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Late Cretaceous and Cenozoic Mammals of North America

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Late Cretaceous and Cenozoic Mammals of North America

Biostratigraphy and Geochronology

Edited by Michael O. Woodburne



Columbia University Press New York



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Contents

Preface M. O. Woodburne vii	
List of Contributors ix	
Definitions xi	
Introduction M. O. Woodburne xv	ii

- Principles and Procedures
 M. O. Woodburne
- 2. Mammalian Biochronology of the Latest Cretaceous
 R. L. Cifelli,* J. J. Eberle, D. L. Lofgren, J. A. Lillegraven, and W. A. Clemens
- Paleocene Biochronology: The Puercan Through Clarkforkian Land Mammal Ages
 D. L. Lofgren,* J. A. Lillegraven, W. A. Clemens, P. D. Gingerich, and T. E. Williamson
- 4. Wasatchian Through Duchesnean Biochronology 106
 P. Robinson,* G. F. Gunnell, S. L. Walsh, W. C. Clyde, J. E. Storer, R. K. Stucky, D. J. Froehlich, I. Ferrusquia-Villafranca, and M. C. McKenna
- 5. The Chadronian, Orellan, and Whitneyan
 North American Land Mammal Ages
 D. R. Prothero and R. J. Emry

- 6. Mammalian Biochronology of the Arikareean Through Hemphillian Interval (Late Oligocene Through Early Pliocene Epochs) 169
 R. H. Tedford,* L. B. Albright III, A. D. Barnosky,
 I. Ferrusquia-Villafranca, R. M. Hunt Jr., J. E. Storer,
 C. C. Swisher III, M. R. Voorhies, S. D. Webb, and D. P. Whistler
 - 7. The Blancan, Irvingtonian, and Rancholabrean Mammal Ages
 E. L. Lundelius Jr. and C. J. Bell,* A. D. Barnosky, R. W. Graham, E. H. Lindsay, D. R. Ruez Jr., H. A. Semken Jr., S. D. Webb, and R. J. Zakrzewski
 - 8. Global Events and the North American
 Mammalian Biochronology 315
 M. O. Woodburne

Systematic Index 345

1

21

43

Subject Index 361

*Chairman of the committee of contributors

Woodburne_00FM 2/1//04 1:31 PM Page VI

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Preface

T HIS BOOK UPDATES the information contained in its 1987 progenitor, *Cenozoic Mammals of North America: Geochronology and Biostratigraphy*, to further refine the tempo and mode of mammalian faunal succession in North America, with the major steps being recognized as discrete intervals known as North American land mammal ages. In the present work, the coverage is extended temporally to include the Lancian part of the Late Cretaceous, as precursor to the Cenozoic, and geographically to include information from Mexico, an integral part of the North American fauna, past and present.

This work incorporates new information on the systematic biology of the fossil record inspected herein but also uses the many advances in geochronologic methods and their results obtained since 1987. It is hoped that what follows here can lead to an increasingly high-resolution stratigraphy in which all available temporally significant data and applications are integrated. Fundamental to achieving this goal are using procedures to enable chronologic units to be recognized and their boundaries defined (no gaps or overlaps), establishing the units in actual field settings so that they are both replicable and realistically complete, and using radioisotopic, cyclostratigraphic, and magnetostratigraphic means to assist in developing as highly refined a correlation network as possible. The goal is a robust high-resolution chronology and, potentially, a chronostratigraphy.

As discussed more fully in the *Introduction*, highresolution chronostratigraphy involves a detailed integration of lithostratigraphic, faunal or (better) biostratigraphic, magnetostratigraphic, cyclostratigraphic, and radioisotopic data to arrive at the best possible interpretation of the age of a given fossiliferous level.

Whereas radioisotopic data used in 1987 had the advantage of the results of the K--Ar method pioneered by Evernden et al. (1964) unavailable to the original promulgation of the mammal age framework developed by Wood et al. (1941), the present effort benefits from the newly developed 40 Ar/39 Ar laser fusion techniques, unavailable before 1987. Similarly, the 1987 work saw the beginning of the now almost ubiquitous application of paleomagnetic stratigraphy to nonmarine mammal-bearing deposits, and a much richer array of this data set is available for the present book. Isotopic geochemistry provides information on changes in isotopes of oxygen and carbon that are proxies for changes in sea level and climate with implications for the nonmarine record, both as an impetus for faunal change and as tools for correlation. Advances in cyclostratigraphy improve the calibration of the magnetic polarity chronology paradigm, with feedback to the nonmarine correlation framework used here.

Thus the present work differs from the earlier volume in representing improvements in all aspects of the data set designed to promote correlation between fossil mammal-bearing successions in North America and thereby to improve our understanding of the times of faunal change represented by the mammal ages and their chronologic relationship to other important geologic, biological, or climatic events that transpired in the past 80 million years or so and may have shaped the tempo and mode of land mammal faunal succession during that time.

viii Preface

The goal of this book, then, is to place in modern context the information by which North American mammalian paleontologists recognize, divide, calibrate, and discuss intervals of mammalian evolution known as North American land mammal ages.

I dedicate this book to the memory of Donald Elvin Savage and Remmert Daams, two persistent advocates from North America and Europe, respectively, of the efforts and approaches documented herein.

Michael O. Woodburne Running Springs, California

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Definitions

- **APTS.** Astronomical polarity time scale. Time scale based on cyclical variations in the stratigraphic record interpreted to reflect astronomical cyclical variations in Earth's orbital progression (Hilgen et al. 1997).
- **ASSEMBLAGE CHRON.** This is a new biochronologic unit based on the antecedent assemblage zone and is an interval of time characterized by a distinctive assemblage or association of three or more fossil taxa that, taken together, distinguishes it in biochronologic character from adjacent intervals of time. To the degree that the replication of boundaries is hindered by the number of taxa involved (derived from the antecedent assemblage zone), the utility in precise correlation for the assemblage chron is diminished thereby. Many mammal ages originally were assemblage chrons with little attention given to biostratigraphic data and therefore are not comparable to the assemblage biochron of Walsh (1998) for which the antecedent assemblage zone (Walsh, 1998:160L and figure 5) is based on a biostratigraphic range zone.
- **ASSEMBLAGE ZONE.** According to Salvador (1994:62–63), this is "a stratum or body of strata characterized by a distinctive assemblage or association of three or more fossil taxa that, taken together, distinguishes it in biostratigraphic character from adjacent strata." This is generally similar to Hedberg's (1976:50–52) definition, except for his explicit biofacies connotation. Because of stratigraphic vagaries in ranges of the associated taxa when considered regionally, stratigraphic limits of assemblage zones may be equally variable (Salvador 1994:63). The North American Commission on Stratigraphic Nomenclature (NACSN 1983:863) considers taxon ranges irrelevant and doesn't define boundaries for assemblage zones, apparently because of their ambiguity, whereas boundaries are defined for interval zones and range zones. This treatment differs from the assemblage zone (as-

semblage fossizone or fossilzone) of Walsh (1998, 2000, respectively) in that the latter are based on specified taxon ranges, an approach that effectively synonymizes assemblage and range zones and differs from the language and concept of Hedberg (1976), Salvador (1994), and NACSN (1983).

- **BIOCHRON.** According to Salvador (1994), this is "The total time represented by a biozone." Williams (1901:579) originally defined this term as an interval of geologic time based on the "duration of organic characters."
- **BIOCHRONOLOGY.** "*Geochronology* based on the relative dating of geologic events by biostratigraphic or paleontologic methods or evidence" (Bates and Jackson 1987:69). To the extent that a biochron is based on a biozone, biochronology has a connection to biostratigraphy because the duration of organic characters cannot be demonstrated usefully without recourse to a stratigraphic framework that includes an ordinal paleontologic scale, with or without the addition of numerical data.
- **BIOSTRATIGRAPHIC UNIT.** A "body of rock strata that [is] defined or characterized on the basis of [its] contained fossils" (Salvador 1994:53). Kinds of biostratigraphic units include range zone, taxon-range zone, concurrent-range zone, interval zone, lineage zone, assemblage zone, and abundance zone (= acme zone). Fossizone of Walsh (1998) or fossilzone (Walsh 2000) is not used here because it is equivalent in concept to a biozone.
- **BIOZONE.** This is a general term for a biostratigraphic zone (Salvador 1994:55).
- **CHRON.** *Chron* is the corresponding geochronologic term for a chronozone, the formal lowest-ranking member of the chronostratigraphic hierarchy (Hedberg 1976:69). This means that the chronostratigraphic unit (chronozone) must be established first in order for the chron (geochronologic unit) to be proposed. On this basis, a biozone (bio-

xii Definitions

stratigraphic unit) must be developed before an equivalent biologically based chronozone can be identified. In that "the time span of a chronozone is usually defined in terms of the time span of a previously designated stratigraphic unit, such as . . . a biozone" (Hedberg 1976:69), that interval of time is a biochron.

- **CHRONOFAUNA.** Following Olson (1952:185), this is a "geographically restricted, natural assemblage of interacting animal populations that has maintained its basic structure over a geologically significant interval of time." See also Tedford (1970), who stresses that chronofaunas are ecologically interpretive units.
- CHRONOSTRATIGRAPHY. Chronostratigraphy is "the element of stratigraphy that deals with the age of strata and their time relations" (Hedberg 1976:66). Salvador (1994:77) replaces strata with rock bodies, which is not appropriate. According to Aubry et al. (1999:99), chronostratigraphy is "the temporal ordering of geologic strata." For the purposes of this book, chronostratigraphy deals with strata. Contrary to Walsh (2001), chronostratigraphy is neither solely a method of age determination nor a means of age classification of strata, nor is it a subset of geochronology. In Hedberg (1976) and Salvador (1994), the purpose of a chronostratigraphic classification is "to organize systematically the Earth's sequence of rock strata into named units (chronostratigraphic units), corresponding to intervals of geologic time (geochronologic units), to serve as a basis for time-correlation and a reference system for recording events of geologic history" (Hedberg 1976:66). Included objectives are to determine local time relations (because this is where the gathering of evidence must begin) and to establish a Standard Global Chronostratigraphic Scale (for global correlation and communication). The determination of the rock record precedes its interpretation (by whatever means) as to the age of that record. The basic chronostratigraphic unit, the stage, therefore precedes the establishment of its geochronologic counterpart, the age, contrary to Walsh (1998, 2001, and references therein).
- **CLASSICAL TIME SCALE (CTS; AUBRY 1995).** Time scale based on radioisotopic dating of the stratigraphic record chosen to characterize certain temporal intervals, such as the system, series, and stage.
- **CONCURRENT-RANGE CHRON.** Following from the antecedent *concurrent-range zone*, this is a new biochronologic term based on the time of the concurrent, coincident, or overlapping parts of the range chrons of two specified taxa selected from among the total forms contained in a temporal array. This is comparable to the strict overlap biochron of Walsh (1998:161, 2000:771) when two taxa are specified.
- **CONCURRENT-RANGE ZONE.** According to Salvador (1994:58) this is "the body of strata including the concurrent, coincident, or overlapping parts of the range zones of two specified taxa selected from among the total forms contained in a sequence of strata." This is preferred over the

definition of Hedberg (1976:55–57) ("parts of the rangezones of two or more . . . taxons") because it simplifies boundary definition and recognition. Still, these zones are not as useful in leading to biochronologic correlations as are others. The present definition is comparable to the strict overlap assemblage fossizone (or fossilzone) of Walsh (1998:161, 2000:770) when two taxa are considered.

- **CORRELATION.** Stratigraphic correlation shows correspondence in character or stratigraphic position (Salvador 1994:15), but as modified from Aubry (1998:43) as "stratigraphic correlation," it must mean temporal correlation as based on temporal analysis. Neither diachrony nor synchrony may be accepted on the basis of stratigraphic correlations alone but must be demonstrated on the basis of temporal analysis (Aubry 1995), and a dual terminology for stratigraphic and temporal terms must obtain.
- **CYCLOSTRATIGRAPHY.** A discipline of stratigraphy wherein successive repetitions of sedimentary features are considered to be cyclical in nature. Some sedimentary cycles (i.e., varves) are interpreted as being annual features of climatic origin. Others are thought to reflect perturbations in orbital precession and obliquity caused by Earth's behavior as it orbits the Sun, commonly known as Milankovitch cycles (Hilgen et al. 1997).
- FAD. First appearance datum. This is a change "in the fossil record with extraordinary geographical limits" (Berggren and Van Couvering 1974:IX). As a chronostratigraphic concept, a FAD expresses an interpretation that the first stratigraphic appearance of a taxon is likely to have been synchronous over a specified geographic region (Woodburne 1996). The origin for a FAD (= appearance) was not constrained by Berggren and Van Couvering (1974, 1978), except that the dispersing taxon would have been newly evolved. For the paleobiotic event to be of "extraordinary geographical limits," dispersal of an organism at a major scale clearly is the primary consideration, presumably from an indigenous source at some location. Aubry (1995:215) paraphrased this as the FAD being the "first (temporal; evolutionary) appearance datum." Also, LO corresponds to FAD if the LO is of global significance (Aubry 1997:18, 22).
- **FAUNA.** For paleontology, this is an assemblage of vertebrate fossils of similar taxonomic composition obtained from a small number sites considered to have a limited temporal range. A fauna is commonly composed of a number of local faunas. See Tedford (1970). Depending on historical context and author intent, stratigraphic limits of a fauna may be supplied.
- **FAUNULE.** Association of taxa interpreted directly or intentionally for its ecological significance. See Tedford (1970).
- **FOD.** First occurrence datum. Aubry (1997:18–19) distinguishes FOD from LO and FAD as a diachronous LO and therefore not an isochronous FAD. The word *datum* in the name signifies the temporal connotation rather than the biostratigraphically descriptive LO. If a given LO can be demonstrated as temporally later than the time of the FAD of that taxon,

then it can segregated from the list of LOs that contribute to the FAD and be designated as a FOD. The FAD is of global significance; the FOD may be regionally important. The FOD is comparable to the dispersal lag of Woodburne and Swisher (1995) if its age can be demonstrated.

- GEOCHRONOLOGY. According to Hedberg (1976) and Salvador (1994), this is defined as "the science of dating and determining the time sequence of events in the history of the Earth" (Hedberg 1976:15). As expressed by Berggren and Van Couvering (1978:40), geochronology is "geologic time as perceived by the progress in one or another ordinal series of events," with those events being parts of irreversible systems, such as organic evolution or radioisotopic decay. It is critically important that these ordinal systems "provide a theoretical basis outside of the preserved geologic record by which the nature and relation of the events in the progression can be recognized or predicted, and according to which missing parts of the record can be identified" (Berggren and Van Couvering 1978:40). Other methods useful to geochronology include paleomagnetic stratigraphy, isotope stratigraphy, and Milankovitch cyclostratigraphy. Geochronology is not merely geochronometry, by which numerical ages are applied to rocks or events.
- **GEOMAGNETIC POLARITY TIME SCALE (GPTS).** A chronology based on counting reversals of Earth's magnetic field (Bates and Jackson 1987:272).
- **HO.** Highest stratigraphic occurrence (Aubry 1997:18–19). This is effectively similar to HSD. An HO may correspond to a LAD (Aubry 1997:22) if it is of effectively global significance. A series of diachronous HOs can become LODs if of regional significance. An HO also may have no temporal significance because of poor representation, scarcity, and truncation by an unconformity (Aubry 1997:22). See also Walsh (2000).
- **HSD.** Highest stratigraphic occurrence of a taxon in a local section (Opdyke et al. 1977). A biostratigraphic term (Lindsay et al. 1987; Woodburne 1996); see *LSD*. Aubry (1997:18–22) prefers to use *HO* for (mostly) the same intent but to reserve the term *datum* for chronologic inference.
- **INTEGRATED MAGNETOBIOCHRONOLOGIC SCALE** (IMBS; Berggren et al. 1985a, 1985b, 1985c, 1995a). A time scale consisting of a magnetochronology, a numerical scale, and a magnetobiochronologic framework.
- **INTERNATIONAL COMMISSION ON STRATIGRAPHY (ICS)**, accepted as such by the International Union of Geological Sciences in 1986. The mandate of the ICS is to develop a standard global stratigraphic scale (Cowie et al. 1986).
- **INTERNATIONAL UNION OF GEOLOGICAL SCIENCES.** The IUGS promotes and supports the study of geological problems of worldwide significance and facilitates international and interdisciplinary cooperation in the Earth sciences.
- **INTERVAL CHRON.** Following from the terminology of the interval zone (Salvador 1994), this is the interval of time

defined on the earliest age of two successive biohorizons and is comparable to that of Walsh (1998) in representing the span of time between the first or last occurrence of one taxon and the first or last occurrence of another taxon. This is interpreted herein to mean that the boundaries of such a unit would be based on the ages of the LO and HO, respectively, of the taxa in question.

- **INTERVAL ZONE.** According to Hedberg (1976:60) this is a biostratigraphic unit defined as the body of fossiliferous strata "between two distinctive biostratigraphic horizons." Salvador (1994:123) defines this as a "biozone consisting of the body of fossiliferous strata between two specified biostratigraphic horizons (biohorizons)." This is interpreted herein to mean that the boundaries of such a unit would be based on the LOs, respectively, of the taxa in question. Although defining a boundary on an HO is theoretically possible, it generally has a greater potential for stratigraphic inconsistency than a LO (but see Cooper et al. 2001).
- **LAD.** Last appearance datum; counterpart to a FAD. A LAD may be identical to the HO if the latter is of global significance (Aubry 1997:22).
- **LINEAGE CHRON.** This is a new biochronologic unit. It is based on the corresponding biostratigraphic unit, the lineage zone (Salvador 1994). Thus a lineage chron is the interval of time defined on the earliest age of a taxon or part thereof in a specific evolutionary lineage and on the earliest age of its evolutionary successor. There is no counterpart in Walsh (1998).
- LINEAGE ZONE. According to Hedberg (1976:58), a lineage zone comprises "the body of strata containing specimens representing a segment of an evolutionary...line or trend, defined above and below by changes in features of the line or trend." In Salvador (1994:125) this is a "body of strata containing specimens representing a specific segment of an evolutionary lineage." These criteria are interpreted herein to mean that the boundaries of such a unit would be based on the LOs, respectively, of the evolutionary first stratigraphic appearance of the taxon in question and the subsequent evolutionary first stratigraphic appearance of the derivative taxon of the lineage in question (see also NACSN 1983:862). Lineage zones "offers one of the best assurances of reliable time-correlation on a biostratigraphic basis" (Hedberg 1976:59).
- **LOCAL FAUNA.** An aggregate of fossil vertebrate species that have a limited distribution in time from a number of closely grouped localities in a limited geographic area. See Tedford (1970). A local fauna could be based on taxa from a single locality.
- **LOD.** Last occurrence datum. A series of regionally diachronous highest stratigraphic occurrences can form a number of LODs if they can be documented. See *FOD*.
- **LO.** Lowest stratigraphic occurrence (Aubry 1995:17). This may be an LSD. It also may equate to an FAD (Aubry 1997:22) if it is of regional significance. Aubry (1995, 1997) differentiates *LO* as a stratigraphic (descriptive) first occur-

xiv Definitions

rence and, although *LSD* is equivalent in concept, reserves the term *datum* to signify a temporal connotation. Aubry (1977:18–19) distinguishes a LO from a FOD as well as an FAD. See also Walsh (2000).

- **LSD.** Lowest stratigraphic datum (Opdyke et al. 1977:324). This is a biostratigraphic concept of the lowest known occurrence of a taxon in a local stratigraphic sequence (see also Lindsay et al. 1987; Lindsay and Tedford 1990:609; Woodburne 1996). The LO (Aubry 1997:18–22) is in part identical to the LSD.
- MAGNETOSTRATIGRAPHIC POLARITY UNITS. Throughout the history of its development, workers applied a variety of names to parts of the Geomagnetic Polarity Time Scale, such as *epoch, event*, or *interval*. Recent codes or guides have stabilized the nomenclature of magnetic polarity units (e.g., Hedberg 1976; Salvador 1994). The following terminology implies that magnetostratigraphic and chronostratigraphic polarity units are analogous to those based on lithostratigraphy (tables 1.1 and 1.2). In practice, however, the original magnetostratigraphic chrons have no lithostratigraphic or chronostratigraphic base because the magnetic interval is inferred to be present in unseen sea floor lavas as sensed from magnetometers towed through the seas by ships.

RECOMMENDED TERMINOLOGY FOR MAGNETOSTRATIGRAPHIC POLARITY UNITS (AFTER SALVADOR 1994:TABLE 2)

MAGNETO- CHRONOSTRATIGRAPHIC STRATIGRAPHIC EQUIVALENT		GEOCHRONOLOGIC Equivalent	
POLARITY UNIT			
Polarity superzone	Chronozone (or superchronozone)	Chron (or equivalent)	
Polarity zone	Chronozone	Chron	
Polarity subzone	Chronozone (or subchronozone)	Chron (or subchron)	

MAMMAL AGES. Mammal ages make up the basic chronologic system used to describe the age and succession of events in mammalian evolution in North America. Mammal ages (commonly known as North American land mammal ages [NALMAs]), are biochronologic units. The interval of time corresponding to each of these is recognized on the basis of mammalian evolution loosely (at least originally) tied to their stratal succession in sedimentary rocks (Wood et al. 1941; Woodburne 1987). In terms of the definitions presented here, mammal ages typically are assemblage chrons, although some have been interval chrons or lineage chrons (Archibald et al. 1987) with varying degrees of biostratigraphic documentation. To the extent that many mammal ages have been defined on the basis of immigrant taxa (Repenning 1967; Woodburne and Swisher 1995), they are effectively interval chrons whose the boundaries are based on first appearance datums. The biostratigraphic

counterpart of most mammal ages is the assemblage zone, "an assemblage zone based on a fossil fauna" (Salvador 1994:63).

- **MEGANNUM (MA).** One million years in the radioisotopic time scale. For example, *10 Ma* refers to the 10-million-year level of the radioisotopic scale.
- **M.Y. (OR m.y.).** A segment of geologic time 1 million years in duration, or the age of an event (e.g., 10 m.y. ago) without reference to a given point or set of points on the radioisotopic time scale.
- **NEOGENE.** This follows Berggren et al. (1995b) to embrace the Miocene through Pleistocene series/epochs.
- **NORTH AMERICAN LAND MAMMAL AGE (NALMA);** see *Mammal ages.*
- **PALEOGENE.** This follows Berggren et al. (1995b) to embrace the Paleocene through Oligocene series/epochs.
- **RANGE CHRON.** This is a biochronologic unit. Following from the language of the antecedent range zone (Salvador 1994), it represents the span of time defined on the age of selected element or elements of a biochronologic sequence. This is interpreted herein to mean that the boundaries of such a unit would be based on the ages of the LO and HO, respectively, of the taxon or taxa in question. The range chron of Walsh (1998) is a subset of the range chron as defined here.
- **RANGE ZONE.** According to Salvador (1994:135) this is a biostratigraphic unit comprising the "body of strata representing the known stratigraphic and geographic range of occurrences of any selected element or elements of the assemblage of fossils present in a stratigraphic sequence." That is interpreted herein to mean that the boundaries of such a unit would be based on the LO and HO, respectively, of the selected element or elements in question.
- **TAXON-RANGE CHRON.** A taxon-range chron is a new biochronologic unit. Following from the language of the antecedent taxon-range zone (Salvador 1994), a taxon-range chron is defined on the known age range of a specified taxon.
- **TAXON-RANGE ZONE.** According to Salvador (1994:140), this is a biostratigraphic unit comprising the "body of strata representing the known range of occurrence (stratigraphic and geographic) of specimens of a certain taxon (species, genus, family, etc.)." That is interpreted herein to mean that the boundaries of such a unit would be based on the LO and HO, respectively, of the taxon in question (see also NACSN 1983:862).

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Introduction

Michael O. Woodburne

PERSPECTIVE

The chronologic framework of the present book remains the North American mammal age concept articulated by Wood et al. (1941) and Savage (1951) and displayed in a great variety of sources, including Woodburne (1987), hereafter identified as the 1987 volume. It is taken as given that practitioners of stratigraphic paleontology or stratigraphic paleobiology recognize and embrace the principle of paleontological correlation (Smith 1815, 1817) and of Steno's (1669) principles of superposition, original horizontality, and original continuity of strata so that the rock record can be used to order the succession of mammalian (and other) taxa and serve as an empirical basis for recording that succession irrespective of theories of evolution or philosophies of systematic analysis. Even though mammal ages are nominally biochrons (Williams 1901:579; intervals of geologic time based on the "duration of organic characters"), their succession (Wood et al. 1941) was framed by the stratigraphic sequences in which they were found (Tedford 1970; Emry 1973 and references cited therein.). Thus the succession of mammal ages depended on the lithostratigraphic framework for their documentation. Similarly, it follows that refinements in the chronology of mammal ages also depend on increasingly refined documentation of the stratigraphic and chronologic framework in which they occur.

Chapters 1 and 2 of the 1987 volume summarized the variety of biostratigraphic and chronostratigraphic proposals developed to describe mammalian faunal succession and correlation up to that time. Chapter 3 of the 1987 volume nominated a succession of new biostratigraphic zones for faunas of nominal Paleocene age, and other 1987 chapters evaluated the mammal succession in early and late (or finer-scale) subdivisions of the traditional mammal ages. These frameworks are essentially followed herein. Woodburne and Swisher (1995) gave an update of the mammal age chronology in North America, with emphasis on evidence for the age of the immigrations that define a majority of the mammal ages and the extent to which these corresponded to major episodes of global sea level lowering. Alroy (1992, 1994, 1998a, 1998b) presented a subdivision of the mammalian faunal record in North America based on quantitative analysis and indicated that whereas immigration is a rapid process, the observed sampling-influenced diachroneity is far too great to allow favoring immigrant first occurrences as time indicators. In Alroy's view, only quantitative analyses of entire faunas have any chance of recovering robust biochronological patterns. However, the only way in which quantitative or any other analyses can be improved is by developing new chronologically significant information with which to assess the age of taxa having a taxonomic precision that is underwritten by the experts directly familiar with the fossils they represent.

HIGH-RESOLUTION STRATIGRAPHY AND BIOCHRONOLOGY

The present work continues with the integration of stratigraphic and other temporally significant data with the mammal record in its primary physical context so as to

xviii Introduction

provide an empirical basis on which the tempo and mode of mammalian evolution can be measured. An underlying concern is the degree to which the patterns of mammalian succession are replicable geographically and found to be chronologically consistent, whether these patterns are described as various kinds of biochrons (mammal ages), subdivisions of them, or biostratigraphic or chronostratigraphic zones.

A goal is the development of a high-resolution chronologic network that, to paraphrase Woodburne (1996), involves the development of a detailed stratigraphic framework for the fossil data, whether they are portrayed in a biostratigraphic array or not, determining an approximate age for the fossiliferous levels with respect to radioisotopic calibration or with respect to a magnetozone whose age limits are confidently known. The independent relative chronologic framework of magnetostratigraphy (and assignment of numerical ages to polarity reversal boundaries by various means; Cande and Kent 1992, 1995; Berggren et al. 1995a, 1995b) allows calibration of the fossil level and temporal correlation with any other similarly placed fossil level in another stratigraphic section. See chapter 1 for further consideration of this topic.

This is not the end of the operation, however. In recent decades, increasing emphasis has been placed on addressing the fidelity of the stratigraphic record through both statistical aspects (Strauss and Sadler 1989; Marshall 1990) and graphic methods (Aubry 1995, 1998; Mann and Lane 1995). Such operations may become increasingly meaningful in recognition of the fact that the ± factor as applied for the 40 Ar/39 Ar radioisotopic dating method can produce ancient ages with very small ± dimensions (e.g., 249.9 \pm 0.1 Ma; Siberian Traps flood basalts; Renne et al. 1998:130). This can lead to the notion that ⁴⁰Ar/³⁹Ar ages are usually better than those derived from, say, the K-Ar method. But as discussed further in chapter 1, this notion can be somewhat misleading. In any case, there are numerous examples wherein mammalian stratigraphers attempt to use accumulation rate reconstructions (based on extrapolations from or interpolations between radioisotopic or magnetic polarity ages) to estimate the age of biostratigraphic or biochronologic units (Woodburne et al. 1990:474), but almost none use the kinds of procedures outlined in Aubry (1995, 1998) to test rigorously for hidden unconformities or other condensations of stratigraphic section, even though it is a given that any sharp geologic boundary (including a magnetic polarity reversal) may reflect an unconformity in the record (Sadler 1999). In fact, the frequent mismatches in the continental magnetostratigraphic record relative to the Geomagnetic Polarity Time Scale must result at least as much as from the effect of apparently unappreciated unconformities in the rock record as from imperfections, overprints, or technical errors in the magnetostratigraphic analysis. Before asserting diachrony in the lowest stratigraphic datum of fossil mammals when considered regionally (Alroy 1998), it is necessary to rule out the effect of imperfections in the stratigraphic record. Finally, in order to be precise, boundaries must be defined and the proposed interval characterized (Woodburne, 1977, 1987, 1996), with single-taxon definitions being preferred over those based on multiple taxa because they are less ambiguous.

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Principles and Procedures

Michael O. Woodburne

DISCUSSION OF THE PRINCIPLES and procedures in ${f A}$ methodology and the goal of producing a time scale based on the evolution of fossil mammals that contains neither gaps nor overlaps is as pertinent now as it was in 1987 or, indeed, in 1941 (Wood et al. 1941). Whether or not it is formally identified as biostratigraphy, students of mammalian chronology in North America have continually worked to improve the stratigraphic framework associated with fossil mammals and to integrate it with other chronologic information. Although still biochrons, mammal ages and subdivisions have become stratigraphically assisted (stratigraphically characterized but not defined) to varying degrees since 1941, and this trend continues here. There still are only a few instances in which sufficient stratigraphic information has been added to the fossil mammal biochronologic concept to support the development of a chronostratigraphic stage, and thus a true geochronologic age, hence the common convention of categorizing the biochrons as mammal ages. The main purpose of this chapter is to review the traditional stratigraphic procedures and some innovations designed to improve the development of a correlation network for fossil mammals that is empirically based and noncircular in reasoning. A thesis developed here is that not only is there a distinct progression from biostratigraphy, through biochronology, to chronostratigraphy, and then to geochronology, but that it is appropriate to use a formalized set of biochronologic units as part of that process. In at least one example cited in this chapter, almost the entire process has been achieved for early Paleocene strata of the Hanna Basin, Wyoming, even though the

final procedural documentation of a chronostratigraphic unit (statement of intent, selection of stratotypes, reference sections) has not been completed. In a much larger set of examples (described elsewhere in this book), the mammal age data set is becoming increasingly documented in detail with respect to stratigraphy and with respect to radioisotopic, paleomagnetic, and stable isotope chronology. It is therefore appropriate to review the fundamentals of stratigraphic classification and correlation here.

THE GEOCHRONOLOGIC FRAMEWORK

This is the framework within which the geologist or paleobiologist understands not only the passage of geologic time but also the age and interrelation of past events important for study. In the present case, interest is focused on mammalian evolution and the means by which the results therefrom can be used to develop a framework of data that lead to a chronologic system by which that evolution can be perceived and documented: an increasingly high-resolution stratigraphy in which all available temporally significant data and applications are integrated. The progression toward this goal begins with a consideration of a chronology derived from a physical stratigraphic framework and turns to its calibration, estimation of completeness or fidelity, operations in correlation, the role of biochronology, and the relationship of these factors to mammal ages.

2 Michael O. Woodburne

STRATIGRAPHIC CLASSIFICATION

A major task of a mammalian stratigrapher is to devise and work within a framework of data that leads to the establishment of a succession of temporal intervals that account for all of geologic time, with no overlaps or hiatuses. The following describes the classification of units

 TABLE 1.1 Conventional Hierarchy of Formal

 Chronostratigraphic and Geochronologic Terms

CHRONOSTRATIGRAPHIC	GEOCHRONOLOGIC
Eonothem	Eon
Erathem	Era
System ^a	Period ^a
Series ^a	Epoch ^a
Stage ^b	Age
Substage	Subage or age
Chronozone	Chron

^aIf additional ranks are needed, the prefixes *sub-* and *super-* may be used with these terms.

^bSeveral adjacent stages may be grouped into a superstage.

Hedberg (1976:69–70) considers *chronozone* and *chron* to be members of the formal hierarchy. Salvador (1994:83–84) treats them as formal but nonhierarchical units. and concepts in the conventional stratigraphic hierarchy. Table 1.1 shows the formal chronostratigraphic and geochronologic terms used in modern stratigraphic guides and codes, and table 1.2 summarizes the classification of units and concepts important to biostratigraphy, chronostratigraphy, and geochronology. The operation of working within this hierarchy to develop a temporal correlation is taken up later in this chapter. With respect to table 1.1, the System–Period pair was the focus of geologists contemporaneous with William Smith, but in subsequent years, increasing attention has been paid to smaller-scale increments of the hierarchy as attempts were made to more finely subdivide (and recognize) intervals of geologic time.

Stratigraphers are increasingly concerned with identifying and using stratigraphically and temporally shorter intervals and use an increasingly sophisticated and refined set of analytical and procedural tools to further those goals. But the first step is to clearly separate physical and tangible units from purely inferential and intangible ones. At one extreme is the lithostratigraphic base on which all other stratigraphic endeavors must be founded. At the other extreme are geochronologic (geologic time) units that are explicitly intangible and inferential. To varying degrees, biostratigraphic units (based

 TABLE 1.2 Independence of Lithostratigraphic Units From and Potential Relationships Between Biostratigraphic,

 Chronostratigraphic, and Geochronologic Units

LITHOSTRATIGRAPHIC ^A	BIOSTRATIGRAPHIC ^B	CHRONOSTRATIGRAPHIC ^C	GEOCHRONOLOGIC^D
Formation	Various kinds of biozones	Chronozone	Chron
Member			
Bed			
Horizon			

^aPhysical unit; descriptive, based on lithological characteristics without regard to age of deposition. A formation may be lithologically heterogeneous or homogeneous. A member usually is lithologically more homogeneous and may be interpreted as to lithogenesis. A bed commonly is of limited thickness and is at least as homogeneous lithologically as a member. A horizon is of very limited (conceptually zero) thickness but is a traceable marker.

^bFundamentally a physical unit, descriptive of the occurrence of fossils in their stratigraphic context. Procedurally independent of other stratigraphic units, biostratigraphic units can be developed for their biochronological significance and ultimately transformed into the paleontological basis for chronostratigraphic units (see text). The biozones most useful in chronostratigraphy are the taxon-range zones and lineage zones that describe the stratigraphic range of a single taxon without regard to sampling factors (e.g., abundance). The interpretive aspect is the subjective identification that the specimens on which the zone is based pertain to a given paleospecies. Thus if Lineage zone α is followed stratigraphic range of each biozone has an interpretive aspect.

^cThis is a physical unit in that it is the rock deposited during an interval of geologic time. It is conceptual in that the means by which the unit is recognized (most commonly fossils) are presumed to have a temporal component that is unique. Once a chronostratigraphic (time–rock) unit is created, the corresponding geochronologic (geologic time) unit of equal rank is thereby defined (Table 1.1). The chronostratigraphic unit (e.g., Ypresian Stage) is defined in a given type section or reference sections, and stratigraphic sequences in other areas are referred to this stage based on having sufficient defining or characteristic criteria (usually fossils) to warrant such a correlation. Chronostratigraphic units are the fundamental means for building a time–rock record that accounts for all of geologic time that has neither overlaps nor hiatuses. In contrast to geochronologic units, chronostratigraphic units are limited by the rock record. The chronozone is the basal element of the hierarchy (Table 1.1).

^dThis is a conceptual and intangible unit that stands for an interval of geologic time. It is not a stratigraphic unit, even though it may correspond to the time span of a stratigraphic unit. Thus one may speak of events that transpired during the Ypresian age without reference to a specific section of strata. The chron is the basal element of the hierarchy (Table 1.1). on the physical disposition of fossils in the rock) and chronostratigraphic units (sections of rock that document intervals of geologic time) are both physical (tangible) and inferential (intangible), as summarized in table 1.2 and as discussed more fully later in this chapter. In brief, lithostratigraphic units provide the objective physical framework for geologic data; biostratigraphic units provide the objective physical framework for paleontologic data; chronostratigraphic units give a physical, stratigraphic record of the passage of time, drawn in large part from biostratigraphic information; and geochronologic units are intangible representations of the intervals of time contained in chronostratigraphic units.

Lithostratigraphic Units With regard to lithostratigraphic units, present North American and international codes and guides are consistent in separating the concepts and operations of lithostratigraphy as distinct from those dealing directly, or potentially, with biostratigraphy, chronostratigraphy, or geochronology. This stems from the conviction that the basic physical and descriptive framework for historical geology should be separate from any interpretive concepts or operations. Schenk and Muller (1941) clearly articulated this principle.

"Lithostratigraphic units are bodies of rock, bedded or unbedded, that are defined and characterized on the basis of their observable lithologic properties" (Salvador 1994:31). The objectively observed lithologic criteria are paramount in establishing a lithostratigraphic unit, regardless of age. Thus whereas fossils can be recognized as an identifying component (e.g., a *coquina*), they are treated as lithologic properties similar to kinds of rocks, minerals, and the like.

A primary purpose of lithostratigraphic units is to demonstrate a physical framework at a level pertinent to the study at hand, not always necessitating the construction of a geologic map. The typically mappable unit is the formation (table 1.2), but other and generally thinner but not necessarily areally less extensive units may be used. Examples of the latter include air-fall or ash-flow tuffs, debris flows, or other (usually thin, measured in meters or less) beds of distinctive lithology relative to those above or below. Whereas formations or other units may be homogenous lithologically, others may be differentiated by being lithologically heterogeneous in contrast to those above and below. Also, it is convenient if the boundaries of the lithologic unit are sharp and unambiguously detected, but in other cases boundaries may be gradational. As Schenk and Muller (1941:1424) point out, boundaries of lithologic units commonly are chosen at unconformities, across which trenchant changes in lithology may be observed. These authors further assert that this is in distinct contrast to the goals of time stratigraphy, in which it is desirable to have a setting in which deposition was effectively continuous, especially at the boundaries between the units. For lithostratigraphic units, the basic issue is developing a physical stratigraphic framework that is empirically constructed and reliably replicable in the district under study. Here, and for other units, base defines boundary. Hedberg (1976) and Salvador (1994) summarize the need to specify stratotypes or type localities of lithostratigraphic units.

Biostratigraphic Units As given in Salvador (1994:53), "biostratigraphic units (biozones) are bodies of rock strata that are defined or characterized on the basis of their contained fossils." As summarized in tables 1.2 and 1.3, biostratigraphic units are material, physical units (also Walsh 1998:163). Determining the base of the unit in places other than the stratotype is only as valid as its definition. As discussed later in this chapter (see "Definition and Characterization"), the best definition is based on the lowest stratigraphic occurrence of a single taxon. Whereas some biozones illustrate variations in abundance of paleospecies, others clearly are intended for use in correlation, including the development of chronostratigraphic units. Some biozones are based on the record of single taxa, others on the occurrence of several.

The reason for establishing biostratigraphic units is to develop an empirical record of taxonomic occurrence in the rock record. Whether codified as a given category (table 1.3) or not, the pattern of biostratigraphic information that may be constructed forms an empirical framework parallel in concept to the development of lithostratigraphic information. Both frameworks are conceptually independent of other kinds of considerations, such as time or ecology, and on this basis can form the legitimate foundation from which those other considerations may be developed. Regarding biostratigraphy, the species from which biozones are described have a distinct, limited sojourn in geologic time. Once described and found to be replicated geographically and consistently with respect to geologically isochronous markers, biostratigraphic data can be interpreted for their temporal significance and form the basis for defining and characterizing chronostratigraphic units (table 1.2). Thus biozones are basically descriptive units but also have the potential for temporal interpretation. This aspect of biostratigraphy is taken up later in this chapter ("The Role of Biochronology").

Salvador (1994:57–64) summarizes the various kinds of biozones. They are categorized as range zone, interval

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(FTER SALVADOR (1994)	AFTER WALSH	(1998, 2000)	THIS BOOK
JIOSTRATIGRAPHIC ATEGORIES	(EU)BIOSTRATIGRAPHIC CATEGORIES	BIOCHRONOLOGIC CATEGORIES	
siostratigraphic units are empirical units ased on the stratigraphic disposition of ossils. The basic unit is the biozone. ^a	As in Biostratigraphic categories.	Biochronologic units are interpretive units; intervals of time as represented by fossils. The basic unit is the biochron (Williams 1901).	Biostratigraphic categories follow Salvador (1994). Biochronologic categories are interpretive units based on the age of the equivalent biostratigraphic unit of Salvador (1994). The basic unit is the biochron.General correspon- dence to certain units of Walsh (1998, 2000) is indi- cated where appropriate.
kange zone: The body of strata containing he total known stratigraphic and geographic ange of any selected elements of the ssemblage of fossils in a stratigraphic equence.	No comparably general unit in Walsh (1998, 2000).		Range chron: Interval of time defined on the age of selected element or elements of a biochronologic sequence, in part inclusive of range chron of Walsh (1998).
 Taxon-range zone: The body of strata containing the total known stratigraphic and cographic range of specimens of a particular axon (species, genus, family, etc.). 	Range zone: The set of strata between the LSD and HSD of a single taxon. ^b	Range chron: The span of time between the FHA and LHA of a single taxon. ^c	Taxon-range chron: Interval of time defined on the known age range of a specified taxon.
 Concurrent-range zone: The body of strata ncluding coincident, or overlapping, parts of he range zones of two taxa selected from hose contained in a sequence of strata. 	Strict overlap assemblage fossizone: Where $N = 2$. The more general case is the thickness of strata between the lowest co-occurrence and highest co-occurrence of every one of a specified set of two or more taxa.	Strict overlap assemblage biochron: The span of time between the FHAs and LHAs of (in the restricted context) two specified taxa.	Concurrent-range chron: Interval of time defined by the concurrent, coincident, or overlapping parts of the range of two specified taxa selected from the total forms contained in a temporal array.
nterval zone: The body of fossiliferous strata wetween two biohorizons. The base is set by he lower biohorizon, the top by the upper.	Interval zone: The set of strata between the LSD or HSD of one taxon and the LSD or HSD of another taxon. ^d	Interval chron: The span of time between the FHA or LHA of one taxon and the FHA or LHA of another taxon.	Interval chron: Interval of time defined on the earliest age of two successive biohorizons.
ineage zone: The body of strata containing pecimens representing a specific segment of n evolutionary lineage. ^e	No specific category in Walsh (1998, 2000). ^f		Lineage chron: Interval of time defined on the earliest age of a taxon or part thereof in a specific evolutionary lineage and on the earliest age of its evolutionary successor.

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Assemblage chron: Interval of time characterized by more fossil taxa that, taken together, distinguishes it in biochronologic character from adjacent intervals a distinctive assemblage or association of three or No specific category. No closely applicable chronologic significance. of time. specified set of two or more taxa is the youngest Disjunctive biochron: The span of time between whichever of the FHAs of a specified set of two combined range biochrons of one, some, or all or more taxa is the oldest and whichever of the between whichever of the FHAs of a specified Strict overlap assemblage biochron: The span Minimal overlap biochron: The span of time set of at least N + 1 taxa is the *n*th oldest and Assemblage biochron: In a given geographic of time between whichever of the FHAs of a area, a span of time based on the partial or whichever of the LHAs is the *n*th youngest the taxa present in a single set of two or and whichever of the LHAs is the oldest LHAs is the youngest. (where $N \leq 2$). more taxa. taxa in a specified set of at least N + 1 taxa where section, a thickness of strata based on the partial all the taxa present in a set of two or more taxa. highest co-occurrence of any combination of nor combined range fossizones of one, some, or thickness of strata between the lowest LSD and includes disjunctive assemblage fossizone (the the highest HSD of whichever taxa are present out of a specified set of two or more taxa) and No closely applicable chronologic significance Assemblage fossizone: In a given superposed Minimal overlap assemblage fossizone (the No specific category in Walsh (1998, 2000). thickness of strata between the lowest and thickness of strata between the lowest and Strict overlap assemblage fossizone (the highest co-occurrence of every one of a specified set of two or more taxa. $N \ge 2$) and nificantly greater than in the adjacent parts of containing a distinctive assemblage of three distinguishes it in biostratigraphic character Abundance zone: A body of strata in which the abundance of a particular taxon is sigthe section regardless of either association or more fossil taxa that, taken together, Assemblage zone: The body of strata from adjacent strata. or range.

FHA; HSD, highest stratigraphic datum; LHA; LSD, lowest stratigraphic datum.

^aWalsh (1998) uses the term *fossizone* for an equivalent concept, modified to *fossilzone* in Walsh (2000).

¹Range zones and interval zones are each divided into a range epizone, range entozone, lineage epizone, and lineage entozone. Epizones are based on LSDk and HSDk (empirical zones based on the LSD and HSD as originally defined by Opdyke at al. (1977). Entozones are based on LSDa, and HSDa, the "actual" occurrence in the rock record, but this is a theoretical concept in that the fossils involved have not yet been found. Even though they are used in a stratal context, LSDa and HSDa are comparable to interpretive, biochronologic units and not recognized here as a separate biostratigraphic category. Range zone of Walsh (1998) is most similar to taxon-range zone of Salvador (1994).

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Range chrons are based on FHA and LHA (first and last historical occurrence as a temporal interpretation). If a taxon is thought to have been present in a given area (FHA), it presumably would leave a potential rock record (LSDa) that, when demonstrated stratigraphically, would become an LSDk. Regardless of being oriented toward a potential rock record rather than a potential temporal record, an LSDk is interpretive to the same extent as is an EHA. Both are interpretive units. Thus entozones are not proper biostratigraphic units and are not used here. Range chron of Walsh (1998) appears most comparable to taxon-range chron as used here.

⁴Walsh (1998) also nominates assemblage interval fossizones and biochrons (renamed in 2000 as multiple-taxon interval fossizones and biochrons). These are not discussed further here.

A lineage zone has strong temporal significance and approaches a chronozone (basic unit of chronostratigraphy). Once defined, however, a chronozone contains all strata that can be shown to correspond to the specified interval of time, regardless of fossil content.

This apparently reflects Walsh's (1988) view that procedures leading to the development of chronostratigraphic units via the usual methods of performing a biochronologic correlation based on biostratigraphic data are irrelevant to finding geochronologic events that can be formalized as a Global Boundary Stratotype Section and Point and then used to define the boundaries of chronostratigraphic units.

6 Michael O. Woodburne

zone, lineage zone, assemblage zone, and abundance zone (table 1.3). Table 1.3 also compares biostratigraphic categories of Salvador (1994) with those of Walsh (1998) and concepts used herein. Either taxon-range zones and concurrent-range zones represent the total stratigraphic and geographic range of taxa. The taxon-range zone (range zone of Walsh 1998) is based on the range of a single taxon, whether of specific rank or greater. Its boundaries therefore are defined on the presence of the taxon in question. Thus the zone begins and ends stratigraphically with the known range of the specified taxon. The concurrent-range zone (strict overlap assemblage fossizone of Walsh 1998) is similar, except that its extent is defined on the shared ranges of two taxa, although other taxa can help characterize the zone. As Salvador (1994:58) notes, a succession of concurrent-range zones can have gaps or overlaps between them.

An interval zone is a unit of fossiliferous rock having boundaries specified by two bounding biohorizons, although the fossil content of the zone within the interval itself is not specified. The interval zone of Walsh (1998) is comparable. This kind of zone appears to be most useful in analyzing cores of subsurface drilling but also has been used in mammalian biochronology (Archibald et al. 1987). This exemplifies the trend reflected in this book whereby mammal paleontologists strive to increase the role of biostratigraphy as applied to rock sequences bearing fossil mammals.

Lineage zones may be chronostratigraphic in character. These comprise a body of strata having specimens of a specific part of an evolutionary lineage, which could include the entire range of a given species. In that evolutionary innovations are temporally unique, this type of zone approaches a chronozone, the basic hierarchical unit of chronostratigraphy (table 1.1). To the extent that limits between species or other parts of the lineage must be interpreted by a paleontologist, there may be an intangible aspect to these zones that could have a temporal ramification (Woodburne 1987b, 1996a). A lineage zone still is empirical in that its presence is recognized solely on the stratigraphic occurrence of the taxon in question and has the additional provision that the base of the lineage defines the base of the zone, and its top is defined by the base of the descendant taxon. A chronozone based on a lineage zone theoretically would have boundaries with neither gaps nor overlaps. Walsh (1998) has no counterpart to the lineage zone.

An assemblage zone is characterized by the co-occurrence of three or more taxa that together distinguish the stratigraphic interval in which they occur from those above or below. In addition to usually being limited to specific areas or regions, the boundaries of assemblage zones are imprecise. In that the zone is based on the ranges of three or more taxa, it is possible that none of them will be necessarily exclusive to the zone. If two or more taxa share the same lowest stratigraphic occurrence (LO), it is likely that this results from extrinsic factors (such as an underlying unconformity) and should be viewed with caution.

In part to address the vagaries of boundary definition for assemblage zones (or assemblage fossilzones), Walsh (1998:160L, 2000:770) proposes three different kinds-disjunctive, minimal overlap, or strict overlap assemblage fossilzones-and proposes to restrict the concept to a the lowest and highest occurrences of a single specified set of two or more taxa. This initiative moves well beyond the apparent consensus (at least among Hedberg 1976; Salvador 1994; NACSN 1983) that assemblage zones are generalized concepts for which boundary precision is unwarranted or at least not relevant. These three works also state or imply that range zones and interval zones are capable of precise boundary definition and also by implication or statement are most relevant as a basis for chronostratigraphic zonation. The formulations of Walsh (1998, 2000) move assemblage zones into the realm of range zone and interval zone, for which definitions already obtain (table 1.3).

Finally, abundance (or acme) zones are self-explanatory, with the abundance of a taxon or group of taxa relative to that of other taxa being distinctive of a certain stratal succession. The subjective nature of the sampling aspect in determining taxon abundance speaks strongly against such zones being precisely replicable stratigraphically; therefore, they are of limited use as a basis for chronostratigraphy. Walsh (1998) has no comparable category to abundance zone.

Chronostratigraphic Units According to Hedberg (1976:67), a chronostratigraphic unit is "a body of rock strata that is unified by being the rocks formed during a specific interval of geologic time, [and] . . . represents all rocks formed during a certain time span of Earth history and only those rocks formed during that time span. Chronostratigraphic units are bounded by isochronous surfaces." Salvador (1994:88) states, "The essential part of the definition of a chronostratigraphic unit is the time span during which the unit described was formed." Contrary to Walsh (2001 and references cited therein) this does not mean that the span of time (and its limits) have been identified before the definition of the chronostratigraphic unit (table 1.4). Salvador (1994:88) continues, "Since the only record of geologic time and of the events of geologic history lies in the rocks themselves, the

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TABLE 1.4	Chronostratigra	phic and G	eochronol	logic C	ategories
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AFTER SALVADOR (1994)	AFTER WALSH (1998, 2001)
CHRONOSTRATIGRAPHIC CATEGORIES	CHRONOSTRATIGRAPHIC CATEGORIES
Bodies of rock formed during a specified interval of geologic time. ^a The basic nonhierarchic unit is the chronozone. Formalized hierarchic units are the System, Series, and Stage. Intervals are based on boundary stratotypes and unit stratotypes; golden spikes (GSSPs) may be used. The boundary stratotype is the same concept as the golden spike. GSSPs are chronostratigraphic entities (also as per the International Commission on Stratigraphy, even if correlation precedes definition).	A set of rocks formed during a chronologic unit Geochronostratigraphic unit: The set of all existing rocks formed during a specified geochronologic unit. ¹ The basic nonhierarchic unit is the geochronozone. ^b Formalized hierarchic units are the System, Series, and Stage. ^c Biochronostratigraphic unit: The set of all existing rocks formed during a specified biochronologic unit. The basic nonhierarchic unit is the biochronozone. ^d Informal hierarchic units are the "System," "Series," and "Stage." ^e
GEOCHRONOLOGIC CATEGORIES	CHRONOLOGIC CATEGORIES
The units of geologic time during which chronostratigraphic units were formed. Limits are established by equivalent and precursor chrono- stratigraphic units. The basic nonhierarchic unit is the chron. Formalized hierarchic units are the Period, Epoch, and Age.	A span of time defined by two historical events. Geochronologic unit: A span of time defined by two geologic events, that is, the deposition of two exactly specified sedimentary layers, marked by golden spikes, in specified stratigraphic sections (boundary stratotypes). GSSPs are geochronologic entities. ^f The basic non hierarchic unit is the geochron. ^g Formalized hierarchic units are the period, epoch, and age. ^h Biochronologic unit: A span of time defined by two paleobiologic events (e.g., evolution, extinction, immigration). The basic nonhier- archic unit is the biochron. ⁱ Informal hierarchic units are the Period, Epoch, and Age.

GSSP, Global Boundary Stratotype Section and Point.

^aIn Salvador (1994) the interval of time is based on evidence intrinsic to the unit in question, as presented in its original formulation and definition. Stage precedes Age. In Walsh (1998) the interval of time is based on evidence extrinsic to the unit in question, on a precedent geochronologic unit. Age precedes Stage.

^bThis is the same concept as chronozone in Salvador (1994). Both are stratigraphically based units representing an interval of time.

^cThese are the same hierarchic units as in chronostratigraphic unit hierarchies of Salvador (1994).

^dThis is effectively the same concept as the biozone in Salvador (1994), a stratigraphic demonstration of paleobiologic phenomena. In that the boundaries of such units in Walsh (1998) are placed on only paleobiologic evidence (biochronologic unit), they are relegated to informal status. This is contrary to Salvador (1994), wherein biozones commonly contain temporal information ultimately taken to define the boundaries of chronostratigraphic units, which then lead to formalized Stages and higher hierarchic units.

"This subordinates paleontologically defined events (biochronologic units) relative to geologically defined events (geochronologic units; boundaries based on GSSPs).

Golden spikes are used in fundamentally different ways: for chronostratigraphic units in Salvador (1994) and for geochronologic units in Walsh (1998).^h

^gWalsh (1998) uses the geochron as a time interval based on the deposition of a body of rock (Williams 1901); it is distinct from the chron of Salvador (1994), a strictly temporal term (Williams 1901). This is consistent with Salvador (1994).

^hImplicit here is that only "geologic" events are appropriate to boundary definition for the Period, Epoch, and Age, with GSSPs being documented in a lithostratigraphic context, rather than these being based on chronostratigraphic data. What formerly were chronostratigraphic procedures now have become those of geochronology.

ⁱThis again implies that paleontologic data are subordinate in importance to GSSPs or other "geologic" events in determining and defining ages of stratigraphic sequences.

best standard for a chronostratigraphic unit is a body of rocks formed between two designated instants of geologic time." Implicit in discussions of both Hedberg (1976) and Salvador (1994) are the fundamental presumptions that rocks are tangible records of the passage of time, that a limit in the rock record implies a limit in time, that chronostratigraphic units are based on marine strata, that the disposition and delimitation of that record is based on criteria meaningful to that situation, and that the defining boundaries are normally based on paleontological data. Addressing the requirement of boundary isochroneity leads to examination of all possibly timesignificant information that, following the examples provided in Aubry (1991, 1995, 1997) and Berggren and Aubry (1996), can lead to consideration of fidelity of the record and identification of phenomena useful in correlation

8 Michael O. Woodburne

that have no intrinsic numerical age connotation, including paleomagnetic pattern. Therefore neither chronostratigraphy or geochronology is hostage to numerical analysis, for which direct evidence is difficult to achieve in marine contexts in any case.

Walsh (1998, 2001) cites some general concerns as to the establishment of chronostratigraphic units (the need for type and reference sections) and their global role in correlation. Actually, there is no confusion between chronostratigraphic units and unit stratotypes because the stratigrapher must proceed from the local to the more regional context for any chronostratigraphic unit, and the location of golden spikes or other formalized important referents must be determined at the end of the process, not at its beginning. To do otherwise presupposes the stratigrapher having prescient knowledge of all globally significant information at the beginning rather than at the end of the operation. The current chronostratigraphic scale has its own historical precedents, and the present-day focus on global geologic events may differ from those considered important when some or most of that scale was first devised. Still, the fact that the stratigraphic community now can provide numerical statements for an increasingly diverse range of geologic situations doesn't mean that the basic principles for establishing and dealing with chronostratigraphic and geochronologic time scales must be abandoned. Stage still must come before Age. By definition, chronostratigraphic units are bounded by isochronous horizons that are everywhere the same age, but demonstration of this goal is a continuing process and ultimately is achievable only within the abilities of a geochronologist to identify the limits of accuracy of a given time indicator (the \pm factor).

Although the basic hierarchical chronostratigraphic unit is the chronozone (table 1.1), the lower boundary of the stage is formally recognized as also setting the basal boundary of the Series and System (Hedberg 1976:71-74), and because the issue of temporal accuracy and repeatability is so important, current codes and guides specify that the stage be defined by its boundary stratotype. This may be based on a Global Boundary Stratotype Section and Point (GSSP; Cowie et al. 1986) because the intent of unit definition is that it is recognizable on a global scale. Therefore the means of identifying the boundary of the unit also should be globally relevant. Here is where the operation of high-resolution chronostratigraphy is paramount because all available means must be organized so as to describe and define an isochronous horizon. Until recently, fossils have been the primary means for age evaluation so that the considerations addressed earlier in this

chapter applied exclusively. The hierarchy of units above and below a stage are given in table 1.1.

In that regard, the chronozone is the most useful chronostratigraphic unit for fine-scale correlation. For all chronostratigraphic units, the means for identifying the span of time they represent must be specified. Critically, base defines boundary, so it is important to specify the basis on which the original (stratotypic) unit was founded and considered to be identifiable in other places around the world. Therefore not only must boundary stratotypes be established for the lower boundary of the stage and the one that succeeds it, but also their locale must be chosen in places where unique instants of geologic time may be recognized stratigraphically in places having a record of effectively continuous (Sadler 1981, 1999) sedimentary accumulation (Salvador 1994:90). Once established, a chronozone, a stage, or any other chronostratigraphic unit is theoretically global in extent. If time-significant criteria can identify the boundaries of the unit in places other than its type area, the unit may be extended laterally regardless of whether the original (e.g., paleontological) criteria are present.

Geochronologic Units In Salvador (1994:16) a geochronologic unit is "a unit of geologic time (time determined by geochronologic methods). It is not a body of rocks and therefore not a stratigraphic unit, although it may correspond to the time span of a stratigraphic unit." Still, as indicated in table 1.1, geochronologic units are the lingua franca of the geologic time scale for general communication and have a formal relationship to chronostratigraphic units. The fact that North American land mammal ages are so designated results from the fact that there is no antecedent chronostratigraphic stage in most cases (Wood et al. 1941; Woodburne 1987a, 1996a). Walsh (1998, 2001) argues in favor of transferring to geochronology many of the operations herein maintained for chronostratigraphy, as indicated in table 1.4. Based on the preceding discussions, these suggestions are not followed here.

THE ⁴⁰AR/³⁹AR DATING SYSTEM IN COMPARISON WITH OTHER GEOCHRONOMETRIC METHODS

The laser total-fusion single-crystal ⁴⁰Ar/³⁹Ar radioisotopic dating method is one of the most widely used and precise methods of geochronologic analysis (Renne et al. 1998), and commonly considered, at least informally, as superior to the K–Ar method, which had such an important role to play in the initial calibration of the mammal age chronology (Evernden et al. 1964). For example, Swisher

et al. (1993) report a mean age of 65.16 ± 0.04 Ma for a volcanic ash in the IRZ coal of Montana, coincident with the iridium anomaly that identified the Cretaceous-Tertiary (K-T) boundary. This can be compared with an ⁴⁰Ar/³⁹Ar age of 15.85 \pm 0.04 Ma for the Oreodont Tuff of the upper Miocene Barstow Formation of California. These dates, of strongly different parts of the Classical Time Scale (CTS), appear to have similarly small \pm factors, but those actually reflect analytical precision alone. Comparisons of these ages are valid as long as only the 40Ar/39Ar or K-Ar system is used. Renne et al. (1998:131) indicate that when dates derived from 40 Ar/39 Ar analyses are compared with those derived from other systems, such as the U/Pb method, additional corrections to the \pm factor should be applied to reflect uncertainties in the decay constants and the absolute ages of standards used in the analyses. In such a situation, recalculation of the IRZ coal date would result in an age of 65.46 ± 0.63 Ma (Renne et al. 1998) and would be more appropriate for comparison with ages derived from other chronometric systems.

Regarding the accuracy of 40 Ar/39 Ar dates and those derived from ⁴⁰K–⁴⁰Ar analysis, Woodburne et al. (1990) and MacFadden et al. (1990) report on reanalyzed ⁴⁰K–⁴⁰Ar ages for some of the tuffs of the Barstow Formation. For example, the 40K-40Ar age given for sanidine crystals in a sample of the Oreodont Tuff in Coon Canyon is 15.8 \pm 0.2 Ma (MacFadden et al. 1990, table 2). This is very close to the 4° Ar/ 3^{9} Ar date of 15.9 ± 0.06 Ma from sanidine of the same sample in Coon Canyon and to a 40 Ar/ 39 Ar date of 15.85 \pm 0.04 Ma from a site in Rainbow Basin, about 1 mile east (MacFadden et al. 1990:489). A similarly close correspondence in age when comparing the ⁴⁰Ar/³⁹Ar and ⁴⁰K-⁴⁰Ar systems is provided by the Dated Tuff of the Barstow Formation. Biotite from this tuff dated by the 40 Ar/39 Ar method yielded an age of 14.8 \pm 0.06 Ma. Analysis of the same biotite by the ⁴⁰K–⁴⁰Ar method yielded an age of 14.8 \pm 0.15 Ma (MacFadden et al. 1990:490). These examples show not only that the ⁴⁰K-⁴⁰Ar and ⁴⁰Ar/³⁹Ar methods are capable of similar results but also that the correspondence in age corroborates the age derived from the ⁴⁰K–⁴⁰Ar system.

THE GEOMAGNETIC POLARITY TIME SCALE (GPTS), THE INTEGRATED MAGNETOBIOSTRATIGRAPHIC SCALE (IMBS), AND ESTIMATING THE AGE OF GEOBIOLOGICAL EVENTS

GPTS and IMBS It is now well known that Earth's magnetic field reverses periodically and that such reversals are recorded in magnetically susceptible minerals of molten

igneous or fluid sedimentary rocks. It also has become obvious that fossil mammals can be found in sequences of nonmarine strata that record patterns of geomagnetic reversals that can be correlated with the global pattern of the GPTS. Extension of the global pattern to mammalbearing sequences provides a major basis by which events important to mammalian paleontologists can be compared with those of other disciplines worldwide, despite the fact that nonmarine sequences generally are considered to be less complete than those deposited in marine environments. Still, Aubry (1995) has shown that even the deep marine record may be significantly incomplete, and a thesis of this book is that in the best examples, stratigraphic and chronologic analysis of nonmarine sequences can approach that embodied by the IMBS of the marine realm. For both the marine and nonmarine realms, correlating an indigenous magnetic reversal pattern to part of the global template is one operation. It is another matter to assign numerical ages to that pattern in any realm.

As illustrated by Aubry (1995), the close link between the stratigraphic record and geologic time is manifested in a number of ways important to our purposes. Most mammalian paleontologists work with elements of the CTS, wherein the age of events in the stratigraphic record is supplied by radioisotopic data. Increasingly, nonmarine stratigraphers also have become accustomed to taking advantage of the GPTS as applied to continental strata. This chronologic scale is derived from a linear distance relationship of the age of magnetic polarity reversals recorded in oceanic basalts preserved on the floors of ocean basins derived from spreading rates calibrated by interpolations between, or extrapolations from, radioisotopic dating of selected magnetic reversals (Cande and Kent 1992, 1995; Berggren et al. 1995a). The radioisotopic information transforms the relative magnetic reversal pattern into a numerical chronology. In that it is almost impossible to directly date the oceanic basalts, the chronologic scale is developed by use of marine or nonmarine stratigraphic sections wherein the polarity pattern can be directly calibrated radioisotopically (see Vine and Matthews 1963; Heirtzler et al. 1968; Berggren et al. 1985; Lindsay et al. 1987; Aubry 1995 for summaries). Whereas initial correlation of a given nonmarine magnetostratigraphic succession typically is based on radioisotopic data, Albright (1999, 2000) gives a recent example in which biostratigraphic and biochronologic data were used for both original and refined age control of a lengthy magnetic polarity sequence in the absence of radioisotopic dates.

Berggren et al. (1995a, 1995b) introduced the concept of the IMBS as consisting of three elements: a magne-

10 Michael O. Woodburne

tochronology, a numerical scale (combined as the GPTS), and a magnetobiochronologic framework. In that the GPTS is independent of biological evolution, the relative magnetic reversal pattern can be applied to the relative biochronologic framework without circularity in reasoning, and the calibration applied to the reversal pattern also can be carried into the biochronologic data set, providing its numerical calibration. Among other operations, the numerical scale allows quantification of geologic (and paleontologic) processes.

Estimating the Age of Biochronologic Events Despite advances in radioisotopic dating, biostratigraphy (augmented by magnetostratigraphy, chemostratigraphy, and cyclostratigraphy) still is the most important and widespread means of obtaining numerical ages from the stratigraphic record. The primary importance of biostratigraphy is that it is noniterative; that is, it is an ordinal scale. This is in contrast to magnetic polarity zones, chemostratigraphic signatures, and so on, which require either biostratigraphy or radioisotopic dating to order the other events in a temporal context.

Because not all biochronologic boundaries are directly calibrated, and because many of them fall within rather than at magnetic polarity reversal boundaries, it is necessary to estimate the ages of the biochronologic framework, either in the deep sea or on land. This operation also can be significant in refining, via feedback, the points at which the GPTS is calibrated and can effect revisions therein (e.g., Cande and Kent 1992, 1995). In this context, the term *estimation* has taken on a formal meaning in chronostratigraphy. Rather than connoting a guess at a reasonable calibration of a biochronologic boundary, estimation (sometimes called temporal analysis; Aubry 1995) means addressing this goal with deliberate attention given to rational means by which it may be achieved. The many examples from Berggren and Van Couvering (1974, 1978), Berggren et al. (1995b), and Aubry (1995, 1998) illustrate that evaluation of accumulation rate (its steadiness or erraticism) in sequences under discussion comprises a primary objective as addressed from any pertinent perspective, including magneto-, bio-, cyclo-, chemo-, and lithostratigraphy. Rather than guesswork, this is a rigorous and time-consuming process. Once stratigraphic completeness has been appraised it is possible (where warranted) to derive numerical ages for paleobiological or other events based on interpolations between, or extrapolations from, parts of the succession that are directly calibrated by radioisotopic means.

In theory, two magnetozones (for instance) may be collapsed into one, or be cut out entirely, by an unconformity (Aubry 1991, 1998; Aubry et al. 1996). Similarly, geochemical profiles or any other pattern may be interrupted and condensed by unconformities, giving spurious results (Aubry 1998). Truncation of taxon ranges may appear to have been diachronous on a regional basis, but this appearance may reflect only an incomplete stratigraphic record. Also, an apparent range truncation might result from parts of a taxon record being eliminated within the stratigraphic extent of the range (preserving both top and bottom). A visually thin biozone thus might translate into spurious estimations of accumulation rate.

To test for hidden unconformities, Aubry (1991, 1995) proposes a method as excerpted here. If the stratigraphic section is continuous, the thickness of the magnetozones and biozones in the stratigraphic record should be proportional to their respective durations as magnetochrons and biochrons of the IMBS. The accumulation curve calculated on this basis should be a straight line. If the record reflects a condensed section, the apparent succession of events still will be recorded, but the accumulation rate constructed from them will be of a shallower slope than that previously or subsequently (figure 1.1). If the record reflects a truncated section (unconformity), the accumulation rate slope will be disjunct within the zone of unconformity (figure 1.2). Whereas it probably is not possible to determine the amount of sediment removed (or not deposited) by the processes that result in an unconformity, it is possible to determine the amount of time represented by the hiatus.

In this exercise, the two surfaces that bound an unconformity are of different genetic significance. The upper surface is the bounding surface that reflects renewed deposition after the hiatus. The lower surface reflects all the events that conspired to form the hiatus in the first place. Dating the surfaces of an unconformity involves three steps (Aubry 1991, 1995).

1. Recognizing the presence of an unconformity as in severe truncation of biozones, magnetozones, and so on (e.g., figure 1.2) or sharp contacts between lithologic units or subunits.

2. Estimating the duration of the hiatus by estimating the duration of the magnetozones or biozones that are not represented in the various stratigraphic sections

3. Dating the age of the boundaries using any information or approach (e.g., accumulation rate) that narrows the level of imprecision as to the likely age of the unconformable surfaces

In an important illustration of the significance of these considerations, Aubry et al. (1996) developed a detailed examination of the fidelity of the core retrieved from Deep Sea Drilling Project (DSDP) site 550. This core contains

Principles and Procedures 11



FIGURE 1.1 Sedimentary history of a section containing successive truncations (stratigraphic gaps), inferred from the sedimentation rate curve. The truncated section is characterized by the anomalous stratigraphic juxtaposition of paleontologic events and magnetic reversals that are temporally well separated. Note the disjunct nature of the sedimentation rate curve in the truncated interval. After Aubry (1995). C.N., calcareous nannofossil; P.F., planktonic foraminiferal.

the data from which a date of 55 m.y. was estimated for the age of the Paleocene-Eocene Series boundary in the GPTS (Cande and Kent 1992, 1995) on the basis of the nannoplankton (NP) 9/10 zonal boundary. This chronozonal boundary occurs 13 m and 7 m, respectively, below ashes dated by the laser total fusion 40 Ar/ 39 Ar method at 54.0 ± 0.53 Ma and 54.51 \pm 0.05 Ma, from which Swisher and Knox (1991) derived an accumulation rate for this part of the DSDP core. This accumulation rate was extrapolated to the part of the section containing the NP9/10 zonal boundary, resulting in its estimated age of 55 Ma. Cande and Kent (1992, 1995) used this age for the NP9/10 chronozonal boundary as one of the nine calibration points from which their GPTS was constructed. But Aubry et al. (1996) showed that there is an unconformity at level 408 m in the core at site 550 and that part of zone NP10 is missing and suggested

that the age of the NP9/10 zonal boundary probably is 0.3-0.4 m.y. older than previously thought. At the same time, one cannot arbitrarily change the age of the NP9/10 chronozonal boundary because that has not yet been demonstrated in a section that is complete across that boundary and because such a change carries implications for the age of all other magnetochrons in that part of the GPTS and thus for all biochronozonal events in the relevant part of the IMBS (Aubry et al. 1996). Wing et al. (2000) explore this situation and also that for the best developed data set for the age of the $\delta^{13}C$ excursion in nonmarine strata of the Fort Union and Willwood formations of the Big Horn Basin, Wyoming. The age of this excursion in the marine realm (55.5 Ma; Aubry et al. 1996) depends on the same data set as that from which an age of 55.0 Ma was derived for the Paleocene-Eocene boundary. Although dif-

12 Michael O. Woodburne



FIGURE 1.2 Sedimentary history of a section containing a condensed interval, inferred from the sedimentation rate curve. The condensed section yields the sequential occurrences of paleontologic events and magnetic reversals that characterize the temporal interval during which it was deposited. After Aubry (1995). C.N., calcareous nannofossil; P.F., planktonic foraminiferal.

ferent in detail, the analysis of sequence and evidence offered by Wing et al. (2000) for the Big Horn Basin succession is comparable in pitfalls and uncertainty to the marine situation under discussion (although for different reasons, including possible variations in local tectonism that might affect accumulation rates used in extrapolations; Bao et al. 1999). Neither the marine nor the nonmarine realm offers a single stratigraphic section that is complete across the interval involved (inclusive of the relevant calibration points), so the proposal that the NP9/10 chronozonal boundary is 55.0 Ma (but might be 55.3 Ma; Berggren and Aubry 1996) cannot be reconciled with the proposal (Wing et al. 2000, table 7.5) that the comparable level in the nonmarine record of the GPTS (two-thirds of the way down in C24r [= C24r.0.66]) is 55.315 Ma. Although the numbers appear similar, either or both might be inaccurate because of uncertainties in each case.

As of this writing, this situation had not been resolved. On one hand, the ages of reversal boundaries for the GPTS are commonly reported to three decimal places (e.g., Berggren et al. 1995b:132–133; chron C29r: 64.745–65.578 Ma). On the other hand, users of the numerical estimates for the age of reversal boundaries of the GPTS should be aware of the methods and the facts by which they are determined and treat them with a level of caution appropriate to the scale of the study for which they are being used.

OPERATIONS IN CORRELATION

The purpose of this section is to outline some further operational aspects basic to developing temporal correlations of paleontological data before turning to a discussion of biochronology. Base Defines Boundary This concept (George et al. 1969) is fundamental to all unit stratigraphic boundaries intended for potential or actual use in correlation. As indicated earlier, boundaries of lithostratigraphic units typically are chosen on sharp or at least replicable changes in lithology. Although not universal, it is common that lithostratigraphic boundaries are based on breaks in the rock record (i.e., at unconformities). As Schenk and Muller (1941) point out, this may be desirable for rock units, but it is definitely undesirable for chronostratigraphic units or related concepts (e.g., table 1.2). When the intent is to develop a succession important for correlation and replication of the passage of time, units and the boundaries between them should be chosen in locations where gaps (unconformities) do not exist or at least are made as minimal as possible.

It is certainly necessary to have a stratotype section for a formalized unit and its boundaries so that subsequent observers can replicate the criteria on which the unit was based originally (Salvador 1994:88). It also is intellectually appealing to have the bottom and top of a particular unit displayed in a single stratigraphic section and to have the type section that forms the basis of the unit to be a single, continuous stratigraphic transect. However, this goal may not be attainable realistically, and rather than having the one-section notion result in loss of important data because of imperfections in the rock record, modern codes and guides (e.g., Hedberg 1976; Salvador 1994) provide for a variety of typical sections to address the situations in which not only the base of the unit (boundary stratotype) but also characteristically typical representations of the unit (composite or component stratotypes) may be portrayed. Thus a given stratigraphic unit could have a boundary stratotype for its base, another for its top (the base of the next overlying unit), and one or more unit stratotypes where the main characterizing features (rocks or taxa) of the unit are well displayed and replicable by subsequent workers (Aubry et al. 1999).

Definition and Characterization The utility of a sequence of chronostratigraphic units for correlation is directly proportional to the degree to which its boundaries may be unambiguously defined and to the interval being characterized for the purpose of general recognition and correlation. In order to have unambiguous utility, the base of a stratigraphic unit must be defined as unambiguously as possible (and therefore must be repeatable and replicable precisely by other workers). A unit is characterized by the joint occurrence of a number of taxa (in this case), so that finding a representative number of them in a rock sequence is sufficient to propose a correlation to somewhere in the unit under discussion. It commonly is convenient to use immigrant taxa as allochthonous novelties (various kinds of datums) in stratigraphic sections as a means for boundary definition (Repenning 1967; Woodburne and Swisher 1995), although this is not always the case, so that taxa resulting from endemic evolution must be considered as well (Murphy 1977; Woodburne 1977, 1987b, 1996a).

Walsh (1998) presents a convenient summary of concerns commonly offered regarding the choice between single-taxon boundary definitions and multiple-taxon characterizations of biostratigraphic or biochronologic units. In short, if the boundary can't be found because the single definition is absent, it is better to increase the chance of finding the boundary with a number of ways (taxa) in which to do so.

If the boundary is to be used in correlation, one logically would seek the least ambiguous (= best) means to identify that point in time. When originally addressing boundaries for fossil mammals, Woodburne (1977) was proposing the best means for that purpose and clearly recognized that a single-taxon definition would be elusive. After all, the best often is a rare entity. Ideally, a single taxon would be widespread, geologically instantaneous in distribution, and abundantly found. The Hippotherium datum is one such candidate (Woodburne 1996a). It also is a rare example of such a phenomenon (Walsh 1998). The *Hippotherium* datum illustrates a fairly common situation regarding such phenomena, at least for the fossil mammal record: Although this datum is of nearly global significance, its source still has not been recognized. Although the North American genus Cormohipparion appears to be the best candidate for the source of the dispersal event known as the Hippotherium datum, neither the species of Cormohipparion that probably was the source for the datum nor its phyletic relationship to sister taxa within Cormohipparion has been securely identified (Woodburne 1996b). Whereas the time of origin in North America of the Old World Hippotherium datum may be unresolved, the age of the regional first appearance datum (FAD) is closely approached at 11.1 Ma (Woodburne 1996a; Garcés et al. 1996; Rögl and Daxner-Höck 1996).

Practical realities suggest that most correlations, as demonstrated by the presence of one or more taxa characteristic of them, are to some point within a chronologic unit or interval. Most correlations are thus centrist in tendency. Still, it is rational to propose the best means by which a biostratigraphic or chronostratigraphic boundary may be recognized, even if having found it means that the boundary already has been crossed to some extent (Walsh 1998). The extent to which such crossing is temporally significant is open to further testing depending on operational goals, and such testing is futile absent an unambiguous, temporally distinctive boundary definition.

THE ROLE OF BIOCHRONOLOGY

Berggren and Van Couvering (1978:40) indicate that "long-distance correlations are geochronologic in substance," and because of the prevalence of fossils over other kinds of chronologically significant data, such longdistance correlations are effectively biochronologic.

Berggren and Van Couvering (1978:40) portray the evidentiary and interpretive progression from biostratigraphy to biochronology and ultimately to chronostratigraphy. In that report, biochronologic correlations are based on recognizing the most widespread and distinctive events in biologic history (mostly FAD and LAD), identifying (replicating) those events in local biostratigraphies (lowest stratigraphic datums [LSDs] or LOs of current terminology) and evaluating their age with respect to as many other criteria as possible, and stratigraphically relating the events to evidence for other biochronologic datum events and to radiometrically dated or calibrated levels such as a volcanic layer or a paleomagnetic boundary in order to justify the interpretation that the event is isochronous throughout its area of extent.

Both Salvador (1994) and Hedberg (1976) state that biostratigraphic units are material and descriptive, rather than interpretive, whereas chronostratigraphic units are interpretive, representing an interval of time as recorded in the strata of the unit. Still, biostratigraphic correlation may approach chronostratigraphic correlation, and biostratigraphic (paleontologic) data give the basic material on which time correlations are based because they are nearly ubiquitous and they reflect the irreversibility of organic evolution.

Implicit in both Salvador (1994) and Hedberg (1976) are the commonly used procedures in developing correlations of rock units based on fossils: Biostratigraphic procedures allow the documentation in a physical framework of the presence and stratigraphic occurrence of a distinctive paleontological event, such as a new species or genus, developed either by in situ evolution or as reflecting dispersal from a possibly unknown source. This situation is conveniently and accurately described as an LSD or LO.

Finding the same paleontological stratigraphic pattern in other geographically distributed sites (other LSDs or LOs) permits the inference that the pattern may be of temporal significance and that the various LSDs or LOs may be correlated on the basis of their biostratigraphic similarity. From the paleontological (including mammal age) standpoint, these correlations are biocorrelations of Salvador (1994:15), which, when demonstrated to be temporally valid, become chronocorrelations. From the perspective of this book, mammalian biostratigraphic information (LO) is proposed to have biochronologic significance. The biochronologic significance is rooted in the irreversibility of organic evolution and documented as to its place in time and space by the stratigraphic framework in which it is manifested. Once frozen in stratigraphy, the biotic properties can be inspected for their relationship to any other kind of potentially significant temporal information and integrated with any iterative or ordinal data so as to eventually arrive at a level of documentation that enables the original biostratigraphic LOs to be awarded a temporal connotation. This operation begins with biostratigraphy, proceeds via biochronology, and leads to chronostratigraphy. In that mammal ages are biochrons, their role in correlation is clear, and a purpose of this book is to identify the quantity and quality of temporally significant information that can be related to mammal ages so that their chronologic utility is increasingly refined and illuminated.

Placing disparate sections (a number of LOs) into a chronologic framework based on stratigraphically adjacent phenomena considered to have their own temporal significance (i.e., other fossil zones, radioisotopic or magnetostratigraphic data) allows the further inference that the boundaries under discussion are isochronous (and at what scale). The resulting FAD is one example of that operation and would define the lower boundary of a given chronostratigraphic unit. Finding the next highest datum (and successfully validating its relevance to correlation; Aubry et al. 1999:113) would permit the designation of a chronozone with both boundaries defined. When this is accomplished, the entire package of strata can be combined into a chronostratigraphic unit of regional scale, with its implication for correlation, which is the purpose of the exercise in the first place.

Thus biostratigraphically based biochronologic correlation is an integral part of assessing age relationships of fossils and the rocks in which they occur, but is not formalized in current codes and guides. The important relationship between biochronology, biostratigraphy, and chronostratigraphy justifies the formalization of biochronologic units, as pioneered by Walsh (1998:158). This is followed here in principle but not in all details of nomenclature (table 1.3). In all cases an attempt has been made to preserve much of the pertinent language of the antecedent biostratigraphic unit, following Salvador (1994). Although the categories nominated by Walsh (1998, 2000) are similar in name and content, they are put to very different uses. In the proposal favored here, biochronologic correlations are of primary importance in establishing formal chronostratigraphic units, which are the necessary precursors to formulating geochronologic units. In the proposals represented by Walsh (1998, 2000, 2001, and references therein), geochronologic units are constructed in advance of chronostratigraphic units, biochronology plays only a subsidiary role, and chronostratigraphic units are "merely abstract sets of material strata" (Walsh 2001:708). One of the most useful aspects of Walsh (1998) is the emphasis on separating empirical and descriptive operations and concepts as distinct from theoretical and interpretive concepts. As Aubry (1997:22) stresses, the goal is to discuss rock and time with a simple but dual nomenclature.

The following biochronologic units are suggested (table 1.3): assemblage chron (reflective of many original mammal ages being effectively assemblage zones: "an assemblage zone based on a fossil fauna" [Salvador 1994:63]), range chron, taxon-range chron, concurrentrange chron, interval chron, and lineage chron. The assemblage chron stems from the assemblage zone of Salvador (1994) rather than that of Walsh (1998; assemblage fossizone) because the latter is directed toward range zones, which are a different category as used here (table 1.3). The range chron stems from the range zone of Salvador (1994). The range zone of Walsh (1998) is effectively the same as the taxon-range zone of Salvador (1994), which here is taken as antecedent to the taxonrange chron. The concurrent-range chron stems from the concurrent-range zone of Salvador (1994), which is the same as the strict overlap assemblage fossizone where the number of taxa is two (Walsh 1998:161). The interval chron stems from the interval zone of Salvador (1994) and is the interval of time defined on the earliest age of two successive biohorizons. This is comparable to that of Walsh (1998), which is a restatement of Salvador (1994). The lineage chron stems from the lineage zone of Salvador (1994) and has no counterpart in Walsh (1998). In any case, the purpose of identifying these biochronologic units is to emphasize their application to interpretive correlation as biochrons subsequent to empirical biostratigraphic documentation.

In this context, *datum* carries a temporal (time = interpretive) connotation and should be kept separate from descriptive and empirical considerations (rock), also as stressed by Walsh (1998). Thus *FAD* is appropriate for a temporal analysis, but LSD is a misnomer because it is a biostratigraphic (empirical, rock) concept (see Definitions). For that reason, LO (Aubry 1995, 1997) is preferred here (also Walsh 2000). Substituting LO for LSD preserves the intent promulgated by Opdyke et al. (1977), Lindsay et al. (1987), and Lindsay and Tedford (1990) but reserves the term datum for temporal interpretations rather than empirical stratigraphy. To paraphrase and substitute as to the proposal of Woodburne (1996a), a FAD is composed of a number of LOs. Each LO is a biostratigraphic record. If the LOs are associated with independent temporally significant information that shows them to be closely time correlative, they collectively support the interpretation that a FAD may be established (and within what temporal limits). If the proposal can be made that the FAD is isochronous over a large geographic area, then that concept (FAD) is appropriate to this interpretation. This is effectively similar to the proposals of Aubry (1995, 1997) except that the FOD (see Definitions) is not addressed here.

Hedberg (1976:86–92) and Salvador (1994:92–97) consider means by which established chronostratigraphic units may be extended away from their boundary or other stratotypes. Except for paleontological or radioisotopic criteria, the remainder¹ fall into various kinds of lithologic or other (paleomagnetic reversal) iterative, rather than ordinal, phenomena that depend on the former two kinds of data for demonstrating their temporal significance. Although mammal ages are not chronostratigraphic units, the means by which they may be correlated are the same because even though they were loosely constrained stratigraphically as originally formulated (Wood et al. 1941), mammal ages still had a stratigraphic component, and this has become increasingly refined ever since (although not necessarily uniformly).

RELATIONSHIP TO MAMMAL AGES

North American land mammal ages (Wood et al. 1941; Savage 1951) typically are identified as biochronologic units constructed to recognize discrete intervals of time based on the evolution of fossil mammals. Historically these biochrons were only loosely tied to a stratigraphic framework. To a real but perhaps originally somewhat limited extent, mammal ages were basically assemblage zones (i.e., there was a biostratigraphic base of sorts), and their correlation made use of the derivative assemblage chrons (although they were not labeled as such). After the work of Savage (1977), various kinds of chronostratigraphic and biostratigraphic units have been proposed for some of these intervals. Savage proposed the

16 Michael O. Woodburne

Wasatchian Stage/Age and its correlation to the European Sparnacian Stage (nominally lower Eocene or upper Paleocene depending on interpretations of the Paleocene–Eocene Series boundary), and although it was provided only in summary form, it is clear that the Wasatchian Stage is represented in Colorado, New Mexico, and Wyoming, as well as in Europe. Although study of the Wasatchian Stage still is not complete, it can be considered as under current discussion (Gingerich and Clyde 2001; Gingerich 2001; Bowen et al. 2001; Clyde 2001; Strait 2001).

Rose (1980, 1981) proposed the Clarkforkian Stage/Age (nominally upper Paleocene, but pre-Wasatchian). Walsh (1998) calls the Wasatchian and Clarkforkian proposals into question on the basis of their having been no boundary stratotype identified for either of them. Still, attention to stratigraphic detail was implicit (Savage 1977) or explicit (Rose 1981) and contributed to the interpretation that the biostratigraphic patterns were chronologically significant. Rose (1981, figures 2 and 3) shows the distribution of measured sections and localities that demonstrate the lower and upper limits of the Clarkforkian Stage, even though type and reference sections are not designated by those names. Thus formalization of the unit remains only a matter of procedural assertion. Rose (1981:26-27) provides additional faunal characterization of the Clarkforkian to facilitate its recognition elsewhere and points out that stratigraphic demonstration of the unit in other areas still is under development. Archibald et al. (1987) indicate that Clarkforkian mammals are rarely found beyond the Big Horn and Clark's Fork basins of Wyoming. The best stratigraphic documentation of elements of the Clarkforkian Stage is provided by Clyde (2001) for the Mc-Cullough Peaks area situated between the Clark's Fork and Big Horn basins (figure 3.1, this volume). The current status of the Clarkforkian Stage is one of further development, documentation, and demonstration.

Archibald et al. (1987) offer a succession of biostratigraphic zones within the four mammal ages that equate about with the Paleocene Epoch. Lacking formal biostratigraphic stratotypes and detailed stratigraphic documentation, these interval zones, lineage zones, and acme zones remain biochronologic units, although their temporal succession still is viable. Williamson (1996) proposes a biostratigraphic zonation for rocks of the same age in the San Juan Basin, New Mexico, that in part validates the biochronology proposed by Archibald et al. (1987) through its explicit use of a physical stratigraphic framework. Although the biostratigraphic data were generalized into intervals, each of which was on the order of 5–10 m thick (or more in some cases) and separated by

apparently unfossiliferous intervals 10 or more meters thick, the stratigraphic order is clear. The suites of locality intervals were physically correlated between the various stratigraphic sections in the southern San Juan Basin and grouped into eight informal biostratigraphic zones, labeled A-H (Williamson 1996:27, figure 18), with many extending laterally up to about 40 km. The physical versus biological correlation of the localities leads these lettered units to be dubbed as paleontologically distinct lithozones by Walsh (2000). The physical correlation also was consistent with its magnetostratigraphic characterization. The physical framework thus constructed was transformed into eight formal biostratigraphic zones as defined paleontologically. The type stratigraphic section was explicitly given for each zone (Williamson 1996:49–53), and the stratigraphic ranges for the taxa on which the zones are based is clearly shown at the indicated level of precision mentioned earlier (Williamson 1996, figure 19). As one example, the stratigraphically lowest biozone was nominated as the Hemithlaeus kowalevskianus-Taeniolabis taoensis Zone. Although not so designated by Williamson (1996), this zone and all of the others are interval zones, save the stratigraphically highest Mixodectes pungens Taxon-range Zone. The biozones are defined on the basis of single taxa and are provided with characterizations based on index taxa and first and last occurrences. As indicated (Williamson 1996, figure 24), these biozones contain taxa correlative with Puercan (but not earliest Puercan) and Torrejonian mammal ages, with the Hemithlaeus-Taeniolabis Zone being about correlative with the Ectoconus-Taeniolabis (Pu2) biochron of Archibald et al. (1987) and the Taeniolabis taoensis-Periptychus carinidens Interval Zone about correlative with the Taeniolabis-Periptychus (Pu3) biochron. Williamson (1996) effectively validates the Pu2 and Pu3 tentative proposals of Archibald et al. (1987; see also chapter 3, this volume), but fossiliferous strata equivalent to Pu1, typified by faunas in Wyoming, Montana, and Colorado (Archibald et al. 1987), are not present in the San Juan Basin.

Superposition of the Puercan interval zones is demonstrated by Eberle and Lillegraven (1998a, 1998b) and Lillegraven and Eberle (1999) in their seminal studies of the Ferris Formation in the Hanna Basin of Wyoming. The Ferris Formation contains a sedimentary succession about 1200 m thick with fossil mammals of Late Cretaceous (Lancian) to early Paleocene (Puercan) age. Puercan fossils occur in the upper 600 m of section, and a detailed biostratigraphic array allows the superpositional demonstration of biochrons Pu1–3 of Archibald et al. (1987), with the content of Pu1 being modified somewhat
to take into account proposals for (Archibald and Lofgren 1990) and against (Lofgren 1995) the recognition of an earliest Puo zone (see also chapter 3, this volume). The Hanna Basin record is sufficient to validate as biostratigraphic interval zones the Pu1–3 biochrons originally proposed by Archibald et al. (1987) and to stabilize the allocation of mammal-bearing sites in other parts of North America to this chronologic scheme. Neither Eberle and Lillegraven (1998a), Lillegraven and Eberle (1999), nor the authors of chapter 3 take the additional steps needed to formalize these Puercan biostratigraphic units.

In a similar fashion, Williamson (1996) validates the Torrejonian biochrons of Archibald et al. (1987). Williamson's (1996) P. carinidens–Protoselene opisthacus Interval Zone is about correlative with the Periptychus-Tetraclaenodon (To1) biochron. Collectively the Williamson (1996) P. opisthacus-Ellipsodon grangeri Interval Zone, the E. grangeri-Arctocyon ferox Interval Zone, the A. ferox-Pantolambda cavirictum Interval Zone, and the P. cavirictum-Mixodextes pungens Interval Zone are about correlative with the Tetraclaenodon-Pantolambda (To2) biochron (chapter 3). The Mixodectes pungens Taxon-range Zone of Williamson (1996) is about correlative with the Pantolambda-Plesiadapis praecursor (To3) biochron. Biostratigraphic validation of the Archibald et al. (1987) biochrons of the Tiffanian mammal age remains to be accomplished.

The biostratigraphic zones of the Fort Union and Willwood formations of the Big Horn Basin, Wyoming (Gingerich 1976, 1980, 1983, 1991), recently have been formalized (Gingerich 2001). Up to this point, these were biochronologic units. As summarized in Bown et al. (1994), P. D. Gingerich and colleagues have embarked on a detailed stratigraphic documentation of fossil-bearing sites of nominally Paleocene and early Eocene age in this region over a period of nearly 30 years. Implicit as well as explicit in these studies has been the correlation of the fossil sites to a number of master stratigraphic sections, with stratigraphic assignments commonly given in meters with respect to a given datum. Although the methods used were those that can lead to biostratigraphic zonations, and the density of biostratigraphic data has greatly increased over time, the proposed zonation has been formally described only recently (Gingerich 2001). Thus the succession of lineage zones, interval zones, and acme zones previously used now is provided with a clear, if terse, definition (lowest range datum [LRD]), stratigraphic documentation, and nominal abbreviation (Cf3 = *Phenacodus–Ectocion* Acme Zone).

Previously, the only procedurally valid (in part) biostratigraphic zonation for part of this succession was proposed by Schankler (1980) for the Willwood Formation of nominally early Eocene age (Bown et al. 1994:35). Following recommendations in Hedberg (1976), a threefold zonation was developed in reference to a measured section approximately 730 m thick, with taxon ranges displayed with respect to the fossil localities that were tied or referred to that master section (grouped into 10-m intervals). The boundaries of the zones were chosen at places showing a marked change in faunal composition. Schankler (1980) chose the boundary between the first two zones, the Haplomylus-Ectocion Range Zone and the Bunophorus Interval Zone at a point labeled biohorizon B, located at a level (380 m) intermediate between a major extinction (370 m) and immigration (390 m) event. In comparable fashion, the boundary between the Bunophorus Interval Zone and the next higher Heptodon Range Zone was placed at a level (530 m) at which another immigration event is recorded. Although Schankler (1980) follows the "base defines boundary" principle, it would have been preferable to begin the Bunophorus Interval Zone at the immigration level (390 m) where data actually are present rather than in the unfossiliferous gap at 380 m. It also would have been preferable had the localities not been lumped into 10-m intervals, an unavoidable procedure at the time. Moreover, Bown et al. (1994:35-36) point out that the stratigraphic section that provided Schankler's zonation was never located on a map; his biostratigraphic zones thus were not provided with a type section and so are of limited utility. The promise of completely demonstrating a viable biostratigraphy was not realized by Schankler (1980), and these are not incorporated in the compilation of Gingerich (2001). Clyde (2001) used the part of the zonations in Gingerich (2001) in the McCullough Peaks Formation, found between the Clark's Fork and southern Big Horn basins. The McCullough Peaks Formation contains fossil mammals that range from Tiffanian (Ti3) through Wasatchian (Wa7) and contributes to the paleomagnetic characterization of these zones in comparison to those from sequences in Polecat Bench. Taking into account the interpolation of zonal boundaries in unfossiliferous parts of the stratigraphic sections, Clyde (2001) proposes two models for age assignment for the biozones of the two regions (also see Wing et al. 2000), based on interpolating zonal boundaries with respect to the magnetostratigraphic zonation. In model 1, the Clarkforkian begins at 56.17 Ma, the Wasatchian zone Wao at 54.96 Ma. In model 2, these ages are 56.47 Ma and 55.23 Ma, respectively.

D. R. Prothero and colleagues have been long involved in a faunal succession of the nominally Oligocene strata in North America. The interval zone framework used in

18 Michael O. Woodburne

chapter 5 for fossil mammals exemplifies the detailed use of magnetostratigraphic information to assist in temporal discrimination of this zonation.

The small number of these and possible other examples reflects, in part, the generally discontinuous record of mammal-bearing deposits in North America but also probably results to some extent from the fact that, overall, mammal age correlations provide results that are satisfactory to their users. In fact it can be argued that valuable refinements can be made to the framework in which mammalian biochronology resides without resorting to the kind of effort needed for their detailed formalization into biostratigraphic or chronostratigraphic units (Lindsay and Tedford 1990). But if for no other reason than to be able to accurately relate events in the fossil mammal time scale to those of global extent (Zachos et al. 2001), close attention still must be given to the chronology of mammal-bearing sequences.

Examples in chapters 3-7 illustrate ongoing refinements in biostratigraphically assisted biochronology, including increased scrutiny of boundaries of mammal ages and their subdivisions, and the principles and practices that can lead to the development of soundly based biostratigraphic and chronostratigraphic units (and the disciplinary rigor needed for this purpose) are exactly those needed to increase the documentation and integration of information with which to assess the quality, validity, and scale of resolution of correlations based on fossil mammals. One of the features of mammalian biochronologies in the 1987 volume and in the current volume is the use of immigration events as defining the boundaries of mammal ages or other units. Whether reflecting endemic genesis or intercontinental correlation, the question of diachroneity is either cited and recognized (Woodburne 1977, 1996a) or emphasized (Alroy 1998). Still, Aubry (1995, 1997) has implied that at basinal (transpose continental here) scale, diachrony is less likely to be an operational problem than is the impact of stratigraphic imperfection on local sections. A major charge to the mammalian biostratigraphic and biochronologic community is to increase the number of pertinent stratigraphic sections and to improve the estimates of age, correlation, and completeness for all of them.

NOTE

 These include physical interrelations of strata (e.g., superposition); lithic correlations, especially volcanogenic units; geomagnetic reversals; climatic change (the δ¹³C excursion, mentioned earlier, could be one such example); eustatic sea level changes or other processes that create unconformities; and subsequent reflooding or other kinds of resumed deposition.

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20 Michael O. Woodburne

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2

Mammalian Biochronology of the Latest Cretaceous

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AMMALIAN DIVERSIFICATION, in both the ecologic **M** and taxonomic senses, sharply increased in the early Tertiary. Consideration of Late Cretaceous assemblages therefore provides essential background to interpretation of the great evolutionary radiations that followed. Most relevant in this connection is the Lancian land mammal age, which preceded the Puercan and is the focus of this summary. However, the Lancian itself must be viewed in the context of preceding land mammal ages and assemblages that have not yet been assigned to a land mammal age. Particularly significant problems remain in identifying the beginning of the Lancian, biochronologically and chronostratigraphically. For this reason, we begin with a brief general review of the record of North American, Late Cretaceous mammals, with particular emphasis on the widely used land mammal ages correlative with the Campanian and Maastrichtian marine stages/ages of Europe. A summary of the age relationships of better-known mammal faunas and ages for the Late Cretaceous of North America is shown in figure 2.1.

Land mammal ages have been established in North America only for the latter part of the Cretaceous period, and for this reason we must make frequent reference to European marine stages in reviewing temporal relationships, especially among the older faunas. The Aquilan, Judithian, "Edmontonian" (not formally recognized at present), and Lancian North American land mammal ages (NALMAs) were proposed initially as true chronostratigraphic ages or stages (Dorf 1942; Russell 1964, 1975). That is, they were based on the physical limits of specific rock bodies and their contained fossils (NACSN 1983), and therefore they differ conceptually from North American land mammal ages (Wood et al. 1941), which are intended to serve as time units. The original definitions of the Cretaceous ages also included other fossils, including plants, molluscs, and lower vertebrates such as dinosaurs. With great increases in knowledge of Late Cretaceous mammals, however, attention later became focused largely on mammalian assemblages in characterizing these ages (Fox 1978). Lillegraven and McKenna (1986) formally proposed Aquilan, Judithian, and Lancian land mammal ages. We follow their definitions and usage herein, modifying the characterization of the Lancian and its principal correlates based on new information.

The beginning of the Puercan land mammal age is defined by the first appearance of Protungulatum donnae (Archibald and Lofgren 1990; chapter 3, this volume). A commonly used marker of the Cretaceous-Tertiary boundary in more global terms is at the base of a clay containing anomalously high levels of iridium in the marine boundary stratotype at El Kef, Tunisia (Keller et al. 1995). The age of the boundary currently is placed at 65.5 ± 0.1 Ma (Obradovich and Hicks 1999), which, because of the use of different standard monitor ages in their calculations, is older than the widely cited age of 65.16 ± 0.04 (Swisher et al. 1993). The Lancian-Puercan and Cretaceous-Tertiary boundaries correspond closely in time, and the two are commonly considered to have been synchronous (see discussion and references in Eberle and Lillegraven 1998b). However, definitions of the Lancian-Puercan and Cretaceous-Tertiary are based on differing criteria, studied in different depositional settings on distant continents. As discussed later in this chapter, at least one transitional mammalian assemblage appears to be a Puercan fauna of Late Creta-



22 Richard L. Cifelli, Jaelyn J. Eberle, Donald L. Lofgren, Jason A. Lillegraven, and William A. Clemens

= Isolated occurrences of single specimens that may be of Lancian age

FIGURE 2.1 Late Cretaceous mammal ages and pre-Aquilan faunas. Polarity and polarity chronozones are from Gradstein et al. (1995); normal polarity chrons are shaded black. Numeric ages for stage boundaries are from Palmer and Geissman (1999). North American land mammal age (NALMA), pre-Aquilan fauna, notable first occurrence, and geographic range information is found in the main text and is based on references cited therein. Shaded boundaries between NALMAs indicate that they are not well defined (see text for discussion).

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ceous age. Radioisotopic ages for chrons of the Geomagnetic Polarity Time Scale (GPTS) as used in our summary follow Berggren et al. (1995). The term *faunule* is used herein as a diminutive form of *fauna*, referring to a fauna known by only a few taxa rather than to an association of taxa interpreted intentionally for its ecological significance (see *Definitions*).

PRE-LANCIAN FAUNAS

ALBIAN-CENOMANIAN INTO SANTONIAN

Until recently, the North American record of Late Cretaceous mammals older than approximately the early Campanian was almost nonexistent, consisting of a few, largely indeterminate specimens (McNulty and Slaughter 1968; Clemens et al. 1979; Krause and Baird 1979; Emry et al. 1981). Several reasonably well-represented mammalian faunas, all from Utah, are now known for the approximately 15-m.y. time span separating the beginning of Cenomanian from the beginning of Campanian time. Oldest of these is the Mussentuchit local fauna, collected from a restricted stratigraphic interval in upper parts of the Cedar Mountain Formation. ⁴⁰Ar/³⁹Ar age determinations indicate the fauna of about 28 mammalian varieties to be about 98.5 Ma, placing it near the Albian–Cenomanian (Early–Late Cretaceous) boundary (Cifelli et al. 1997, 1999b).

A somewhat younger fauna is known from the Dakota Formation, southern Utah. Mammalian fossils come from the middle member of the unit and are considered late Cenomanian in age, based on invertebrate fossils from marine facies in parts of the Dakota Formation itself (Eaton 1991). The next youngest, reasonably well-known mammalian fauna comes from the Smoky Hollow Member of the Straight Cliffs Formation, also in southern Utah. The age of this assemblage is Turonian, based on molluscs from sub- and superjacent marine units (Eaton 1987, 1991). Late Cretaceous, pre-Campanian faunules, as yet not well known, have been reported from the John Henry Member (Coniacian–Santonian) of the Straight Cliffs Formation, which overlies the Smoky Hollow Member (Eaton et al. 1999a); an unspecified unit of ?Coniacian–Santonian age (Eaton et al. 1999b); and various horizons in the Iron Springs Formation, southwestern Utah, possibly including mammals of Turonian and Coniacian–Santonian age (Eaton 1999a).

The discontinuous record, limited geographic distribution, and in most cases scant sampling of these faunas, together with the preliminary nature of much of the taxonomic information available about them, severely limit interpretation of mammalian biochronology of these older strata. Accordingly, we limit ourselves in this summary to general observations on pre-Campanian mammals of North America. Members of Triconodontidae, represented by an endemic North American clade (Alticonodontinae), are reasonably abundant in the Albian-Cenomanian (Cifelli and Madsen 1998). However, they are lacking from all later faunas except an Aquilan assemblage from Canada (Fox 1976a). Spalacotheriid symmetrodonts are present in all pre-Campanian faunas (Cifelli and Gordon 1999). Multituberculate assemblages are dominated by species of the "Paracimexomys group." Relictual "plagiaulacidans" may be present in the Albian-Cenomanian, when Neoplagiaulacidae first appear (Eaton and Cifelli, unpublished data). Cimolodontidae are possibly present as early as the Cenomanian and, more securely, by the Coniacian-Santonian, when Cimolomyidae first appear (Eaton 1995, 1999a, 1999b; Eaton et al. 1999a, 1999b). Marsupials are present from the Albian-Cenomanian onward (Cifelli et al. 1999b), with Stagodontidae appearing by the Cenomanian (Cifelli and Eaton 1987) and the paraphyletic "Pediomyidae" by the Santonian (Eaton et al. 1999b). Notable by their absence throughout are Eutheria, which may have been present in the Aptian-Albian of North America but do not reappear until the early Campanian (Cifelli 1999).

AQUILAN

The Aquilan, the oldest of North America's formally defined Late Cretaceous land mammal ages, was characterized on the basis of a mammalian fauna from Verdigris Coulee, in upper parts of the Milk River Formation, Alberta (Lillegraven and McKenna 1986). The age of the fauna is conventionally regarded as early Campanian, although placement of the Santonian-Campanian boundary has been disputed (Lillegraven 1991). An alternative interpretation would place the upper Milk River Formation in late Santonian time (Leahy and Lerbekmo 1995). The mammalian fauna, described in a series of papers by Fox (1971a, 1971b, 1976a, 1980b, 1982, 1984a, 1984b, 1987), is highly distinctive. In large part, this is almost surely a result of artifacts caused by hiatuses in the fossil record. The Aquilan is not immediately preceded by any wellknown mammalian fauna and, because it is probably at least 80 Ma in age, it antedates Judithian assemblages by several million years. In addition to the fauna of some 31 mammalian varieties from Verdigris Coulee, the Aquilan is represented by several smaller assemblages from Utah. Of these, the most diverse is from the Wahweap Formation of the Kaiparowits Plateau (Cifelli and Madsen 1986; Eaton 1987; Cifelli 1990b, 1990c); faunules also are known from the ?Wahweap Formation, Paunsaugunt Plateau (Eaton et al. 1998), and the Masuk Formation, Henry Mountains (Eaton 1990).

The Aquilan includes representations of a number of archaic mammalian lineages; most notable among last appearances are the spalacotheriid symmetrodonts and Triconodontidae. Nonetheless, the Aquilan differs significantly from older Late Cretaceous assemblages, particularly in the greater diversity of more advanced forms, including cimolodontid, cimolomyid, and neoplagiaulacid multituberculates (Fox 1971a; Eaton 1987), along with pediomyid marsupials (Fox 1971b). Notable first occurrences include the multituberculate Mesodma, the stagodontid marsupial Eodelphis, and the lipotyphlan insectivore Paranyctoides (see Fox 1984a; Cifelli 1990c). A species referred to Paranyctoides also has been described from Coniacian strata of Uzbekistan (Nessov 1993). This suggests the possibility that Paranyctoides arrived via dispersal from Asia rather than having evolved in situ in North America. Given that it is widely distributed among Aquilan (and later) faunas, Paranyctoides may eventually prove useful as a first appearance datum (FAD) for the Aquilan.

JUDITHIAN

The basis of the Judithian land mammal age (Lillegraven and McKenna 1986) is a fauna from three localities situated near the top of the Judith River Formation, Choteau and Blaine counties, north-central Montana (Sahni 1972). Stratigraphic correlation of the type Judithian (and presumed correlatives mentioned later in this chapter) with adjacent marine units has yielded mixed interpretations for the age of the Judithian because of conflicting zonations based on foraminiferans and ammonites (see references and discussion in Lillegraven and McKenna 1986; Lillegraven and Ostresh 1990). Radioisotopic dates for a correlative assemblage (the Hill County Local Fauna), together with correlations based on ammonites, suggest that the Judithian had a duration of at least 5 m.y. and extended back to at least 78 Ma, placing it within standard chronology of the European Campanian (Goodwin and Deino 1989). Weil (1999) summarizes available biostratigraphic and geochronologic data and concludes that known Judithian faunas span the interval from approximately 79 to 74 Ma.

Geographically, the Judithian is the most widely represented of North America's Late Cretaceous land mammal ages. Correlative faunas from the Judith River Formation in Montana include a well-sampled assemblage from the northern part of the state, the Hill County Local Fauna (Montellano 1992), as well as a faunule from near the Mussellshell River, Wheatland and Golden counties (Fiorillo 1989; Fiorillo and Currie 1994), in south-central Montana. The Egg Mountain locality, in the Two Medicine Formation, northern Montana, has yielded rare but more complete specimens (Montellano 1988; Montellano et al. 2000). To the north, in Alberta, correlative faunas (arbitrarily grouped, for present purposes, as the Oldman assemblage) have been recovered from what is now called the Judith River Group (Eberth and Hamblin 1993). Best represented of these are fossils from the Dinosaur Park (upper Oldman) Formation (Fox 1979a, 1979b, 1979c, 1980a, 1981); a few specimens have been collected from the underlying Oldman and Foremost formations (lower Oldman of Fox 1976b). A few mammalian specimens also have been collected from the Judith River Group in Saskatchewan (Storer 1993). Principal correlatives to the south of the type Judithian include faunas from the "Mesaverde" Formation, Wind River and Bighorn basins, Wyoming (Lillegraven and McKenna 1986); Kaiparowits Formation, southern Utah (Cifelli 1990a, 1990c; Eaton 1993; Eaton et al. 1999a); upper part of the Fruitland Formation and transition zone between Fruitland and Kirtland formations, New Mexico (Clemens 1973; Flynn 1986; Rigby and Wolberg 1987); and Aguja Formation, southern Texas (Rowe et al. 1992; Weil 1992; Cifelli 1994; Sankey 1998).

The Judithian is highly distinctive, sharing few species with other land mammal ages (Lillegraven and McKenna 1986; see table 2.2), and it appears to have been stable

through its duration (Goodwin and Deino 1989). Perhaps the biochronologically most useful first appearances are those of the multituberculates Meniscoessus major, M. intermedius, Mesodma primaeva, and Cimolomys clarki; marsupial Turgidodon; and leptictoid eutherian Gypsonictops. On the basis of dinosaur assemblages, Lehman (1997) defines northern and southern faunal provinces for the Judithian, corresponding to the Aquilapollenites and Normapolles palynofloras, respectively. Heterogeneity in composition of Judithian mammalian assemblages also appears to be related, at least in part, to latitudinal provinciality. Pediomyid and stagodontid marsupials, for example, are rare or lacking in southern assemblages. Statistical analyses of the Judithian mammalian assemblages show that available data do not permit formal recognition of one or more southern faunal provinces (Weil 1999), but mammalian local faunas of the San Juan Basin, New Mexico, await full description and modern systematic analyses of all their members.

"EDMONTONIAN"

It is generally recognized that a significant temporal hiatus separates typical Judithian from Lancian faunas (Lillegraven and McKenna 1986). Indeed, given the age range for the Judithian recognized here (ca. 79–74 Ma) and the fact that known Lancian local faunas correlate with the late Maastrichtian (ca. 67.5–65.5 Ma), it seems probable that the two land mammal ages are separated by as much as 7 m.y. Russell (1964, 1975) proposes an intervening terrestrial vertebrate stage, the "Edmontonian." Formal recognition of the "Edmontonian" as a land mammal age is not yet possible, however, and the term is used in quotation marks here, following Lillegraven and McKenna (1986). Fossiliferous nonmarine strata of probable "Edmontonian" age are not common in the Western Interior because of a late Campanian-early Maastrichtian marine transgression. In Montana, for example, this interval is represented by the Bearpaw Shale, which in most areas of outcrop lies stratigraphically between the largely terrestrial Judith River and Hell Creek formations (Lillegraven 1987). A second problem in recognizing an "Edmontonian" land mammal age is that a high proportion of the few mammals represented is either inadequately known or conspecific with Lancian taxa, so the species are not temporally diagnostic (Lillegraven and McKenna 1986). Fortunately, discoveries in recent years have greatly improved knowledge of this poorly understood interval, and we suggest that a defensible basis for definition of the "Edmontonian" soon may be possible.

The first mammalian assemblage to be referred to the "Edmontonian" was the Scabby Butte Local Fauna from the St. Mary River Formation, Alberta (Sloan and Russell 1974; Russell 1975); a second occurrence in the same formation is near Lundbreck, Alberta (Russell 1975). Two sites of probable "Edmontonian" age, also in Alberta, are known from the Horseshoe Canyon Formation (Fox and Naylor 1986). A small mammalian assemblage from the St. Mary River Formation in Montana remains under study (Heinrich et al. 1998). Most recently, a diverse mammalian assemblage has been reported from the Williams Fork Formation, northwestern Colorado. Correlation based on cephalopods indicates the fauna to be intermediate in age between the Judithian and Lancian (Lillegraven 1987). Although study of the fauna is still in progress (Archibald 1987a; Diem 1999), the mammals of the Williams Fork Formation show great promise for resolving problems inherent in defining the "Edmontonian" as a land mammal age. At present, the most diagnostic "Edmontonian" mammals are species of the multituberculate Meniscoessus and the stagodontid marsupial Didelphodon (see Fox and Naylor 1986; Lillegraven 1987).

The age of the Lower Hunter Wash fauna (from the upper part of the Fruitland Formation and lower part of the Kirtland Formation), New Mexico, has been disputed (see Butler et al. 1977; Butler and Lindsay 1985; Flynn 1986; Rigby and Wolberg 1987). As noted earlier, the range of ages of Judithian local faunas is estimated at 79-74 Ma, but paleontological criteria for recognition of a boundary between the Judithian and "Edmontonian" have yet to be established. The ages of the Lower Hunter Wash local faunas appear to approximate this undefined boundary. In addition to revisions of biostratigraphic correlations by Rowe et al. (1992), Fassett and Obradovich (1996) and Fassett and Steiner (1997) report ⁴⁰Ar/³⁹Ar determinations that constrain the age of at least some of the localities yielding the Lower Hunter Wash fauna to the interval 74.56-74.11 Ma and show that they were deposited during chron C33n. Contrary to arguments presented by Lillegraven (1987) and Lillegraven and Ostresh (1990), this fauna is herein tentatively considered to be Judithian in age. A second biogeographically highly significant Judithian-"Edmontonian" boundary local fauna comes from three localities in the "El Gallo Formation" in Baja California del Norte (Lillegraven 1972). All the localities are above a tuff dated at 73 Ma, and ammonites from within and above the El Gallo Formation suggest a Campanian age. Finally, a possible Judithian (or ?"Edmontonian") correlative,

dated at 71.6 Ma, is known from the Marshalltown Formation, New Jersey (Grandstaff et al. 1992).

LANCIAN LAND MAMMAL AGE

"The Lancian 'age' is a new (or modified) provincial time term, based upon mammalian fauna from type Lance Formation of east-central Wyoming in Niobrara County, faunal type areas in valleys of Lance Creek and its tributaries north of town of Lance Creek" (Lillegraven and McKenna 1986:51). The first discovered Cretaceous mammals are Lancian in age (Van Valen 1967), and occurrences of Lancian mammals account for nearly a quarter of the entire record of Mesozoic mammals worldwide. As is true for most Cretaceous mammals from North America, Lancian mammals have been collected principally through use of underwater screenwashing and associated techniques (e.g., Lillegraven 1969). Thus, despite the enormous samples now known, most fossils are fragmentary, consisting largely of dentulous jaw fragments and isolated teeth. Identification and interpretation of such material must be approached with caution.

Many Lancian localities yielding individual specimens, faunules, or well-represented local faunas are known (see Webb 1998). Herein (figure 2.2, table 2.1), we treat only principal correlates or those that are of special interest for other reasons (i.e., geographic or stratigraphic distribution, availability of geochronologic data). Mammalian fossils are known from many localities in the type Lance Formation, but the majority of specimens comes from three main sites in upper parts of the unit (Clemens 1963, 1966, 1973). Additional specimens and faunules from the Lance Formation are known from several nearby areas not far to the north of the type area (Clemens et al. 1979; Whitmore 1985; Whitmore and Martin 1986) and in southern Wyoming (Breithaupt 1982), the Bighorn Basin area (Webb 1998, 2001), and south-central Montana (Clemens et al. 1979).

The Hell Creek Formation of Montana and adjacent parts of the Dakotas is distinguished from the Lance Formation mainly on the basis of discontinuity in exposure between the two (Clemens 1963; Clemens et al. 1979). Many Lancian localities in the upper part of the Hell Creek Formation are known from vicinity of the Fort Peck Reservoir, Montana; the Flat Creek Local Fauna (principally from one of five included sites) is the bestsampled assemblage (Archibald 1982). Currently, G. P. Wilson (Museum of Paleontology, University of Califor-



FIGURE 2.2 Principal Lancian localities, local faunas, and areal assemblages. Numbered areas are the same as those used in tables 2.1 and 2.2.

nia Berkeley) is having success in discovering and sampling mammalian local faunas from the middle and lower parts of the formation. Another cluster of sites in the upper Hell Creek Formation occurs to the southeast, in Carter and Fallon counties. Some, such as the Claw Butte and Blacktail local faunas, are well represented, including 25–30 mammalian species (Hunter and Archibald 2002). Only individual specimens or faunules have been reported from other localities (Clemens 1973; Clemens et al. 1979; Archibald 1982). The Muddy Tork Local Fauna, from the upper Hell Creek Formation, Williston Basin, eastern Montana, includes only nine mammalian taxa but is well documented through study of palynomorphs, nonmarine molluscs, and paleomagnetic stratigraphy (Hunter et al. 1997).

Additional occurrences of Lancian mammals from the Hell Creek Formation are known from North Dakota

(Hoganson et al. 1994; Murphy et al. 1995; Hunter and Archibald 2002) and South Dakota (Wilson 1965, 1983). Mammals also are known from at least two localities in the Fox Hills Formation, South Dakota (Waage 1968; Wilson 1983). The Red Owl Local Fauna, Meade County, is in the lower part of the unit and therefore probably is equivalent, stratigraphically, to a part of the Fox Hills Formation in the area of the type Lance Formation, Wyoming (Wilson 1987). The Red Owl Local Fauna therefore is noteworthy because it is almost surely older than typical Lancian assemblages from upper parts of the Lance and Hell Creek formations.

Three principal correlative faunas are known from the prairies of Canada. The Trochu Local Fauna, Red Deer River Valley, Alberta, is in lower parts of the Scollard Formation (see review by Clemens et al. 1979). The fauna includes 22 mammalian varieties, several of which are represented by complete jaws (Lillegraven 1969). The other two faunas are from closely spaced sites on opposite sides of the Frenchman River, Cypress Hills region, Saskatchewan. The Gryde and Wounded Knee local faunas are diverse, well-represented assemblages from slightly different horizons in the upper Frenchman Formation (Fox 1989; Storer 1991). Two other localities in Saskatchewan, Fr-1 and Long Fall, have yielded mammals from the Ravenscrag or Frenchman formation (Johnston and Fox 1984; Fox 1989). The age and correlation of Fr-1 and Long Fall have been contentious; as discussed later in this chapter, they have been interpreted as Cretaceous by some workers and Paleocene by others. We refer both localities to the Puercan land mammal age on the basis of key mammalian fossils.

The most northerly known occurrence of Late Cretaceous mammals is from a site in the Prince Creek Formation, northern Alaska. Although only three mammalian species are yet known, the occurrence is notable for its high paleolatitude, which during the Cretaceous was greater than the present position near 70°N (Clemens 1995). Precise correlation of this northern local fauna with those to the south is bedeviled by faunal and floral provincialism and the lack of a formal definition of a boundary between the "Edmontonian" and Lancian. The site that has yielded mammals is estimated but not clearly demonstrated to lie stratigraphically below the major dinosaurbearing sites near Ocean Point. Interbedded strata of tephra at the major dinosaur bearing sites yielded K-Ar and ⁴⁰Ar/³⁹Ar age determinations of 69.1 ± 0.3 Ma (weighted mean of all analyses, Conrad et al. 1992). This radiometric age determination indicates that the Alaskan mammalian fauna is older than most Lancian faunas in the northern Western Interior. To the southwest of the

TABLE 2.1 Major Areal Assemblages, Local Faunas, and Localities of the Lancian Land Mammal Age

Areas are numbered generally north to south then east to west and agree with the numbers used in figure 2.2 and table 2.2. Prince Creek Formation, Alaska o. Colville River (not shown on map) Reference: Clemens 1995 Scollard Formation, Alberta 1. Trochu local fauna Reference: Lillegraven 1969 Frenchman Formation, Saskatchewan 2. Wounded Knee local fauna 3. Gryde local fauna References: Fox 1989; Storer 1991 Hell Creek Formation, Montana and North Dakota 4. Vicinity of Fort Peck Reservoir, Montana 5. Muddy Tork local fauna, Williston Basin, Montana 6. Powderville, Montana 7. Claw Butte local fauna, Montana 8. Blacktail local fauna, Montana 9. Localities in the Little Missouri badlands, Montana and North Dakota References: Clemens et al. 1979; Archibald 1982; Lofgren 1995; Hunter and Pearson 1996; Hunter et al. 1997; Hunter and Archibald 2002 Fox Hills Formation, South Dakota 10. Iron Lightning 11. Red Owl local fauna References: Waage 1968; Clemens et al. 1979; Wilson 1983, 1987 Hell Creek Formation, South Dakota 12. Joe Painter Quarry 13. Eureka Quarry Reference: Wilson 1983 Lance Formation, Wyoming 14. Localities near Mule Creek Junction 15. Localities in Lance Creek drainage, type Lance Formation 16. Hewitt's Foresight 17. Black Butte Station References: Clemens 1963, 1966, 1973; Breithaupt 1982; Whitmore 1985; Webb 1998, 2001 Ferris Formation, Wyoming 18. Localities in Hanna Basin References: Eberle and Lillegraven 1998a, 1998b; Lillegraven and Eberle 1999 Laramie Formation, Colorado 19. Site in Weld County Reference: Carpenter 1979 North Horn Formation, Utah 20. Localities on North Horn Mountain and in South Dragon Canyon References: Clemens 1961; Cifelli and Muizon 1998; Cifelli et al. 1999a Kirtland Formation, New Mexico 21. Alamo Wash local fauna, San Juan Basin References: Lehman 1981; Flynn 1986

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type Lance Formation, an assemblage of Lancian mammals from the Ferris Formation of the Hanna Basin, Wyoming, is particularly notable because the sequence also includes mammals of early Puercan age in unequivocal superposition (Eberle and Lillegraven 1998a, 1998b; Lillegraven and Eberle 1999). Smaller Lancian faunules are known from the Laramie Formation, Colorado (Carpenter 1979), and North Horn Formation, Utah (Cifelli et al. 1999a). For many years only a few isolated teeth documented the mammalian fauna of the Naashoibito Member of the Kirtland Formation, New Mexico (Flynn 1986). Isolated occurrences of single specimens that may be of Lancian age are known from the Kemp Clay Formation, Texas (Tokaryk 1987), and the Mount Laurel Formation, New Jersey (Krause and Baird 1979).

Despite this broad geographic spread, currently wellrepresented and published Lancian assemblages are confined to north-central parts of the Western Interior, so that biogeographic variation among the mammals remains difficult to assess. Dinosaurian and floral distributions suggest some degree of latitudinal provinciality, as was true for mammals in the older Judithian (Lehman 1987; Clemens 2002) and younger Puercan (Eberle and Lillegraven 1998a) ages. Some geographic variation of mammals is seen among the well-sampled local faunas of central and northern parts of the Western Interior. Eutherians, for example, are generally more abundant and diverse in northerly assemblages, such as Trochu and Wounded Knee (see Hunter and Pearson 1996; Clemens 2002). The Flat Creek Local Fauna of Montana is geographically intermediate between Trochu (to the north) and the type Lance (to the south), and this is reflected in distribution of mammalian species among the three faunas (Archibald 1982).

DEFINITION AND CHARACTERIZATION

Definition of the beginning of the Lancian age through designation of an FAD is problematic. The principal problem is questionable occurrences in older faunas, especially inadequate knowledge and characterization of the preceding "Edmontonian." Local ancestry for most firstappearing Lancian taxa appears probable. However, Weil and Clemens (1998; see also Clemens 2002) identify the eutherian Batodon and the marsupial Glasbius as Lancian "aliens" that lack records in preceding faunas of the northern Western Interior. To this list we add the multituberculate Essonodon, which appears to be closely related to known North American taxa (Weil 1999) but nonetheless is highly distinctive and has no known close morphologic antecedent in preceding faunas. We do not formally propose an FAD for the Lancian, but Batodon, Glasbius, and Essonodon appear to be the best candidates based on evidence in hand. Onset of the succeeding Puercan age is defined by first appearance of the archaic ungulatomorph Protungulatum donnae (see Archibald and Lofgren 1990; Eberle and Lillegraven 1998a, 1998b; Clemens 2002; and chapter 3). We provisionally characterize the Lancian here (also see tables 2.2 and 2.3). Note in what follows that taxa listed as possible appearances or occurrences may appear in more than one category.

- First appearances: Cimexomys minor, Parectypodus, Alphadon jasoni, and Gypsonictops illuminatus; possible other first appearances: Essonodon, Mesodma formosa, M. hensleighi, Neoplagiaulax, Kimbetohia campi, Pediomys elegans, "P." krejcii, Cimolestes cerberoides, and C. stirtoni
- Last appearances: Paracimexomys, P. priscus, Meniscoessus collomensis, M. conquistus, cf. Deltatheridium sp., Alphadon wilsoni, Protalphadon, P. lulli, Turgidodon, T. rhaister, "Pediomys" cooki, "P." hatcheri, "P." krejcii, Stagodontidae, and Didelphodon; possible other last appearances: Cimolomyidae, Cimolomys, C. gracilis, Meniscoessus robustus, Cimolestes cerberoides, C. stirtoni, and Paranyctoides
- Unique occurrences: Bubodens magnus, Cimolomys trochuus, Essonodon browni, Meniscoessus seminoensis, Clemensodon, C. megaloba, ?Neoplagiaulax burgessi, Parectypodus foxi, Alphadon eatoni, Glasbius, G. intricatus, G. twitchelli, Protalphadon foxi, Turgidodon petaminis, "Pediomys" florencae, Didelphodon padanicus, D. vorax, Cimolestes incisus, C. magnus, C. propalaeoryctes, Telacodon, T. laevis, Gypsonictops hypoconus, Batodon, B. tenuis, Alostera, and A. saskatchewanensis; possible other unique occurrences: Essonodon, "Pediomys" hatcheri, "P." krejcii, Cimolestes cerberoides, and C. stirtoni

AGE RELATIONSHIPS BETWEEN LANCIAN LOCAL FAUNAS

With a few exceptions noted earlier, Lancian local faunas are highly similar in composition across northwestern North America. Some of the few known differences may reflect age variation between sites rather than biogeographic provinciality or geographic distance (Hunter and Archibald 2002), but it is not yet possible to propose a defensible zonation to subdivide the Lancian land mammal age. Detailed, multidisciplinary studies of age relationships have been conducted for Lancian and Puercan faunas in the Hell Creek and Tullock formations near Ft. Peck Reservoir, Montana (see Clemens 2002 and references therein). Stratigraphic positions commonly are determined by thickness below the local Hell Creek-Tullock contact, with most Lancian sites being in upper parts of the Hell Creek Formation, 3.5 to 45 m below the contact.

Reference to the presumed K–T iridium anomaly has proven of limited utility in the area because its presence depends on local depositional settings. Iridium anomalies are preserved in lignites near the base of the Z coal complex (which defines the formational contact) at sev \oplus

TAXON	JU	"ED"	LA	P	U	LOCALITIES
				PU1	PU2+	
Multituberculata						
Family incertae sedis						
Bubodens			Х			11
B. magnus			Х			11
?Bryceomys	Х					
Cimexomys	Х	Х	Х	Х	Х	4, 11, 15, 17
C. gregorvi	Х					
C. judithae	х	х				
C. minor			х	x		4, 15, 16, 17
Paracimexomys	х	х	X			1, 2, 3, 4, 20
P priscus	X	0	x			1, 2, 3, 4, 20
P magnus	X	Ũ	A			1, 2, 3, 4
Cimolodontidae	Λ					
Cimolodon	v	v	v	v	v	0 1 0 0 4 7 8 0 11
Cimolouon	А	Λ	Λ	Λ	А	0, 1, 2, 3, 4, /, 8, 9, 11, 13, 14, 15, 18
C. electus	?	Х				
C. nitidus	?	Х	Х	Т		0, 1, 2, 3, 4, 7, 8, 9, 11, ?13, 14, 15, 16, 18
C. similis	?					
Cimolomyidae						
Cimolomvs	Х	х	Х	х		1, 3, 4, 8, 13, 15, 19, 20
C. clarki	х					
C. oracilis		х	х	?Т		1. 3. 4. 8. 13. 15. 16
C. milliensis	х					-, ;, ;, -, -;, -,, -*
C trochuus			x			1
Fssonadan		2	x			2 4 7 15 17 21
E browni		·	X X			4, 7, 15, 17, 21
E. browni Manisconscue	v	v	A V	т		4, /, 15, 21
Meniscoessus	л	л	л	1		2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 17, 18, 19, 21
M. collomensis		X	X			19
M. conquistus		Х	Х			
M. intermedius	Х	Х				
M. major	Х	Х				
M. robustus		Х	Х	?Т		2, ?3, 4, 5, 6, 7, 8, 9, 10, 11, 12, ?13, 14, 15, 16, 17
M. seminoensis			Х			18
Eucosmodontidae						
Clemensodon			Х			15
C. megaloba			Х			15
Stygimys		Х	0	Х	Х	
S. cupressus				Х		
Neoplagiaulacidae						
Mesodma	Х	Х	Х	Х	Х	1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 12, 13, 15, 17, 20, 21
M. formosa	?	?	Х	Х	Х	1, 2, 3, ?4, 7, 8, 11, 12, 13, 15, 16, 17, 18, 21
M. hensleighi	?	0	Х	Х		1, 3, 7, 8, 11, 12, ?13, 15, 16, 17, 18, ?20
M. primaeva	Х					
M. senecta	?	?				
M. thompsoni		Х	Х	Х	Х	1, ?2, ?3, 4, ?5, 6, ?7, 8, 9, ?11, 12, 13, 15, 16, 17

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TABLE 2.2 Temporal Ranges for Judithian Through Puercan Mammals

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TABLE 2.2 (continued)

TAXON	JU	"ED"	LA	F	יט	LOCALITIES
				PU1	PU2+	
Neoplagiaulax			?	0	Х	?4
?N. burgessi			Х			4, 16
Parectypodus			Х	0	Х	3
P. foxi			Х			3
Ptilodontidae						
Kimbetohia	?		Х	0	Х	15
K. campi			Х	0	Х	15
Taeniolabididae						,
Catopsalis				Х	Х	
C. jovneri				Х	Х	
C. johnstoni				Х		
'Eupantotheria"						
Drvolestidae	х					
Boreosphenida <i>incertae sedis</i>	11					
Deltatheridiidae						
cf. Deltatheridium	v	0	v			1 15
En Denumertan cadic	А	0	Λ			1, 15
Falling incertive setus	v					
Fulepeirus	A V					
F. barwini	Λ	V				
Bistius		X				
B. bondi	X	Х				
Palaeomolops	X					
P. langstoni	Х					
Marsupialia						
Alphadontidae						
Aenigmadelphys	Х	Х				
A. archeri	Х					
Alphadon	Х	Х	Х	Т		1, 2, 3, 4, 7, 8, 9, 11, 12, 13, 17, 20, 21
A. attaragos	Х					
A. eatoni			Х			20
A. halleyi	Х	Х				
A. jasoni			Х	Т		1, 2, 3, 4, 15, 16
A. marshi	Х		Х	Т		1, 4, 7, 8, 9, 11, ?12,
						15, 16, 17, 21
A. perexiguus	Х					
A. sahnii	Х					
A. wilsoni	?	Х	Х			1, 4, ?7, 8, 15
Glasbius			Х			1, 4, 7, 15
G. intricatus			Х			15, 16
G. twitchelli			Х			1, 4, 7
Protalphadon	х	0	X			4, 7, 8, 11, 15, 18
P. foxi		č	x			4
P. Julli	x	0	x			T 7. 8. ?11 15 16 18
Turgidodon	x	x	x			1. 3. 4 5 7 8 15
T lillegraveni	X X	Λ	Λ			1, 3, 4, 3, /, 0, 13
T. madsoui	A V					
	Λ	v				
1. parapraesagus		Λ	v			
1. petaminis	37		Х			3
1. praesagus	Х		37			
1. rhaister		X	Х			1, 4, 5, 7, 8, 15, 16
T. russelli	Х	Х				

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TAXON	UL	"ED"	LA	P	Ū	LOCALITIES
				PU1	PU2+	
Varalphadon	Х					
V. wahweapensis	Х					
"Pediomyidae"						
Aquiladelphis	О	Х				
A. incus	О	Х				
A. paraminor		Х				
"Pediomys"	Х	Х	Х	Т		1, 2, 3, 4, 5, 6, 7, 8, 9, ?10, 11, 12, 13, 14, 15, 17, 20
"P."clemensi	Х					
"P."cooki	Х	Х	Х			4, 7, 8, 11, 15, 16
"P."elegans	?	0	Х	Т		1, 2, 3, 4, 7, 8, 12, 13, 15, 16, 17
"P."fassetti		Х				
"P."florencae			Х			4, 5, ?6, 7, 8, 9, 13, 15, 16
"P."hatcheri	?	0	Х			1, ?3, 4, 5, ?6, 7, 8, 11, 12, 13, 14, 15, 20
"P. "krejcii		Ş	Х			1, 3, 4, ?5, 7, 8, ?11, 12, 15
"P." prokrejcii	Х					
Stagodontidae						
Didelphodon		Х	Х			1, 2, 3, 4, 5, 6, 8, 9, 11, ?12, 13, 14, 15
D. covi		Х				
D. padanicus			Х			
D. vorax			Х			1, 2, 3, 4, 5, 6, 8, 9, ?11, ?13, 14, 15, 16
Eodelphis	Х	Х				
E. browni	Х					
E. cutleri	Х					
Eutheria						
Arctocyonidae						
Baioconodon				Х	Х	
Oxyprimus				Х		
O. erikseni				Х		
Protungulatum				Х	Х	
P. donnae				Х	Х	
Cimolestidae						
Cimolestes	?	Х	Х	Х	Х	1, 2, 3, 4, 8, 9, ?14, 15, 18
C. cerberoides			Х	?Т		1, ?4
C. incisus			Х			?2, 3, 4, 8, 15, 16
C. magnus			Х			1, 3, 4, 9, 15, 16
C. propalaeoryctes			Х			1, ?2, 4, 8, 16
C. stirtoni			Х	?T		2, 4, 8, 15
Procerberus				Х	Х	
P. formicarum				Х		
Telacodon			Х			15
T. laevis			Х			15
Gypsonictopidae						
Gypsonictops	Х	Х	Х	Т		0, 1, 2, 3, 4, 6, 7, 8, 9, 11, 12, 13, 15, 17, 18, 19
G. clemensi		Х				
G. hypoconus			Х			1, 4, 7, 11, 12, 13, 15, 16, 17
G. illuminatus			Х	Т		1, ?2, 3, 4, ?6, 9, 16
G. lewisi	Х	?				

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32 Richard L. Cifelli, Jaelyn J. Eberle, Donald L. Lofgren, Jason A. Lillegraven, and William A. Clemens

TABLE 2.2 (continued)

TAXON	JU	"ED"	LA	Р	U	LOCALITIES	
				PU1	PU2+		
Periptychidae							
Mimatuta				Х	Х		
Soricomorpha, family incertae sedis							
Batodon			Х			1, 3, 4, 7, 8, 15	
B. tenuis			Х			1, 3, 4, 7, 8, 15	
Paranyctoides	Х	Х	?			?8	
P. maleficus	Х						
P. megakeros	Х						
P. sternbergi	Х	?					
Ungulatomorpha, family incertae sedis							
Alostera			Х			1, 2, 3, 4	
A. saskatchewanensis			Х			1, 2, 3, 4	
Avitotherium	Х						
A. utahensis	Х						
Gallolestes	Х	Х					
G. agujaensis	Х						
G. pachymandibularis		Х					

Puercan taxa include only those also known from older faunas or those appearing in the earliest Puercan. See table 2.1 for references and suites of localities. "Ed," "Edmontonian"; Ju, Judithian; La, Lancian; Pu (and first two subdivisions), Puercan.

X, presence; O, absence; ?, questionable occurrence; T, otherwise Lancian taxon with Puercan occurrence only in one of the transitional faunas of Saskatchewan (Long Fall, Fr1).

eral sites near Hell Creek; a weighted mean age determination for the horizon is 65.14 ± 0.04 Ma (Swisher et al. 1993). However, the base of the Z coal complex is not synchronous from place to place; it is about 200 k.y. younger to the east, in vicinity of McGuire Creek, where it overlies Puercan faunas recovered from the uppermost Hell Creek Formation. In absence of the iridium anomaly (which often has been assumed to be synchronous on a hemispheric basis), palynological criteria have been used to recognize the local Cretaceous-Tertiary boundary (Lofgren 1995). As far as is known, Lancian assemblages in vicinity of the Ft. Peck Reservoir lie within the youngest Late Cretaceous palynological zone of the Western Interior, the Wodehousia spinata Assemblage Zone, and in sediments deposited during magnetic polarity chron 29r. A chemostratigraphic method of correlation, based on carbon isotope excursions before and associated with the K-T boundary, gives great promise of providing precise correlations of terrestrial sections in the Western Interior (Arens and Jahren 2000). In the Dakotas, Montana, and adjacent areas the Hell Creek Formation probably spans about 1.75 m.y. (Hicks et al. 1999a), but the time represented by the better sampled Lancian faunas in the area is far less, insofar as these known localities are concentrated in upper parts of the unit.

Some Lancian faunas from the Hell Creek Formation further to the east (in easternmost Montana and southwestern North Dakota) appear to be somewhat older, representing younger parts of magnetic polarity chron 30n (Hunter et al. 1997; Hicks et al. 1999a). Where correlation to the GPTS is known or can be reasonably inferred, Lancian faunas from most other units also appear to lie within strata representing chron 29r or the younger parts of chron 30n (table 2.4). All known Lancian faunas are older than the generally accepted Cretaceous-Tertiary boundary, placed at 65.5 Ma by Obradovich and Hicks (1999). Given the age of chron 30n (65.58-67.61 Ma; Berggren et al. 1995), a maximum duration for the Lancian, based on these limited data from the Hell Creek Formation, would be about 2 m.y. To our knowledge, the only radioisotopic date that in part constrains the age of the Lancian is a determination of 66.8 \pm 1.1 Ma from the Kneehills Tuff, considered to represent the base of the Triceratops zone in the lower part of the Scollard Formation (Obradovich 1993). Again it must be stressed that establishment of a boundary between the Lancian and the older "Edmontonian" remains a challenge for future research.

The two Lancian mammal localities in the Fox Hills Formation of South Dakota—Red Owl Quarry (Wilson 1983, 1987) and the Iron Lightning locality (Waage 1968)

Multituberculata family <i>incertae sedis</i>	A.marshi	
Bubodens	A. wilsoni (*L)	
B.magnus (U)	Glasbius	
Cimexomys	G. intricatus (U)	
<i>C. minor</i> (*F)	<i>G. twitchelli</i> (*U)	
Paracimexomys (*L)	Protalphadon (*L)	
P. priscus (*L)	P. foxi (U)	
Cimolodontidae	P. lulli (*L)	
Cimolodon	Turgidodon (*L)	
C.nitidus	T. petaminis (U)	
Cimolomyidae	T. rhaister (*L)	
Cimolomys	"Pediomyidae"	
C. gracilis (*?L)	"Pediomys"	
C.trochuus (U)	"P." cooki (*L)	
Essonodon (?U)	<i>P. elegans</i> (*?F)	
E. browni (*U)	"P." florencae (*U)	
Meniscoessus	"P." hatcheri (?U)	
<i>M. collomensis</i> (L)	"P." krejcii (?U)	
<i>M. conquistus</i> (L)	Stagodontidae (*L)	
M. robustus (*?L)	Didelphodon (*L)	
M. seminoensis (U)	D. padanicus (U)	
Eucosmodontidae	D. vorax (*U)	
Clemensodon	Eutheria	
C. megaloba (U)	Cimolestidae	
Neoplagiaulacidae	Cimolestes	
Mesodma	C. cerberoides (?U)	
<i>M. formosa</i> (*?F)	C. incisus (*U)	
M. hensleighi (*?F)	C. magnus (*U)	
M.thompsoni	C. propalaeoryctes (*U)	
Neoplagiaulax (?F)	C. stirtoni (?U)	
?N. burgessi (U)	Telacodon	
Parectypodus (F)	T. laevis (U)	
P. foxi (U)	Gypsonictopidae	
Ptilodontidae	Gypsonictops	
Kimbetohia	G. hypoconus (*U)	
K. campi (?F)	G. illuminatus (*F)	
Boreosphenida, <i>incertae sedis</i>	Soricomorpha, family incertae sedis	
Deltatheridiidae	Batodon	
cf. Deltatheridium sp. (L)	B. tenuis (*U)	
Marsupialia	cf. Paranyctoides (?L)	
Alphadontidae	Ungulatomorpha, family incertae sedis	
Alphadon	Alostera	
A. eatoni (U)	A. saskatchewanensis (*U)	
A. jasoni (*F)		

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TABLE 2.3 Taxonomic List of Lancian Mammals and Their Biochronologic Significance

Taxa not surely identified are excluded unless their occurrences are significant. First (F), last (L), and unique (U) occurrences in the Lancian are designated for supraspecific taxa only when their occurrences differ from those of included species. F, L, and U occurrences are queried if the respective taxon is tentatively recorded from another land mammal age; asterisked taxa are known from more than one Lancian assemblage and therefore are more useful biostratigraphically.

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34 Richard L. Cifelli, Jaelyn J. Eberle, Donald L. Lofgren, Jason A. Lillegraven, and William A. Clemens

LITHOLOGIC UNIT AND LOCATION	TEMPORAL CORRELATION AND REFERENCES
Scollard Formation, Alberta	According to Lerbekmo et al. (1979) and Lerbekmo (1985), Cretaceous strata of Scollard Formation in Red Deer Valley, Alberta, are in younger half of chron 30n and 29r.
Hell Creek Formation, vicinity of Fort Peck Reservoir, Montana	Chron 29r; see Clemens (2002) and references therein.
Hell Creek Formation, Muddy Tork local fauna, Montana	Younger part of chron 30n (Hunter et al. 1997).
Hell Creek Formation, SW North Dakota (loc. PTRM-V92067 of Hunter and Pearson 1996)	Youngest chron 30n (K. R. Johnson, pers. comm., 2000; Hicks et al. 1999a).
Lance Formation, Wyoming	According to Keating and Helsey (1983), strata of the Lance Formation in east-central Wyoming are of reversed polarity, but no mention is made of correlation to the Geomagnetic Polarity Time Scale or to chron 29r.
Upper part of Laramie Formation, Weld County, Colorado	No study was done in Weld County, but paleomagnetic data from else- where in the Denver Basin (Castle Pines core and Jimmy Camp Creek Section) suggest normal polarity rocks, probably representing C30n or possibly C31n (K. R. Johnson, pers. comm. 2000).
Fox Hills Formation, South Dakota	Indirect correlation to section at Red Bird, Wyoming (this chapter), suggests placement of Red Owl and Iron Lightning faunas in chron 31N (see Wilson 1987; Hicks et al. 1999b).
Alamo Wash local fauna, Naashoibito Member of Kirtland Formation, San Juan Basin, New Mexico	Chron 29r (see Butler and Lindsay 1985; Flynn 1986).

Locality suites listed in table 2.1 but not appearing here lack available paleomagnetic information.

warrant further discussion. Indirect evidence suggests that both sites may be older than other Lancian local faunas in the Western Interior and consequently may be useful for constraining the earlier age limit of the Lancian NALMA. The Iron Lightning locality is in the type section for the Iron Lightning Member (Waage 1968), and Red Owl Quarry is in the Fairpoint Member (Wilson 1987), which "is equivalent to at least part of the Colgate and Bullhead Members and perhaps to the Trail City and Timber Lake Members farther east" (Pettyjohn 1967:1367). Red Owl Quarry is lower in the local section than the Iron Lightning locality (Wilson 1983). Wilson (1987) surmised that strata containing Red Owl Quarry probably are equivalent to some part of the Fox Hills Formation in the Lance Creek area and that the mammalian fauna from Red Owl therefore is older than that of the type Lance Formation.

Correlation of the ammonite zonation preserved in members of the Fox Hills Formation to the GPTS (Gradstein et al. 1995) appears to support Wilson's (1987) interpretation. The *Jeletzkytes nebrascensis* Range Zone, the youngest ammonite zone in the Western Interior, begins with the first appearance of *J. nebrascensis* in the uppermost Trail City Member and extends through the Iron Lightning Member of the upper Fox Hills Formation (Cobban and Reeside 1952; Landman and Waage 1993). Landman and Waage report that the *J. nebrascensis* Range Zone locally extends into the basal Hell Creek Formation. According to Gradstein et al. (1995, figure 8), the *J. ne-brascensis* Range Zone occurs within C31. At Red Bird, approximately 40 km northeast of Lance Creek, Hicks et al. (1999b) place the C31r–C31n boundary in the upper part of the Fox Hills Formation, within the *Hoploscaphites birkelundi* Range Zone (see Landman and Waage 1993, called the *H.* aff. *nicoletti* Range Zone by Gradstein et al. 1995), and estimate the age of the boundary to be 69.01 \pm 0.5 Ma. The *J. nebrascensis* Range Zone overlies the *H. birkelundi* Range Zone and thus presumably lies within C31n.

As discussed earlier, other Lancian localities for which correlation to the GPTS has been proposed are placed in the younger part of C30n or in C29r, thus suggesting that the mammalian assemblages of the Iron Lightning Formation are somewhat older. Given an estimated 1.02-m.y. duration for C31n (Berggren et al. 1995) and an estimated age of 69.01 Ma for the C31r–C31n boundary (Hicks et al. 1999b), the mammals of the Fox Hills Formation would fall within the range 69.01–67.99 Ma. Thus if the ammonite-based correlation of the Fox Hills strata were to be confirmed (a possibility reflected in figure 2.1), the 2-m.y. duration of the Lancian would be nearly doubled. The mammalian fauna of the Iron Lightning locality is poorly known, including four varieties, only one of which (the common Lancian multituberculate *Meniscoessus robustus*) is identified at the species level (Clemens et al. 1979). Fourteen kinds of mammals have been reported from Red Owl Quarry (Wilson 1983, 1987). None of these suggests a temporal difference from other Lancian faunas. One species, the large multituberculate *Bubodens magnus*, is endemic to Red Owl Quarry, however. Specimens referred to another multituberculate, *Meniscoessus robustus*, have somewhat smaller average dimensions than those from other Lancian localities (Eberle and Lillegraven 1998b). Wilson (1983) also noted the absence at Red Owl of the marsupial *Pediomys elegans* as unusual.

PROBLEMATIC LANCIAN-PUERCAN FAUNAS

Several mammalian faunas or assemblages include a mixture of species that are typical of the Lancian on one hand and Puercan on the other. Most celebrated are the Bug Creek assemblages, from several localities in northeastern Montana. When first described, they were interpreted as a temporally ordered series (from oldest to youngest: Bug Creek Anthills, Bug Creek West, Harbicht Hill), apparently documenting appearance of mammalian taxa typical of the Paleocene during latest Cretaceous time (Sloan and Van Valen 1965). Subsequently, the issue of ecological versus temporal differences between Cretaceous and Tertiary faunas (see Matthew 1937) was reopened, and the Bug Creek assemblages were then suggested to represent a faunal facies that was contemporaneous with "typical" Lancian faunas (see also Clemens et al. 1979; Archibald 1982). Still later, the Bug Creek assemblages were assigned to their own, slightly younger land mammal age, the "Bugcreekian" (Archibald 1987b; Sloan 1987). Subsequently, the "Bugcreekian" mammal age was abandoned, with the Bug Creek assemblages being placed within the Puercan NALMA, and Protungulatum donnae was recognized as the FAD for advent of the Puercan's initial interval zone (Archibald and Lofgren 1990). The original Bug Creek "faunas" and their correlatives (see Sloan et al. 1986, Rigby 1989, and Lofgren 1995 for correlatives) are now interpreted to represent time-averaged assemblages that include both Lancian and Puercan elements mixed together through reworking caused by the incision of large Paleocene channels into fossiliferous Cretaceous strata (Lofgren 1995). The result of this reworking is that older Lancian fossils are present as sedimentary particles in younger

channel fills, deposited during the Puercan, that also yield *Protungulatum* (see Lofgren 1995). Thus Lancian taxa in the original Bug Creek assemblages, and their correlatives probably are represented by reworked fossils. As a practical issue, these fossils must be ignored for purposes of biochronology because it cannot be determined to what extent reworking might have extended their apparent geologic range.

The other two problematic faunas, both from the Cypress Hills of southwestern Saskatchewan, also include a mixture of Lancian species with those that are more typical of the Puercan. The sites in question, Long Fall (Medicine Hat Brick and Tile Quarry) and Fr-1, have been interpreted as late Lancian in age (Johnston 1980; Johnston and Fox 1984; Fox 1989, 1997) and therefore were considered to have been faunally transitional between the Lancian and Puercan NALMAs. Long Fall lies about 3 m stratigraphically below another site, Rav W-1 (Lerbekmo 1985), the latter of which yielded an assemblage of Puercan mammals.

Sloan (1987) interprets Long Fall as earliest Paleocene in age. Similarly, Lerbekmo (1985) considers both Long Fall and Rav W-1 to be in the same point bar deposit in the Frenchman Formation and suggests that the Lancian fossils were reworked during Puercan time (see also Lofgren 1995). Lerbekmo's (1985) interpretation was vigorously challenged by Fox (1989, 1997), however, who argued that the sites are separated by a disconformity and that both lie in the Ravenscrag Formation. The regional, traditionally used marker bed for recognizing the Cretaceous-Tertiary boundary, the Ferris (= No. 1) Coal Seam (Lerbekmo and Coulter 1985), unfortunately is not found in the section that included Long Fall and Rav w-1, and attempts to recover palynomorphs were unsuccessful (Fox 1997). Magnetostratigraphic studies by Lerbekmo (1985) place the Long Fall site within chron 29r, which spans both the Lancian–Puercan and globally recognized Cretaceous-Tertiary boundaries. Unfortunately, the two localities have since been destroyed through mining operations (Fox 1997), so questions regarding the age of Long Fall remain unanswered.

The Fr-1 site lies unequivocally in the Frenchman Formation. The Ferris Coal Seam is absent from vicinity of this site as well, and no sampling for iridium concentrations has been done. However, palynomorphs that are typical of strata in the Western Interior considered to be of Maastrichtian age have been recovered from Fr-1 (Fox 1997). In addition, articulated dinosaur remains have been reported from what appears to represent the same horizon several hundred meters east of Fr-1 (Fox 1989). Also, the relative abundance of mammals typical of the Lancian at Fr-1 is high (Fox 1989), much higher than in the mixed assemblages from the Bug Creek area of Montana. These relationships make it difficult to dismiss the mixture of Lancian and Puercan mammals at Fr-1 as having resulted from reworking (see criteria and discussion by Lofgren 1995).

We assign both the Long Fall and Fr-1 localities to the Puercan land mammal age on the basis of presence of Protungulatum cf. P. donnae (see discussion by Eberle and Lillegraven 1998a); at least two other taxa characteristic of the Puercan are known from Fr-1, and many more, including a moderate diversity of archaic ungulates, are known from the Long Fall site (Fox 1989). But both sites also include several varieties of vertebrates that are otherwise known only from the Lancian (see table 2.2). Taken at face value, available data suggest the working hypotheses that (1) one or both of these transitional assemblages are of Cretaceous age and are therefore older than Puercan fossils from elsewhere (notably the Tullock Formation and the uppermost strata of the Hell Creek Formation in some areas of Montana); (2) the beginning of Puercan time is diachronous between the prairie provinces and northern Montana, at the level of resolution currently available; and (3) Protungulatum and a few other mammalian genera thought to be exclusively Paleocene in age apparently occur in the Late Cretaceous of southwestern Saskatchewan.

PROSPECTS FOR FUTURE RESEARCH ON THE LANCIAN AGE

Definition of the onset of Lancian time continues to be problematic because of inadequate knowledge and characterization of the preceding, informally recognized "Edmontonian." This is particularly unfortunate because it has direct bearing on the duration of the Lancian and therefore of the magnitude of faunal change through that age. Such information would provide an important baseline for comparison to apparently much greater evolutionary rates for mammals during the Puercan. Field research focused on lower parts of the Lance, Ferris, Hell Creek, and contemporaneous formations and older units is a priority.

Problems of correlation of the Lancian–Puercan boundary (see chapter 3) with the Cretaceous–Tertiary boundary have resulted from a wealth of data and application of different correlation techniques. In the northern Western Interior, Brown's (1952) widely applied "formula" placed the Cretaceous–Tertiary boundary at the base of the first regionally continuous lignite found stratigraphically above the last record of dinosaurs. Subsequently, biostratigraphic criteria for recognition of the Cretaceous–Tertiary boundary (e.g., marked changes in palynofloras) have been used. On a global basis, mineralogic and chemostratigraphic evidence of the impact of an extraterrestrial body, as well as radiometric age determinations, have been used in attempts to correlate the Cretaceous–Tertiary boundary (as defined at the stratotype in Tunisia) with particular levels in sections in the Western Interior. Changes in carbon isotope ratios are providing another tool for long-range correlations (Arens and Jahren 2000).

Given the increased precision of correlation methods, it is not surprising that formation boundaries long held to mark the Cretaceous–Tertiary boundary (e.g., the Hell Creek–Tullock boundary) can now be shown to be time transgressive (Lofgren 1995). An example of Puercan local faunas of possible Late Cretaceous age was discussed in a preceding section of this chapter. As Lillegraven and Eberle (1999) emphasize, although the Lancian–Puercan boundary appears to approximate the Cretaceous– Tertiary boundary, greater care must be exercised in defining units and their boundaries and applying different methods of correlation with the stratotype of the Cretaceous–Tertiary boundary.

One of the most serious shortcomings of the Lancian as a provincial time term has been restriction of its definition to faunas in north-central parts of the Western Interior. Only a few minor faunules were known outside this region and, as a result, little was known of biogeographic variation. Given the clearly recognized latitudinal and biogeographic differences that characterize Judithian and Puercan faunas (Weil 1999; Clemens 2002), the hypothesis that such provinciality also characterized Lancian mammals–as apparently was the case with dinosaurs (Lehman 1987)–was open to testing.

Recent discoveries by Weil and Williamson (2000) provide the first extensive sample of a mammalian fauna in the uppermost Kirtland Formation (Naashoibito Member) of the San Juan Basin, New Mexico. In their initial report on this collection they document the common occurrence of the multituberculate *Essonodon*, whose first occurrence has been suggested as a FAD for the Lancian; and as yet unidentified therian mammals. The composition of the mammalian fauna is reported to be distinctly different from that of Lancian faunas in the northern Western Interior. Additional collecting in the San Juan Basin, along with a geographically expanded program of sampling of Lancian and older Late Cretaceous formations, will provide additional insights into biogeographic deployment of highly distinctive taxa such as *Essonodon* and *Glasbius*. These genera appear in the fossil record without obvious antecedents, and it will be important to determine the extent to which appearance of such taxa in different parts of the continent was synchronous.

Renewed field investigations in known fossiliferous Lancian units in southerly realms such as Colorado, Utah, New Mexico, and Texas offer promise for more complete documentation of Lancian biogeography in western North America. Extending still farther south, Mexico's highly diverse Late Cretaceous dinosaurian faunas show marked similarities to correlatives to the north (Ferrusquia-Villafranca 1998). To what extent do Lancian mammalian assemblages show faunal continuity between Canada and Mexico?

Compositions of North American Late Cretaceous faunas are providing pivotal data for analyses of macroevolutionary patterns of terrestrial vertebrates before and across the Cretaceous-Tertiary boundary. Debate swirls around conflicts between analyses of the available fossil record (suggesting that most of the major ordinal clades of mammals did not differentiate until after the Cretaceous-Tertiary boundary; Foote et al. 1999) and comparative molecular studies (suggesting much more ancient times of divergence; Kumar and Hedges 1998). Recent studies of the patterns of mammalian extinction at the Cretaceous-Tertiary boundary and restoration of their taxonomic diversity during the early Paleocene (Alroy 1999; Lillegraven and Eberle 1999; Clemens 2002) are based primarily, if not exclusively, on the fossil record available from the northern Western Interior.

How adequately does the Lancian and Puercan fossil record from the Western Interior represent the global pattern of evolution of mammalian faunas across the Cretaceous—Tertiary boundary? On a worldwide basis, a survey of known latest Cretaceous (Maastrichtian) mammalian faunas highlights significant additions since they were surveyed by Clemens et al. (1979). Various localities have been added to the record from the Western Interior, and new discoveries provide glimpses of contemporaneous faunas in eastern North America. Discoveries in Europe (e.g., Gheerbrant and Astibia 1999) are beginning to document Maastrichtian local faunas of distinctly different compositions. Increased exploration of Late Cretaceous and Paleocene faunas of South America (see Bonaparte 1996; Rougier et al. 2000) reveals endemism.

Unfortunately, we continue to lack detailed records of mammalian evolution across the Cretaceous–Tertiary boundary from continents other than North America. Knowledge of mammalian evolution during this interval is limited almost exclusively to a major window encompassing only the North American Western Interior and much more limited data from South America and Europe. All of these records indicate that immigration from unsampled areas played major roles in establishing earliest Paleocene faunas on other continents. Despite contrary suggestions (e.g., Fara and Benton 2000), the incompleteness and geographic bias of the available fossil record must be considered in studies of patterns of mammalian evolution.

Studies of the mammalian fossil record in the Western Interior highlight the rapid rate of increase in taxonomic diversity and appearance of major groups of multituberculates and eutherian mammals in the Puercan. The heightened diversity becomes particularly clear during Pu2 and Pu3 times (see chapter 3 and Alroy 1999). Does this rapid increase in taxonomic diversity represent a high rate of evolutionary radiation of locally surviving lineages of multituberculates and eutherians after they were freed from dinosaurian tyranny? Or are we seeing effects of the immigration of new taxa from outside the Western Interior?

As noted earlier, the vertebrate fossil record of the northern Western Interior for approximately the last 2 million years of the Cretaceous suggests that its mammalian fauna remained stable in composition, even though the flora of the area changed markedly (Johnson and Hickey 1990). Most Lancian mammals were closely related to those known from Judithian strata; only a few genera appear to qualify as FADs for the Lancian land mammal age.

Analyses of phylogenetic relationships both of multituberculates and eutherians in earliest Puercan (Pui, see chapter 3) local faunas show that most species are not closely related to known Lancian mammals (Weil and Clemens 1998; Clemens 2002). Unexpectedly, among Puercan representatives are various early ungulates that appear to be most closely related to Cretaceous forms known from Campanian local faunas in Texas and Baja California as well as members of older assemblages in Asia. Among the FADs for Pu1, the multituberculate Stygimys kuszmauli is not closely related to any known species in Lancian or Judithian local faunas of the northern Western Interior. However, that genus (if not the same species) is represented in the Campanian local fauna known from Baja California. Pre-Lancian records of primitive ungulatomorphs (such as Gallolestes) and the lipotyphlan soricomorph Paranyctoides suggest that the evolutionary radiation of eutherians had roots well within the Late Cretaceous and therefore was not solely the product of post-Cretaceous diversification.

In summary, both direct and indirect evidence (including analyses of phylogenetic relationships of immigrant taxa) points to extensive biogeographic diversification throughout Late Cretaceous mammalian faunas of the world. Although the specific groups of mammals differ, patterns of mammalian evolution across the Cretaceous-Tertiary boundary in other parts of the world show some basic similarities to those documented in the Western Interior. In the few areas currently sampled, Cretaceous extinctions appear to have terminated many lineages. Recovery of taxonomic diversity in the earliest Paleocene appears to have been the combined product of evolutionary radiations of locally surviving stocks and immigration of new groups. Although we may be approaching comprehensive knowledge of Lancian mammalian diversification in northern parts of the Western Interior, much remains to be discovered there and in other areas outside this small window of current knowledge.

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3

Paleocene Biochronology: The Puercan Through Clarkforkian Land Mammal Ages

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ALEOCENE CONTINENTAL STRATA of the Western Interior of North America preserve the world's most complete and most thoroughly studied record of early Cenozoic mammalian evolution. We examine this record. Our examination updates and amplifies earlier ones, specifically Wood et al. (1941) and Archibald et al. (1987) on the first four North American land mammal ages (NALMAs) of the Cenozoic era: the Puercan, Torrejonian, Tiffanian, and Clarkforkian. For brevity, we refer to these as NALMAs or individually as mammal ages. Wood et al. (1941) recognized a fifth mammal age, the Dragonian, between the Puercan and Torrejonian mammal ages. Van Valen (1978) later proposed another, the Mantuan, preceding the Puercan mammal age. Also, Sloan (1987) and Archibald (1987a, 1987b) both tentatively proposed a Bugcreekian mammal age preceding the Puercan (and Mantuan). Archibald et al. (1987) considered the Dragonian mammal age to be part of the Torrejonian and the Mantuan mammal age to be part of the Puercan, and we follow that usage. Also, we follow Archibald and Lofgren (1990) and consider the Bugcreekian to be part of the Puercan.

Wood et al. (1941) correlated the advent of the Paleocene Epoch with the beginning of the Puercan mammal age and the end of the Paleocene Epoch with the end of the Clarkforkian mammal age. Archibald et al. (1987) also correlated the beginning of the Puercan with that of the Paleocene but placed the Clarkforkian mammal age as straddling the Paleocene–Eocene boundary based on correlations by Gingerich (1976) and Rose (1980, 1981a). More recent developments in geochronology based on presumed unique geochemical phenomena indicate that the Puercan may have begun in the latest Cretaceous, and the beginning of the Wasatchian mammal age (which followed the Clarkforkian) correlates closely to the advent of the Eocene. These geochemical phenomena are an elevated concentration of iridium at the Cretaceous– Paleocene boundary (see Clemens 2002 and references therein) and carbon isotope excursions at both the Cretaceous–Tertiary boundary (Arens and Jahren 1999; Arens et al. 2000) and the Paleocene–Eocene boundary (see Gingerich 2000, 2001, 2003 and references therein).

In this chapter, we are concerned with two types of geochronologic units: the mammal age and the mammal zone or biochron (treated as a subdivision of a mammal age). Mammal ages and mammal zones or biochrons are types of biochronologic units, units that are not used by the North American Stratigraphic Code (NACSN 1983) and are only briefly considered in the International Stratigraphic Guide (ISG; Hedberg 1976). Mammal ages and mammal zones are biochronologic units characterized by faunal content and thus are not chronostratigraphic units because they are not tied to a body of rock established to serve as the material reference for all strata deposited during the same span of time. For this reason, Savage (1962) advocated that the word ages in North American land mammal ages be placed in quotes to reflect the fundamental difference between North American land mammal "ages" and ages as later defined by the NACSN (1983). We agree with this reasoning but omit the quotes as unnecessarily repetitive in this chapter.

The Puercan, Torrejonian, Tiffanian, and Clarkforkian NALMAs differ from one another in their historical development, but their defining and characterizing criteria are procedurally similar. However, three different kinds of zones are used to subdivide them. The first kind is illustrated by subdivisions of the Puercan and Torrejonian mammal ages and the oldest zone of the Clarkforkian mammal age. Both the Puercan and Torrejonian are subdivided into three zones, all of which are defined and limited by successive first appearances of unrelated taxa (first appearance datum [FAD]). The oldest zone of the Clarkforkian, for example, is defined by the first appearance of Rodentia. Zones such as these are recognized by the NACSN and ISG as one type of interval zone.

The second kind of zone is recognized for all six of the Tiffanian zones and for the second oldest Clarkforkian zone. These seven zones conform to the concept of a range zone according to the ISG and to a type of interval zone according to the NACSN. Both codes are in agreement on lineage zones because the successive earliest appearances defining the zones form a presumed phylogenetic lineage. The final type of zone is represented by the youngest of the three zones in the Clarkforkian mammal age and is called an abundance zone by the NACSN and an acme zone by the ISG.

We follow Archibald et al. (1987) in their use of ISG terminology and refer to the three types of zones as interval zones, lineage zones, and acme zones. We also follow Archibald et al. (1987) in naming and subsequent usage of zonal names by including the name of the commencing taxon and the closing taxon for both the interval and lineage zones. The oldest zone in the Puercan mammal age, for example, is the Protungulatum/Ectoconus Interval Zone, and the oldest in the Tiffanian mammal age is the Plesiadapis praecursor/Plesiadapis anceps Lineage Zone. Also, each zone can be referred to by an abbreviation of the mammal age in which it occurs plus a number indicating its temporal sequence within the given mammal age. For example, the two zones just mentioned are known informally as the Pu1 interval zone and the Ti1 lineage zone, or simply Pu1 and Ti1, respectively.

For each of the four mammal ages and fifteen zones discussed in this chapter, we provide a standardized definition and characterization. A formal definition is not given for the fifteenth zone, the *Phenacodus–Ectocion* Acme Zone. The definitions for all four mammal ages and for the remaining fourteen zones are based on the first appearance of a single taxon. Characterization for each age and zone consists of five parts: "first appearances" for taxa that appear for the first time within a mammal age or zone (but not necessarily in the oldest faunas of that mammal age or zone), "last appearances" for taxa that appear for the last time within a mammal age or zone (but not necessarily in the youngest faunas of that mammal age or zone), "index fossils" for taxa limited to a mammal age or zone, "characteristic fossils" for all taxa (not just common taxa) that occur within a mammal age or zone (but do not belong to one of the three preceding categories), and taxa that are recognized before and after a given mammal age or zone but not within it.

We follow the recently published classification of mammals by McKenna and Bell (1997). Also, we limit our review to Paleocene mammalian biochronology of North America, associated magnetostratigraphic and radioisotopic data, and intercontinental correlations. Thus for discussion of community structure of Mammalia during the Paleocene, rates of origination and turnover, diversity histories, and effects of climate change on mammalian evolution in North America, we recommend use of Alroy (1999, 2000), Alroy et al. (2000), Wilf (2000), Maas and Krause (1994), Maas et al. (1995), and Wing et al. (1995) as starting points.

We present two figures and two tables to augment the text. In general, they are updates of the two figures and two tables provided by Archibald et al. (1987). Figure 3.1



FIGURE 3.1 Map showing approximate locations of Puercan through Clarkforkian mammal-bearing regions in western North America. Each number refers to a region in which known mammal localities are present (not shown are Louisiana and South Carolina) and relates to a stratigraphic column presented in figure 3.2.

is a map of western North America showing the approximate location of areas from which Puercan through Clarkforkian mammalian faunas have been recovered (equivalent to figure 3.1 of Archibald et al. 1987). Figure 3.2 is a biochronologic correlation of Puercan through Clarkforkian localities clustered according to geographic and geologic features (equivalent to figure 3.2 of Archibald et al. 1987). Table 3.1 is a list of localities and references for each locality (equivalent to table 3.1 of Archibald et al. 1987). Table 3.2 is a list of taxa and their temporal ranges (similar to table 3.2 of Archibald et al. 1987 but lacking the locality component).

We would be remiss if we did not formally acknowledge that the organizational content of this chapter closely follows that of Archibald et al. (1987). We owe them a tremendous debt for compiling and producing the first update of Paleocene NALMAs since Wood et al. (1941). We were able to build on their framework. As we present our version of the current state of knowledge concerning the Puercan through Clarkforkian NALMAs, we hope our work is also a worthy framework for a future update. All interpretations, as well as errors or inaccuracies in the text or figures, are our own and not attributable to Archibald et al. (1987).

PUERCAN MAMMAL AGE

The concepts of the Puercan and Torrejonian NALMAs grew out of work done in the San Juan Basin, New Mexico, in the late nineteenth century with fossils supplied to E. D. Cope from the "Puerco Marls" (Cope 1875) by professional collector David Baldwin (Cope 1884, 1888). Cope's "Puerco Marls" were subsequently subdivided into two formations, the Puerco and overlying Torrejon (Matthew 1897). When naming the Puercan mammal age, Wood et al. (1941) based it on the Puerco Formation and named the type locality the Rio Puerco area (near Cuba, New Mexico). They also noted that the "most typical and only fossiliferous exposures" of the Puercan are "the escarpment running from northwest of Ojo Alamo about 25 miles to Arroyo Eduardo, east of Kimbetoh" (1941:8). Similarly, Wood et al. (1941:9) based the Torrejonian mammal age on the Torrejon Formation, described the type locality as situated at "the heads of Arroyo Torrejon," and stated that the "typical area runs from there northwest to Ojo Alamo, with additional, poorer localities scattered to the north." After much discussion concerning the difficulty of differentiating the Puerco and Torrejon formations based on lithologic criteria, it was discovered that the type locality of the Puercan mammal age in the Rio Puerco area, as recognized by Wood et al. (1941), yielded fossils that were Torrejonian in age (Simpson 1959).

Simpson (1959) further noted that the "Puerco" and "Torrejon" formations could not be differentiated based on lithologic criteria and suggested that the Nacimiento Formation of Gardner (1910) be used in a restricted sense to replace them. This usage was adopted by subsequent workers, although the Nacimiento Formation was later subdivided into three members, the Arroyo Chijuillita, Ojo Encino, and Escavada (Williamson and Lucas 1992). Thus since 1959 only the exposures on the escarpment running from northwest of Ojo Alamo about 25 miles to Arroyo Eduardo, east of Kimbetoh have been recognized as yielding the type Puercan fauna (Simpson 1959; Archibald et al. 1987; Williamson 1996). These Puercan sites are all restricted to the Arroyo Chijuillita Member of the Nacimiento Formation (Williamson and Lucas 1992; Williamson 1996). For purposes of discussion, we divide these exposures geographically into the De-na-zin (= Barrel Spring Arroyo), Alamo, Kimbeto, and Betonnie-Tsosie washes and the West Fork of Gallegos Canyon.

The only correlative of the Puercan assemblages recognized by Wood et al. (1941) is what Archibald et al. (1987) called the Mantua Lentil Local Fauna from the Fort Union Formation (= Polecat Bench Formation of Jepsen 1940), Wyoming. Archibald et al. (1987) retained the Mantua Lentil Local Fauna in the Puercan mammal age, although they demonstrated that it was older than the type Puercan assemblage (sensu Simpson 1959) of the San Juan Basin, basing their correlation on the stage of evolution of the mammals, the demonstrable superposition in northeastern Montana of type Puercan-like local faunas over Mantua-like local faunas, and faunal and magnetostratigraphic correlation between type Puercan-like local faunas of Montana and the type Puercan fauna of New Mexico. Thus, when dividing the Puercan into three interval zones, Archibald et al. (1987) referred the Mantua Lentil Local Fauna to the oldest (Pu1) and the type Puercan to the youngest (Pu2–Pu3) rather than accepting the argument by Van Valen (1978; further supported by Williamson 1996) that the Mantua Lentil Local Fauna should be the basis for a new Mammal Age, the "Mantuan." Thus Archibald et al. (1987) defined the beginning of Pu1 interval zone, the initial interval zone of the Puercan mammal age, as occurring with the first appearance of the marsupial Peradectes.

However, in 1987, when Archibald et al. was published, there was much uncertainty about the age of a series of localities in eastern Montana and western Canada that contained unusual mammalian assemblages with taxa indicative of both the Lancian and Puercan NALMAs. These



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tween faunas is based on biochronology or biostratigraphy. Between regions, correlation is biochronologic except in areas where magnetostratigraphic studies have been conducted. The approximate geochronologic ages and epochal and magnetic chronal boundaries are after Berggren et al. (1995) and Cande and Kent (1995). Note that for some sections (e.g., Clark's FIGURE 3.2 Correlation of Puercan through Clarkforkian faunas and mammal-bearing strata in United States and Canada, with localities clustered according to geographic or geologic features (often sedimentary basins). Each column is denoted by a number matching those used in figure 3.1. Number 18, in Louisiana and South Carolina, is not shown in figure 3.1. Mammal-bearing localities or suites of localities in each region are designated by letters. Letters L and W indicate Lancian and Wasatchian sites, respectively. Letters that are circled indicate that strata containing the localities or suite of localities have undergone paleomagnetic analysis and have been correlated to a magnetic anomaly. Within regions, correlation becontinued on next page)

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H CLARKFORKIAN STRATA IN THE U.S.A. AI H CLARKFORKIAN STRATA IN THE U.S.A. AI ALBERTA, SASKATCHEWAN, GOLER BASIN, CANADA ALBERTA, SASKATCHEWAN, GOLER BASIN, CANADA A L M M A LERTA, SASKATCHEWAN, GOLER BASIN, CANADA A LERTA, CANADA CANADA A LERTA, CANADA CANAD
BH CLARKFORKIAN STRATA -1516161616
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Certain areas (e.g., Fort Peck area of Williston Basin) provide both magnetostratigraphy and radioisotopic dating as means of placement of biochronologically recognized mammal ages and zones into geochronologic context. Such correlations provide some degree of confidence to chronostratigraphic and geochronologic assignments for certain strata. However, this is not possible for most sections. Thus a given segment of a formation should not be assumed to correlate across the chart to a given mammal age or zone (e.g., in the absence of relevant (continued from previous page) Fork and Bighorn basins) biochronologically recognized mammal ages and zones can be placed in a geochronologic context using magnetostratigraphy. data, the lowermost Hoback Formation should not be assumed to be latest Torrejonian in age at all places of occurrence). TABLE 3.1 List of Regions in Which Mammal-Bearing Strata Occur and Known Localities in Each Region

I. SAN JUAN BASIN, NEW MEXICO-COLORADO

PUERCAN

- A. West Fork of Gallegos Canyon, AMNH locality 4 (Pu3)
- B. De-na-zin Wash AMNH locality 2, lower fossil level (Pu2)
- C. De-na-zin Wash AMNH locality 2, upper fossil level (Pu3)
- D. West Flank Kimbeto Wash AMNH locality 5 (Pu2)
- E. East Flank Kimbeto Wash AMNH localities 6 and 7 (Pu2)
- F. Betonnie–Tsosie Wash including Mammalon Hill NMMNH L-317 (Pu2)

TORREJONIAN

- G. Kutz Canyon NMMNH localities 2659, 2660 (To1)
- H. Kutz Canyon AMNH locality "Sec. 3, T27N, R11W," KU locality 14 (To2)
- I. KU Locality 13, "Big Pocket" (To2)
- J. AMNH localities "1 or 2 miles west of Angel Peak" (To2)
- K. NMMNH localities 1482, 2658 (To2)
- L. De-na-zin Wash AMNH locality 3 (To1)
- M. Gallegos Canyon AMNH locality 1 (To2)
- N. Lowest Torrejonian of Kimbeto Wash, NMMNH 692 (= UALP 77113) (To1)
- O. Head of Kimbeto Wash AMNH locality 8 in part, KU 9 "Little Pocket" (To2)
- P. Betonnie–Tsosie Wash ("lowest Torrejonian") (To1)
- Q. 44 store localities low and high, AMNH locality 9 in part? (To2)
- R. Escavada Wash AMNH locality 14 in part, lower horizon (To2)
- S. Escavada Wash AMNH locality 14 (head of Escavada Wash) (To3)
- T. Torrejon Wash NMMNH localities 2693, 2714 (To2)
- U. Torrejon Wash NMMNH locality 2723 (To2)
- V. Torrejon Wash NMMNH locality 2709 (To2)
- W. East Branch of Torrejon Wash NMMNH 2724 (AMNH locality 11 in part?) (To2)
- X. East Branch of Torrejon Wash AMNH locality 11 lower horizon (To2)
- Y. West Branch of Torrejon Wash AMNH locality 10 upper horizon, including Tsentas Microvertebrate locality NMMNH L-312 (To3)
- Z. East Branch of Torrejon Wash AMNH locality 10 upper horizon (To3)
- AA. Mesa Chijuilla AMNH locality 17 (To3)
- BB. Mesa de Cuba and Mesa Portales AMNH localities 222, 226, 229, 230 (To2)

TIFFANIAN

- CC. Mason Pocket near Tiffany (Ti4) DD. Bayfield and others (Ti5)
- References: Simmons 1987; Thewissen 1990 (DD); Williamson and Lucas 1993; Gunnell 1994 (CC); Van Valen 1994; Williamson 1996; Lucas et al. 1997; Rose and Lucas 2000

II. BIG BEND, TEXAS

- A. Dogie LSUMG VL-108 (Pu3–To1?)
 B. Tom's Top LSUMG VL-111 (Pu3–To1?)
 C. Glenn Eleven LSUMG VL-107 (Pu3–To3)
 D. C-Con and Schiebout–Reeves Quarry (TMM 41274, 41377) (Ti1)
 E. The Middle Peak and Alligator Alley (TMM 40147) (To2?)
 F. Ray's Bonebed (TMM 40536, 40537) (Ti3)
 G. Joe's Bonebed (TMM 41365, 41366) (Ti5)
 H. New Taeniodont Site (TMM 41364) (Ti or Cf)
- References: Schiebout 1974; Schoch 1986 (H); Schiebout et al. 1987; Thewissen 1990 (D, F); Standhardt 1986; Williamson 1996

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III. WASATCH PLATEAU, UTAH

A. Gas Tank Hill local fauna (Pu2?)
B. Wagonroad; lower part of Gazin's locality 4 (Pu3)
C. Dragon; upper part of Gazin's locality 4 (To1)
D. Dragon; locality 2 of Gazin (To1)

References: Robison 1986; Cifelli et al. 1995, 1999; Lucas et al. 1997; Williamson 1996

IV. PICEANCE CREEK BASIN, COLORADO

A. Plateau Valley local fauna (Cf2)B. Big Rock Ranch local fauna (Cf2?)C. Later Clarkforkian local fauna (including Flynn Hill, Oval Hill) (Cf3)

References: Kihm 1984; Thewissen and Gingerich 1987 (A)

V. DENVER BASIN, COLORADO

A. Littleton local fauna (Alexander and South Table Mountain) (Pu1)B. Coral Bluffs, Jimmy Camp Creek, West Bijou Creek (Pu2–3)

References: Middleton 1982, 1983; Williamson 1996

VI. FOSSIL AND GREEN RIVER BASINS, WYOMING

A. Little Muddy Creek (Ti1)B. Twin Creek (Ti3)C. Chappo Type Locality (Chappo 17) (Ti3)D. Buckman Hollow Locality (Chappo 1, Chappo 12) (Cf2)

References: Dorr and Gingerich 1980 (C, D); Gunnell 1989 (B), 1994 (B, C); Krause 1987b (D); Williamson 1996 (A); Gingerich 1976 (A, B)

VII. BISON AND WASHAKIE BASINS, WYOMING

BISON BASIN

A. Saddle Locality (Ti2)B. Ledge Locality, Saddle Annex, West End (Ti3)C. *Titanoides* Locality (Ti5)

WASHAKIE BASIN

D. University of Wyoming Localities V77009–10, 12, 14, V78055 (To3)
E. Swain Quarry (To2?)
F. University of Wyoming Localities V77005–8, 13, 15–16, V77061 (Ti4)
G. University of Wyoming Localities V76008, V77059–60, V78052–54 (Ti5)
H. Big Multi Quarry (Cf1)

References: Gunnell 1994 (A); Gingerich 1976, 1983 (A, B, C); Rigby 1980 (E); Winterfeld 1982 (D, F, G); Rose 1981a (H); Thewissen 1990 (E); Williamson 1996 (E); Dawson and Beard 1996 (H); Wilf et al. 1998 (H)

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VIII. HOBACK AND WIND RIVER BASINS, WYOMING

A. Battle Mountain (Ti3)
B. Dell Creek Quarry (Ti5)
C. UM-Sub-Wy localities 7, 10, 20 (Cf2) (locality plotted in #6 column of figure 3.2)
D. Love Locality (Ti3)
E. Low Locality, Rohrer Locality (Ti6–Cf1)

F. Purdy Basin (Red Creek Localities) (Cf2)

G. Keefer Hill (Twin Buttes) (Ti1)

H. West Side of Shotgun Butte (Cf2?)

I. "Malcolm's Locality" (Badwater Locality) (Ti4)

References: Gunnell 1989 (G), 1994 (A, D, J); Gingerich 1976; 1983 (A, B); Thewissen and Gingerich 1987 (C); Rose and Krause 1982 (E); Cifelli et al. 1989 (F); Rose 1981a (F)

IX. HANNA AND CARBON BASINS, WYOMING

HANNA BASIN

A. Ferris Formation Pu1 Level (Pu1)B. Ferris Formation Pu2 Level (Pu2)C. Ferris Formation Pu3 Level (Pu3)D. The Breaks local fauna (To3–Ti3)

CARBON BASIN

E. Grayson Ridge fauna (Ti1?)F. Halfway Hill fauna (Ti1?)G. Sand Creek fauna (Ti3–Ti5)

References: Eberle 1999 (B); Eberle and Lillegraven 1998a (A–C), 1998b (A–C); Higgins 2000 (D–G); Lillegraven and Eberle 1999 (A–C); Secord 1998 (D–G)

X. CLARK'S FORK AND BIGHORN BASINS, WYOMING AND MONTANA

WEST AND NORTHWEST OF POLECAT BENCH

A. Cub Creek (To3)

B. Seaboard Well (Ti3)

C. Princeton Quarry, Schaff Quarry, Fossil Hollow, Brice Canyon, Fritz Quarry, Jepsen Valley (Ti5)

D. Little Sand Coulee (Cf1), various UM localities (including 52a) (Cf1), Bear Creek (Cf1), various UM localities (Ti6)

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E. Franimys Hill, Phil's Hill, Paint Creek, Krause Quarry, Holly's Microsite, various other localities (Cf2)

F. Granger Mountain, Rainbow Valley, various UM localities (Cf3)

VICINITY OF POLECAT BENCH AND POWELL, WYOMING

G. Mantua Lentil (Pu1)
H. Rock Bench Quarry (To2)
I. UM Locality 263 (Ti2)
J. Various UM localities (Ti3)
K. Airport Locality, Long Draw Quarry (Ti4)
L. Various UM localities (Ti5)
M. Various UM localities (Cf1)
N. Various UM localities (Cf2)
O. Various UM localities (Cf3)

SOUTH AND EAST OF POWELL, WYOMING

P. Cedar Point Quarry, Jepsen Quarry (Ti3)
Q. Lower Sand Draw, Witter Quarry (Croc Tooth), Divide Quarry, Sand Draw Anthill (Ti4)
R. Middle Sand Draw, Sunday Locality (Ti5)
S. Foster Gulch (Cleopatra Reservoir Quarry), Rough Gulch, Upper Sand Draw (Cf2)
T. Ries Locality, Foster Gulch Oil Well #1 (Cf, but zone uncertain)

SOUTHERN BIGHORN BASIN

U. Leidy Quarry (Pu1)

V. Cedar Mountain Sites, low in Fort Union Formation (Pu, but zone uncertain)

W. Cedar Mountain Sites, high in Fort Union Formation (To3 or Ti1)X. Grass Creek–Blue Mesa #1 (To2–To3)Y. Grass Creek Blue Mesa #2 (Ti3–Ti5)

References: Thewissen 1990; Gunnell 1988, 1989, 1994; Krause 1987a, 1987b; Gingerich 1976, 1987, 1989; Cifelli et al. 1989; J. E. Hartman 1986 (V–W); Leite 1992 (X–Y); Gunnell and Gingerich 1991; Rose 1981a; Van Valen 1978; Williamson 1996 (H); Bloch et al. 2001 (Q); Bloch et al. 2002

XI. CRAZY MOUNTAINS BASIN, MONTANA (BANGTAIL LOCALITY LOCATED IN BRIDGER RANGE)

A. Bangtail Locality (Ti1)
B. Gidley Quarry (To2)
C. Silberling Quarry (To2)
D. Douglass Quarry (Ti1)
E. Scarritt Quarry (Ti2)
F. Simpson Locality 13 (= Melville Locality) (Ti3)
G. Simpson Locality 65 (To1)
H. Simpson Quarry (Pu2 or Pu3)
I. Glennie and Bingo localities (Ti1)

References: Hartman and Krause 1993; Hartman et al. 1989 (H); Buckley 1994 (H), 1995 (H), 1997 (H); Hartman 1999; Butler et al. 1987; Krause and Maas 1990; Gunnell 1994; Thewissen 1990; Wall and Krause 1992 (C); Williamson 1996 (B, H)

XII. FORT PECK AREA, WILLISTON BASIN, MONTANA

A. Bug Creek Anthills (Pu1)

B. Bug Creek West, Harbicht Hill, Ferguson Ranch, Chris's Bonebed (Pu1)

C. Morales 1 and Herpijunk Promontory (Pu1)

D. McKeever Ranch localities (Pu1)

E. Hell's Hollow local fauna (including Worm Coulee #1) (Pu1)

F. Garbani Channel localities (including Garbani Quarry) (Pu3?)

G. Mosquito Gulch localities (including Farrand Channel) (To1)

H. Purgatory Hill (Pu3?)

I. McGuire Creek local faunas (Little Roundtop, Black Spring Coulee, Shiprock, Brown Grey, Second Level, Up Up the Creek) (Pu1)

J. Z-Line Channel local fauna (Pu1)

K. Jacks Channel local fauna (Pu1)

References: Lofgren 1995; Archibald 1982; Archibald and Lofgren 1990; Clemens 2002; Van Valen 1978, 1994; Swisher et al. 1993; Rigby 1987, 1989; Rigby et al. 1987; Sloan et al. 1986; Lupton et al. 1980 (B); Simmons 1987 (F, H); Luo 1991 (A); Fox 1989 (A)

XIII. WILLISTON AND POWDER RIVER BASINS, SOUTHEAST MONTANA

A. Olive (Ti4)

B. Circle (Ti4)

C. Bechtold Site (Pu3?)

D. Medicine Rocks 1, Mehling Site (To3?)

E. White Site, 7-Up Butte, Highway Blowout (Ti2)

F. Newell's Nook (USGS D-2003) (Ti1)

G. Hiatt local fauna (Pu2)

H. School Well local fauna (To, but zone uncertain)

References: Hunter et al. 1997 (G–H); Robinson and Honey 1987 (F); Simmons 1987 (C); Thewissen 1990; Gunnell 1989, 1994; Krause 1987a (D); Gingerich 1976; Rose 1975

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XIV. WILLISTON BASIN, NORTH DAKOTA

A. Wannagan Creek Quarry (Ti4)
B. Donnybrook (To or Ti)
C. Lloyd and Hares Site (= Heart Butte) (To3 or Ti1)
D. Judson (Ti4)
E. Brisbane (Ti3)
F. Riverdale (Ti4)
G. Cross Locality (L5377 a and b) (Ti4)
H. White's River Basin Survey Site 3 (Ti3?)
I. Red Spring Locality (Ti4)
J. Locality L5500b (Ti4)
K. Witter Locality (Ti4)
L. Pita Flats (Pu2–Pu3)
M. Brown Ranch localities (To2)
N. X-X Locality (Ti2)

References: Hartman and Kihm 1991, 1992, 1995, 1999; J. H. Hartman 1999; Erickson 1991 (A), 1999 (A); Gunnell 1994 (D–F); Thewissen 1990 (D, F); Krause 1987b (D); Hunter 1999 (L–N)

XV. ALBERTA, CANADA

A. R.C.A. Corehole 66-1 (Balzac) (Pu2?)
B. Diss (To3?)
C. Calgary 2E (inc. Calgary 7E) (To3?)
D. Cochrane 1, Cochrane 2 (Ti1)
E. Aaron's Locality (Ti1 or Ti2)
F. Hand Hills West lower level (Ti1 or Ti2)
G. Hand Hills West upper level (Ti3)
H. Blindman River localities (DW-1, DW-2, DW-3, Mel's Place) (Ti3)
I. Burbank (Ti3)
J. Joffe Bridge localities (including Erickson's Landing) (Ti3)
K. Crestomere School (Ti4)
L. Canyon Ski Quarry (Ti4)
M. Swan Hills Site (Ti4)
N. Birchwood Locality (Ti3)

References: Fox 1990a, 1990b, 1990c, 1997; Webb 1995 (N); MacDonald 1995 (F, G); Gunnell 1994 (M); Thewissen 1990 (D, J); Williamson 1996 (B)

XVI. SASKATCHEWAN, CANADA (POLICE POINT LOCATED IN SOUTHEAST ALBERTA)

A. Frenchman 1 (Pu1)
B. MHBT Quarry, Long Fall (Pu1)
C. MHBT Quarry, Rav W-1 (Pu3?)
D. Croc Pot (Pu3)
E. Police Point (Ti3)
F. Roche Percée (Ti4)

References: Fox 1990c, 1997; Lofgren 1995 (A, B); Gunnell 1989 (C), 1994 (F, G); Krause 1987a (C), 1987b (G); Simmons 1987 (C); Williamson 1996 (C)

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XVII. GOLER BASIN, CALIFORNIA

A. Laudate local fauna (Ti2–Ti3)B. Edentulous Jaw Site (Ti2–Ti3)

References: McKenna et al. 1987 (A); Lofgren et al. 1999 (A, B); McKenna and Lofgren in press (A)

XVIII. LOUISIANA AND SOUTH CAROLINA (NOT SHOWN IN FIGURE 2)

A. Junior Oil Co. Beard #1 Well (Louisiana) (To2?)B. Santee River Rediversion Project (South Carolina) (Ti5)

References: Russell 1967 (A); Simpson 1932 (A); Schoch 1985, 1998 (B)

The same convention of numbering (region) and lettering (locality) used in figures 3.1 and 3.2 is used here. The abbreviation in parentheses after each locality is the zone to which the fauna from that locality is referred. References follow each numbered section; those listed are seminal works that refer to most of the relevant localities or are references that appeared after publication of Archibald et al. (1987). References followed by a letter or letters in parentheses denote the specific locality or localities to which each reference relates. For a more extensive list of cited literature, see table 3.1 in Archibald et al. (1987).

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were the Bug Creek Faunas (Bug Creek Anthills, Bug Creek West, Harbicht Hill) from the upper Hell Creek Formation of eastern Montana, first described by Sloan and Van Valen (1965), and the Frenchman 1 (Frenchman Formation) and Long Fall (Ravenscrag Formation) sites in southern Saskatchewan, described by Johnston (1980) and Johnston and Fox (1984). Archibald et al. (1987) tentatively recognized the Bug Creek Faunas and correlatives as Lancian in age because their stratigraphic position was thought to be laterally equivalent to nearby Lancian sites (Archibald 1982). But they also suspected that they "may be younger than known typical Lancian localities" (Archibald et al. 1987;41).

Subsequently, Archibald (1987a, 1987b) and Sloan (1987) both proposed a Bugcreekian mammal age preceding the Puercan, based on the Bug Creek Faunas and presumed correlatives (i.e., Frenchman 1 and Long Fall). As defined, the Bugcreekian began with the first appearance of the ungulate Protungulatum (Archibald 1987a, 1987b). It should be noted that when the Bugcreekian mammal age was proposed, the first appearance of Protungulatum was in channel fillings in the upper Hell Creek Formation that were thought to be of Cretaceous age. The stratigraphically lowest record of Peradectes was in the lowest part of the overlying Tullock Formation and was recognized to be of Puercan age. Shortly thereafter, Lofgren (1995) reported the co-occurrence of Protungulatum and Peradectes at a number of sites in the upper Hell Creek Formation in the McGuire Creek area, which is 3 miles south of Bug Creek, where two of the three original

Bug Creek sites are located. Based primarily on the cooccurrence of Protungulatum and Peradectes in the upper Hell Creek Formation at McGuire Creek, the Bugcreekian mammal age was abandoned and the Puo interval zone of the Puercan NALMA was proposed to replace it (Archibald and Lofgren 1990). Thus the first occurrence of Protungulatum defined the beginning of both the Puo interval zone and the Puercan mammal age (Archibald and Lofgren 1990). Later, Lofgren (1995) discussed the practical difficulties of paleontologically distinguishing Puo from Pui, noting that Puo involves no genera of unique occurrence and must be differentiated from Pu1 by the absence of Peradectes, a typically rare genus. Also, as noted, Puo and Pu1 faunas are found in the same stratigraphic interval in Montana, the upper Hell Creek Formation, and further complicating the biostratigraphy is that Puo and Pu1 faunas in the Bug Creek and McGuire Creek areas contain reworked Lancian fossils (Lofgren 1995). Thus in both a biostratigraphic and biochronologic sense the Puo interval zone, although demonstrably older in two cases than any Pu1 site (based on faunal content at Bug Creek Anthills [Lofgren 1995] and palynology at Frenchman 1 [Fox 1995, 1997]), is still too similar to the Put interval zone to be of practical use. Therefore we merge Puo and Pu1 and recognize the advent of the Puercan mammal age as beginning with the first occurrence of the ungulate Protungulatum.

A recent test of the utility of the Puo interval zone that supports our decision to merge the Puo and Pu1 interval zones comes from the type Ferris Formation, roughly 2 \oplus

TAXON	L+	PU1	PU2	PU3	T01	т02	тоз	TI1	T12	TI3	TI4	T15	T16	CF1	CF2	CF3	W+
MULTITUBERCUL	ATA																
Ptilodontidae																	
Mesodma	\leftarrow	Х	Х	Х	0	?	Х	Х	Х	Х	Х						
Neoplagiaulax	?	0	Х	Х	0	Х	Х	Х	Х	Х	Х	Х					
Ectypodus			Х	0	0	Х	Х	Х	Х	Х	Х	Х	0	Х	Х	Х	\rightarrow
Parectypodus	\leftarrow	0	Х	Х	Х	Х	Х	Х	0	Х	0	Х	Ο	Х	Х	0	\rightarrow
Mimetodon							Х	Х	0	Х	Х	Х					
Xanclomys						Х											
Kimbetohia	\leftarrow	0	Х	Х													
Krauseia							Х	Х									
Ptilodus			Х	0	Х	Х	Х	Х	Х	Х	Х	Х					
Xyronomys			Х	0	0	Х											
Baiotomeus							Х	Х	0	Х							
Prochetodon										Х	Х	Х	Х	Х	Х	Х	
Viridomys	\leftarrow	0	0	?	?												
Sloanbaataridae																	
Pentacosmodon												Х					
Cimolodontidae																	
Cimolodon	\leftarrow	0	0	?													
Anconodon						Х	Х	Х	Х								
Cimolomyidae																	
Cimolomys	\leftarrow	?															
Eucosmodontidae																	
Essonodon	\leftarrow	?															
Acheronodon		Х															
Microcosmodon			Х	Х	0	0	0	Х	Х	Х	Х	Х	0	Х	Х		
Eucosmodon			Х	Х	Х	Х	Х	?									
Stygimys	\leftarrow	Х	Х	Х	0	Х											
Liotomus								Х									
Neoliotomus									?	?	0	Х	Х	Х	Х	0	\rightarrow
Taeniolabididae																	
Meniscoessus	\leftarrow	?															
Catopsalis		Х	Х	Х	Х	Х	Х	Х	0	0	Х						
Taeniolabis				Х													
Family indetermin	ate																
Cimexomvs	←	Х	Х	Х													
Fractinus								Х									
MARSUPIALIA																	
Didelphidae																	
Peradectes		Х	Х	Х	0	Х	Х	Х	Х	Х	Х	Х	0	Х	Х	Х	\rightarrow
Mimoperadectes															?	\rightarrow	
Swaindelphys							Х										
Alphadon	\leftarrow	?															
Turgidodon	\leftarrow	?															

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 TABLE 3.2
 List of Puercan Through Clarkforkian Mammalian Genera and Their Known Temporal Ranges

TAXON	L+	PU1	PU2	PU3	T01	то2	тоз	TI1	TI2	тіз	T14	T15	T16	CF1	CF2	CF3	W+
Glasbiidae																	
Glasbius	\leftarrow	?															
Pediomyidae																	
Pediomys	~	?															
Stagodontidae																	
Didelphodon	←	?															
LEPTICTIDA																	
Gypsonictopidae																	
Gypsonictops Stilpnodon	\leftarrow	?				X	0	0	0	ş							
Leptictidae																	
Leptonysson Prodiacodon Palaeictops Myrmecoboides Xenacodon				X X	0 0	X X X X	X ? X	X O X	X O O	X O X	O X O X	X X X	0 0	0 0	? O	? O	\rightarrow \rightarrow
ANAGALIDA																	
Pseudictopidae																	
Mingotherium												Х					
RODENTIA																	
Alagomyidae																	
Alagomys														Х			
Ischyromyidae																	
Acritoparamys Microparamys Paramys Franimys Apatosciuravus														X X X	O X X X X X	O X X O X	$\begin{array}{c} \rightarrow \\ \rightarrow \\ \rightarrow \\ \rightarrow \\ \rightarrow \\ \rightarrow \end{array}$
Reithroparamyidad	е																
Reithroparamys															Х	0	\rightarrow
CIMOLESTA																	
Family indetermin	ate																
Alostera Ravenictis Pararyctes	~	?		Х			х	х	X	Х	х						
Palaeoryctidae																	
Palaeoryctes Aaptoryctes						Х	Х	Х	0	Х	X	X X	0	Х	X	X	

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TAXON	L+	PU1	PU2	PU3	T01	T02	тоз	TI1	TI2	тіз	TI4	T15	т16	CF1	CF2	CF3	W+
DIDELPHODONTA																	
Cimolestidae																	
Cimolestes	\leftarrow	Х	Х	Х													
Alveugena			Х														
Procerberus		Х	?	Х													
Gelastops						Х	Х	Х	0	Х							
Avunculus						Х	Х										
Acmeodon					Х	Х	Х	Х	0	Х							
Paleotomus						Х	Х	Х	Х	Х	0	Х					
Protentomodon														Х			
Apatemyidae																	
Jepsenella						Х	Х	Х									
Apatemys										Х	Х	0	0	Х	Х	Х	\rightarrow
Unuchinia						Х	0	0	Х	Х	Х	Х					
PANTOLESTA																	
Pantolestidae																	
Corithague						v	v	v									
Aphronorus					x	x	X	x	0	x							
Pentacodon					Α	X	x	x	0	Λ							
Bisonalveus						11	n	x	x	x							
Propalaeosinopa						х	х	x	x	x	х	x					
Palaeosinopa						11	21	11	x	x	x	x	x	x	x	x	\rightarrow
Thelvsia									21	11	11	11		1	X	21	,
Fpoicotheriidae																	
Ameletelee											v						
Amelotabes											Λ						
Metacheiromyidae																	
Propalaeanodon												Х					
Palaeanodon														Х	Х	Х	\rightarrow
Escavadodontidae																	
Escavadodon							Х										
Family indetermind	ate																
Melaniella										Х							
TAENIODONTA																	
Stylinodontidae																	
Onychodectes			Х	Х													
Conoryctella					Х	Х											
Schochia			Х														
Wortmania			Х	Х													
Psittacotherium						Х	Х	Х	0	Х	0	?					
Ectoganus												Х	Х	Х	Х	Х	\rightarrow
Conoryctes						Х	Х										
Huerfanodon						Х											

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TAXON	L+	PU1	PU2	PU3	T01	то2	тоз	T11	TI2	тіз	т14	T15	T16	CF1	CF2	CF3	W+
TILLODONTIA																	
Tillotheriidae																	
Esthonyx Deltatherium						Х							?	Х	Х	Х	\rightarrow
PANTODONTA																	
Titanoideidae																	
Titanoides								Х	Х	Х	Х	Х	0	?			
Pantolambidae																	
Pantolambda Caenolambda						Х	Х	Х	х	х							
Barylambdidae																	
Barylambda Haplolambda Ignatiolambda										Х	X X X	X X X	0 0	X X	Х	?	\rightarrow
Cyriacotheriidae																	
Cyriacotherium										Х	Х	Х	Х	Х	Х	Х	
Coryphodontidae																	
Coryphodon														Х	Х	Х	\rightarrow
CREODONTA																	
Oxyaenidae																	
Oxyaena Dipsalidictides Tytthaena Dipsalodon										Х		X X	X ?	X X O	X X X	X X ?	\rightarrow \rightarrow
Palaeonictis																Х	
CARNIVORA																	
Viverravidae																	
Pristinictis Simpsonictis Viverravus						х	0	X X	?			Х	0	Х	Х	Х	\rightarrow
Ictidopappus Didymictis Protictis Raphictis			?	0	O X	x x	x	Х	х	X X	X X	X X	Х	х	Х	Х	\rightarrow
Miacidae																	
Uintacyon															Х	Х	\rightarrow

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TAXON	L+	PU1	PU2	PU3	т01	то2	тоз	T11	TI2	тіз	TI4	TI5	т16	CF1	CF2	CF3	W+
LIPOTYPHLA ERINACEOMORP	HA																
Family indetermin	iate																
Adunator						Х	Х	Х	0	Х	Х	Х	Х	Х	Х	Х	
Litocherus							Х	Х	Х	Х	Х	Х					
Diacodon						?	?	?	0	0	0	Х	0	0	?	0	\rightarrow
Leipsanolestes														Х	Х	Х	\rightarrow
Erinaceidae																	
Litolestes										Х	Х	Х					
Cedrocherus										Х							
Entomolestes											Х	0	0	0	0	0	\rightarrow
SORICOMORPHA																	
Geolabididae																	
Batodon	\leftarrow	;															
Nyctitheriidae																	
Plagioctenodon														Х	?	0	\rightarrow
Ceutholestes														Х	0	Х	
Limaconyssus								Х	0	0	0	0	0	Х	0	Х	
Wyonycteris														Х	0	Х	
Leptacodon				?	0	?	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	\rightarrow
Pontifactor															?	0	\rightarrow
ARCHONTA CHIROPTERA																	
Archaeonycteridae	?																
Icaronycteris																?	\rightarrow
PRIMATES																	
Purgatoriidae																	
Purgatorius		;	Х	Х													
Microsyopidae																	
Niptomomys															Х	Х	\rightarrow
Navajovius								Х	0	Х	Х	Х					
Arctodontomys														Х	Х	Х	\rightarrow
Micromomyidae																	
Micromomys										Х	Х	Х	0	0	0	0	\rightarrow
Tinimomys														Х	Х	0	\rightarrow
Chalicomomys														Х	0	0	\rightarrow
Plesiadapidae																	
Pandemonium			Х	Х													
Saxonella										Х							
Pronothodectes						Х	Х	Х									
Chiromyoides										Х	Х	Х	Х	Х	Х		

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TAXON	L+	PU1	PU2	PU3	T01	т02	тоз	T11	TI2	тіз	T14	T15	T16	CF1	CF2	CF3	W+
Nannodectes Plesiadapis								X X	X X	X X	X X	X X	х	х	х	Х	\rightarrow
Palaechthonidae																	
Palaechthon Premnoides Anasazia Palenochtha Plesiolestes					X X	X X X	X X X X X X	X X X	0	Х							
Picrodontidae																	
Draconodus Picrodus Zanycteris					Х	x	Х	X	x	x x	O X	x					
Paromomyidae Paromomys Ignacius Dillerlemur Phenacolemur Acidomomys					X	X X	X X	X X	? X	? X	X ?	X X O	O X O	X X X	X X X X X	X X X	\rightarrow \rightarrow \rightarrow
Plagiomenidae																	
Elpidophorus Eudaemonema Planetetherium Worlandia Plagiomene						х	X X	X X	X O	X X	Х			Х	? X X	X X	\rightarrow \rightarrow
Mixodectidae																	
Mixodectes Dracontolestes					Х	Х	Х										
Family indetermina	ite																
Thylacaelurus								?	0	0	0	0	0	0	0	0	\rightarrow
Elphidotarsius Carpodaptes Carpolestes Carpocristes Carpomegodon						X	X	X X	O X	x x x	X X X	X X X	x	x	x	X	
UNGULATA																	
Protungulatum DINOCERATA		X	Х	X													
Uintatheriidae																	
Prodinoceras												Х	Х	Х	Х	Х	\rightarrow

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TAXON	L+	PU1	PU2	PU3	т01	т02	тоз	T11	TI2	тіз	т14	T15	T16	CF1	CF2	CF3	W+
PROCREODI																	
Oxyclaenidae																	
Oxyprimus		Х															
Carcinodon			Х	Х													
Chriacus			Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	0	Х	?	?	\rightarrow
Oxyclaenus		Х	Х	Х	Х												
Oxytomodon					Х												
Prothryptacodor	1					Х	Х	Х									
Princetonia												Х	0	0	Х	0	\rightarrow
Thryptacodon								Х	Х	Х	Х	Х	0	Х	Х	Х	\rightarrow
Arctocyonidae																	
Platymastus			Х														
Desmatoclaenus			Х	Х	Х	0	0	Х	Х								
Baioconodon		Х	Х	Х													
Loxolophus			Х	Х	Х	Х	Х										
Mimotricentes			Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х				
Deuterogonodor	1					Х	Х										
Neoclaenodon						V	X	X	X	37	V	V					
Claenodon						Х	Х	Х	X	X	Х	Х					
Amacadam	1								А	Λ	v	v	0	0	v		
Lambartacuon										v	л v	л v	0	v	Λ		
Colpoclaenus						?	Х	Х	0	X	Α	Α	0	Α			
CONDYLARTHRA																	
Hyopsodontidae																	
Litomylus			Х	0	Х	Х	Х	Х	Х	Х	Х						
Aletodon										Х	Х	Х	0	Х	Х	Х	
Haplaletes				Х	0	Х	Х	Х	Х	Х	Х	Х					
Dorraletes										Х	0	Х					
Utemylus											Х						
Hyopsodus																Х	\rightarrow
Haplomylus														Х	Х	Х	\rightarrow
Phenacodaptes											Х	Х	0	Х			
Apheliscus														Х	Х	Х	\rightarrow
Mioclaenidae																	
Protoselene				?	Х	Х	Х	Х	Х	Х							
Litaletes				?	Х	Х	Х	Х									
Ellipsodon			Х	Х	0	Х											
Choeroclaenus			Х	Х													
Bubogonia			Х	Х													
Tiznatzinia			Х	Х													
Promioclaenus			Х	Х	Х	Х	Х	Х	Х	Х							
Mioclaenus					Х	Х	Х										
Phenacodontidae																	
Tetraclaenodon					Х	Х	Х	Х									
Phenacodus							Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	\rightarrow

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Paleocene Biochronology: The Puercan Through Clarkforkian Land Mammal Ages 61

TABLE 3.2 (continued)

TAXON	L+	PU1	PU2	PU3	T01	T02	тоз	T11	TI2	TI3	TI4	T15	T16	CF1	CF2	CF3	W+
Ectocion								Х	Х	Х	Х	Х	Х	Х	Х	Х	\rightarrow
Meniscotherium																Х	\rightarrow
Copecion										Х							
Periptychidae																	
Mimatuta		Х	Х														
Anisonchus			Х	Х	Х	Х	Х	Х									
Haploconus			Х	Х	Х	Х	Х										
Mithrandir			Х	Х													
Hemithlaeus		?	Х														
Ampliconus		Х	Х														
Auraria		Х															
Ectoconus			Х	Х													
Alticonus			Х														
Maiorana		Х															
Periptychus			Х	Х	Х	Х	Х	Х	0	Х	Х						
Tinuviel		?	Х	Х													
Oxyacodon		Х	Х	Х													
Conacodon		Х	Х	Х	0	0	0	0	?	;							
ARCTOSTYLOPIDA	4																
Arctostylopidae																	
Arctostylops												Х	0	0	Х	Х	
CETE																	
Family indetermina	te																
Microclaenodon						Х	Х										
Triisodontidae																	
Goniacodon				Х	Х	Х	Х										
Eoconodon		Х	Х	Х													
Triisodon					Х	Х											
Stelocyon							Х										
Mesonychidae																	
Ankalagon						Х	Х										
Dissacus						Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	\rightarrow

Arrows indicate documented ranges earlier than Puercan or later than Clarkforkian. Genera listed have been reported in published literature or are in press (except *Auraria* from Middleton 1983). Unpublished faunal data from dissertations are included in a few cases. Symbols: X, known from zone; ?, questionably present; O, not known. Taxa are listed following McKenna and Bell (1997). It is beyond the scope of this work to provide a locality list for each genus listed. For a partial list of localities for each genus, see tables 3.1 and 3.2 in Archibald et al. (1987) and the more recently published references listed in table 3.1.

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km thick, exposed in the Hanna Basin of Wyoming (Eberle and Lillegraven 1998a, 1998b). Eberle and Lillegraven report a series of 39 localities referable to the Lancian and interval zones Pu1, Pu2, and Pu3 of the Puercan. A mammalian assemblage referable to the Puo interval zone was not found in the Ferris Formation, even in this unusually thick package of sedimentary rock.

Finally, in contrast to our decision to refer faunas with *Protungulatum* to the Puercan mammal age, Fox (1990c, 1997) argued that the mammalian assemblages contain-

ing Protungulatum from the Frenchman 1 and Long Fall sites in western Canada are Cretaceous in age and referable to the Lancian mammal age. Their Cretaceous age assignment was based on stratigraphic position (Johnston 1980; Johnston and Fox 1984; Fox 1990c, 1997) and palynology (Fox 1995, 1997). Thus, as we recognize it, the Puercan mammal age may span the Cretaceous-Tertiary boundary (i.e., the first occurrence of Protungulatum may have occurred in the Cretaceous in Canada or elsewhere in North America). In any case, the first appearance of ungulates (i.e., the advent of the Puercan mammal age) signals the beginning of a dramatic shift in composition of mammalian assemblages in North America (Alroy 1999). We see no conceptual reason why the Lancian-Puercan and Cretaceous-Tertiary boundaries should necessarily coincide. Also, we see no reason why the first appearance of Protungulatum could not have occurred in the Late Cretaceous.

The number of known Puercan localities has increased greatly since publication of Wood et al. (1941) and Archibald et al. (1987). New Puercan faunas or additional taxa reported from previously known sites have been reported from the Javelina Member of the Tornillo Formation of Texas (Standhardt 1986; Schiebout et al. 1987), the North Horn Formation of central Utah (Robison 1986; Cifelli et al. 1995, 1999), the Ferris Formation of south-central Wyoming (Eberle 1999; Eberle and Lillegraven 1998a, 1998b; Lillegraven and Eberle 1999), the Fort Union Formation near Cedar Mountain, Wyoming (Hartman 1986), the Bear Formation in south central Montana (Buckley 1994, 1995, 1997), the upper Hell Creek and lower Tullock formations of eastern Montana (Lofgren 1995; Rigby 1989; Sloan et al. 1986), the Ludlow Member of the Fort Union Formation of southeastern Montana (Hunter et al. 1997), the Ludlow Formation of North Dakota (Hunter 1999), the Ravenscrag Formation of Saskatchewan (Fox 1990c, 1997), and the Nacimiento Formation of New Mexico (Williamson 1996).

DEFINITION AND CHARACTERIZATION

We define the Puercan mammal age to include faunas that occurred between first appearance of the arctocyonid condylarth *Protungulatum* and first appearance of the periptychid condylarth *Periptychus carinidens*.

Wood et al. (1941) noted that the following taxa first appeared in the Puercan mammal age: *Anisonchus*, Condylarthra, Creodonta, *Eucosmodon*, *Oxyclaenus*, Taeniodonta, and Taligrada. The taxa in this list are still thought to have appeared during Puercan time, although not necessarily at the earliest sites referable to this age. Of the four orders listed as first appearances, only the Taeniodonta retains a taxonomic usage comparable to that applied by Wood et al. in 1941 (Archibald et al. 1987). This order is still considered to have appeared in the Puercan mammal age but not at the earliest sites (Eberle 1999). Assuming that Wood et al. (1941) followed Matthew's (1937) concept of the Condylarthra, Creodonta, and Taligrada, then, following the classification by McKenna and Bell (1997), Puercan representatives of Matthew's Condylarthra are now included in the condylarthran families Mioclaenidae (Protoselene, Ellipsodon) and Periptychidae (Oxyacodon). According to McKenna and Bell (1997), Matthew's Creodonta are now included in the orders Procreodi (Oxyclaenidae: Carcinodon, Oxyclaenus, Chriacus including Tricentes, and Arctocyonidae: Loxolophus) and Cete (Triisodontidae: Eoconodon, Goniacodon), and Matthew's Taligrada are now included in the condylarthran family Periptychidae (Haploconus, Anisonchus, Hemithlaeus, Periptychus, Ectoconus, Conacodon). Taligrada is no longer used in standard mammalian taxonomy (see McKenna and Bell 1997).

In addition to first appearances, Wood et al. (1941) identified the following as index fossils thought to have been limited to the Puercan mammal age: Carsioptychus, Conacodon, Ectoconus, Eoconodon, Loxolophus, Onychodectes, Oxyacodon, Taeniolabis, and Wortmania. Of these genera, three are now known to occur in the Torrejonian or Torrejonian and Tiffanian mammal ages. Loxolophus has been reported from the Dragon Local Fauna, North Horn Formation of Utah (Gazin 1941; Robison 1986) and Swain Quarry of Wyoming (Rigby 1980), both of Torrejonian age (Archibald et al. 1987). Conacodon has been identified from the Laudate Local Fauna in the Tiffanian part of the Goler Formation of California (McKenna 1955; McKenna and Lofgren in press). McKenna and Bell (1997) consider Carsioptychus a junior synonym of *Periptychus*, which extended into the Tiffanian mammal age (Archibald et al. 1987).

Archibald et al. (1987) presented a list of first and last appearances, index fossils, and characteristic fossils for the Puercan mammal age. Our updated list reflects new knowledge of temporal ranges, new genera described since 1987, and the following taxonomic and biostratigraphic considerations. First, in addition to the synonymy of *Periptychus* and *Carsioptychus*, McKenna and Bell (1997) recognized the following generic synonyms: *Mithrandir* (*Gillisonchus*), *Oxyclaenus* (*Thangorodrim*), *Oxyacodon* (*Escatepos*), *Mimatuta* (*Earendil*), and *Ellipsodon* (*Bomburia*). Second, we recognize *Ragnarok* as a junior synonym of *Baioconodon*, an idea first proposed by Middleton (1983), formalized by Hunter et al. (1997), and accepted by McKenna and Bell (1997). Third, the occurrence of *Gypsonictops, Alostera, Batodon, Didelphodon, Glasbius, Pediomys, Alphadon, Turgidodon, Essonodon, Meniscoessus,* and *Cimolomys* in strata representing the Puercan mammal age probably is the result of reworking because their Puercan records are limited to channels that were incised into Lancian strata (Lofgren 1995). Finally, as a result of changing the definition of the beginning of the Puercan mammal age to the first appearance of *Protungulatum,* the following genera represent Puercan index fossils rather than taxa that first appeared in the Lancian and last appeared in the Puercan mammal ages: *Baioconodon* (including *Ragnarok*), *Mimatuta, Oxyprimus, Procerberus, Protungulatum,* and *Purgatorius.*

A combined biochronologic–magnetostratigraphic correlation of Puercan local faunas from the Nacimiento Formation, San Juan Basin, New Mexico (Butler and Lindsay 1985; Williamson and Lucas 1992; Williamson 1996); North Horn Formation, central Utah (Tomida and Butler 1980); Tullock Formation, northeastern Montana (Archibald et al. 1982; Swisher et al. 1993); Fort Union Formation, northern Wyoming (Butler et al. 1987); and Ludlow Formation, southeastern Montana (Hunter et al. 1997) indicates that Puercan mammals first occur and last occur in strata of reversed polarity (Tomida and Butler 1980; Swisher et al. 1993). We interpret these data to signify that the Puercan mammal age (Pu1 interval zone) began during magnetic polarity chron C29r and ended (To1 interval zone) in chron C28r.

Puercan local faunas in the upper Hell Creek and Tullock formations in eastern Montana have been correlated to stratigraphic units (in this case lignites) that contain bentonitic and volcanic crystal rich partings suitable for argon–argon dating (Swisher et al. 1993). These data indicate that the entire Puercan mammal age was approximately 1 million years in duration (Swisher et al. 1993).

Further discussion of biochronologic–paleomagnetic correlations is provided in the appropriate sections of this chapter dealing with interval zones Pu1, Pu2, and Pu3 of the Puercan mammal age.

First and last appearances, index fossils, and fossils characteristic of the Puercan mammal age are as follows.

First appearances: Anisonchus, Catopsalis, Chriacus, Conacodon, Desmatoclaenus, Ectypodus, Ellipsodon, Eucosmodon, Goniacodon, Haplaletes, Haploconus, Ictidopappus?, Leptacodon?, Litaletes?, Litomylus, Loxolophus, Microcosmodon, Mimotricentes, Oxyclaenus, Palaeictops, Peradectes, Periptychus, Prodiacodon, Promioclaenus, Protoselene?, Ptilodus, and Xyronomys

- Last appearances: Alostera?, Alphadon?, Batodon?, Cimexomys, Cimolestes, Cimolodon?, Cimolomys?, Didelphodon?, Essonodon?, Glasbius?, Gypsonictops?, Kimbetohia, Meniscoessus?, Pediomys?, Turgidodon?, and Viridomys
- Index fossils: Acheronodon, Alticonus, Alveugena, Ampliconus, Auraria, Baioconodon, Bubogonia, Carcinodon, Choeroclaenus, Ectoconus, Eoconodon, Hemithlaeus, Maiorana, Mimatuta, Mithrandir, Onychodectes, Oxyacodon, Oxyprimus, Pandemonium, Platymastus, Procerberus, Protungulatum, Purgatorius, Ravenictis, Schochia, Taeniolabis, Tinuviel, Tiznatzinia, and Wortmania
- Characteristic fossils: Mesodma, Neoplagiaulax?, Parectypodus, and Stygimys

ZONATION

We recognize three interval zones in the Puercan mammal age. From oldest to youngest, they are the *Protungulatum/Ectoconus* Interval Zone (Pu1), the *Ectoconus/ Taeniolabis taoensis* Interval Zone (Pu2), and the *Taeniolabis taoensis/Periptychus carinidens* Interval Zone (Pu3).

Protungulatum/Ectoconus Interval Zone (Pu1) We define the Protungulatum/Ectoconus Interval Zone to include faunas that occurred between the first appearance of Protungulatum and the first appearance of Ectoconus. The Pu1 interval zone is represented by the following sets of localities and local faunas: Mantua Lentil Local Fauna, Leidy Quarry, and sites low in the Fort Union Formation near Cedar Mountain, Bighorn Basin, northern Wyoming; Hell's Hollow Local Fauna, McKeever Ranch localities, Bug Creek Anthills and correlatives (Bug Creek West, Harbicht Hill, Ferguson Ranch, Chris's Bonebed), Morales 1 and Herpijunk Promontory, McGuire Creek local faunas, Z-line Channel Local Fauna, Jacks Channel Local Fauna, northeastern Montana; Littleton Local Fauna, Denver Basin, central Colorado; Long Fall and Frenchman 1 sites in western Canada; and a series of localities in the Hanna Basin, south-central Wyoming.

The Mantua Lentil Local Fauna from the Fort Union (= Polecat Bench) Formation was first described by Jepsen (1930, 1940). Van Valen (1978) later provided abbreviated descriptions of a number of new species of ungulates and a list of ungulates present in the local fauna (*Oxyprimus, Baioconodon, Eoconodon, Maiorana, Mimatuta*, and *Oxyacodon*). Van Valen (1978) also briefly described the mammalian fauna from the Leidy Quarry in the southern Bighorn Basin, a locality also referable to the Pu1 interval zone. Leidy Quarry yielded specimens 64 Donald L. Lofgren, Jason A. Lillegraven, William A. Clemens, Philip D. Gingerich, and Thomas E. Williamson

that are referable to *Baioconodon* and *Mimatuta*. More recently, J. E. Hartman (1986) described a sparse fauna containing *Mesodma*, *Baiotomeus*, *Peradectes*, *Oxyclaenus*, and *Oxyprimus* from four sites low in the Fort Union Formation near Cedar Mountain, also in the southern Bighorn Basin. Presence of the ungulate *Oxyprimus* suggests an early Puercan age because this is an index fossil for the Pu1 interval zone based on current knowledge. However, *Baiotomeus* is reported from the same locality (Hartman 1986), and this genus is known only from the early Tiffanian elsewhere. Thus these sites low in the Fort Union Formation from Cedar Mountain probably are Puercan in age (Hartman 1986), but there are not enough data available to refer them to a specific interval zone.

Beginning with a brief description of the mammalian fauna from Bug Creek Anthills and correlatives by Sloan and Van Valen in 1965, the uppermost Hell Creek and the lower Tullock formations in northeastern Montana have yielded many sites referable to the Pu1 interval zone. From the lower Tullock Formation in Garfield County, Archibald (1982) described the Hell's Hollow Local Fauna and a sparse fauna from the McKeever Ranch localities, and he noted the presence of Baioconodon from Morales 1. From McCone County further to the east, Sloan and Van Valen (1965), Lupton et al. (1980), Sloan et al. (1986), Rigby (1989), Fox (1989), Luo (1991), and Lofgren (1995) provided lists or descriptions of taxa from the Bug Creek Anthills locality and nearby correlatives (Bug Creek West, Harbicht Hill, Ferguson Ranch, Chris's Bonebed) from the upper Hell Creek Formation. Also, Lofgren (1995) described a series of mammalian faunas from the upper Hell Creek Formation from the McGuire Creek area just south of Bug Creek, which are referred to here as the McGuire Creek and Z-line local faunas. Lofgren (1995) also provided a list of the small mammalian assemblage from the Jacks Channel Local Fauna, which consists of two sites in the lower Tullock Formation near McGuire Creek. All these sites or local faunas are referred to the Pu1 interval zone based on presence of the multituberculates Stygimys, Catopsalis, Mesodma, Cimexomys, and Acheronodon (Hells Hollow only), the cimolestid Procerberus, the marsupial Peradectes, the ungulates Protungulatum, Baioconodon, Oxyprimus, and Mimatuta, and the primate Purgatorius (occurrence at Harbicht Hill is questionable). The presence of Lancian taxa at some of these sites (i.e., Meniscoessus, Essonodon, Cimolodon, Cimolomys, Alphadon, Turgidodon, Pediomys, Glasbius, Didelphodon, Gypsonictops, Alostera, and Batodon) probably is the result of reworking (Lofgren 1995).

The Littleton Local Fauna from the Denver Formation in central Colorado was described by Middleton (1983) based on specimens collected from South Table Mountain and the Alexander Locality. In this mostly unpublished dissertation, Middleton (1983) described 13 new mammalian species and two new genera (*Auraria* and *Ampliconus*). He also argued based on phyletic relationships that the Littleton Local Fauna is younger than the Mantua Lentil Local Fauna but older than the type Puercan faunas of the San Juan Basin or the faunas that define the Pu2 and Pu3 interval zones. Therefore Archibald et al. (1987) assigned the Littleton Local Fauna to the Pu1 interval zone.

Two sites from southern Saskatchewan are of special interest to discussions of the Cretaceous-Tertiary and Lancian-Puercan boundaries. These localities are Frenchman 1, Frenchman Formation, and Long Fall, Ravenscrag Formation. The sample of mammals from Frenchman 1 is small and contains Protungulatum and mammals previously restricted to Lancian-aged strata (Meniscoessus and Cimolodon) along with the bones and teeth of dinosaurs (Johnston 1980; Fox 1988, 1990c, 1997). The mammalian sample from Long Fall is much larger and yields the ungulates Protungulatum, Oxyprimus, Baioconodon, and Mimatuta, Lancian mammals (Alphadon, Pediomys, Meniscoessus, Cimolomys, Cimolodon, and Gypsonictops), and dinosaurs (Johnston and Fox 1984; Fox 1988, 1990c, 1997). We assign these sites to the Pu1 interval zone based on the presence of Protungulatum (and in the case of Long Fall, the other ungulates as well). Fox (1988, 1990c, 1997) argued that these sites are both Cretaceous and Lancian in age. A Cretaceous age for Frenchman 1 is further supported by a preliminary report based on palynology (Fox 1995). The Frenchman 1 and Long Fall sites may indeed be Cretaceous in age. However, we choose to define the boundaries of biochronologic units based on new appearances of mammals (see Woodburne 1977, 1987 for further discussion). Thus age assignment of assemblages such as Frenchman 1, Long Fall, and Bug Creek Anthills from eastern Montana to a particular interval zone does not require one to first determine whether the Lancian mammal component of the fauna may have been reworked (see Lofgren 1995 for discussion). Also, the first appearance of ungulates in North America signals the advent of a dramatic change in the taxonomic composition of its mammalian faunas. We use that event to define the beginning of the Puercan mammal age (i.e., the first appearance of Protungulatum) whether or not it occurs in the late Cretaceous or early Paleocene. This line of reasoning was first proposed by Archibald and Lofgren (1990) and further advocated by Lofgren (1995), Eberle and Lillegraven (1998a), and Lillegraven and Eberle (1999).

Recently, Eberle and Lillegraven (1998a, 1998b) documented a series of stratigraphically superposed localities containing mammals typical of the Puercan mammal age from the type Ferris Formation in the Hanna Basin of south-central Wyoming. These mammalian fossils allowed a detailed biostratigraphic zonation of the Puercan section of the formation, which is approximately 540 m thick, an order of magnitude thicker than any other known of that age (Eberle and Lillegraven 1998a). Preserved in this thick section are mammalian assemblages that represent all three Puercan interval zones (Pu1 as defined here and Pu2 and Pu3 as defined by Archibald et al. 1987). In the Ferris Formation, Eberle and Lillegraven (1998a, 1998b) used the lowest stratigraphic occurrences of Puercan interval zone FADs Protungulatum (Pu1), Ectoconus (Pu2), and Taeniolabis taoensis (Pu₃) to determine the bases of their three respective Puercan interval zones. As Eberle and Lillegraven (1998a, 1998b) noted, the lowest stratigraphic occurrence of Ectoconus is 77 m above that of Protungulatum, whereas the lowest stratigraphic occurrence of Taeniolabis taoensis is 240 m above that of Ectoconus. No other section in North America has mammalian faunas that represent Puercan interval zones Pu1, Pu2, and Pu3 in direct superposition. Documented differences in mammalian assemblages combined with unequivocal superposition of fossilbearing localities from the Ferris Formation in the Hanna Basin help to confirm the distinctiveness of all three Puercan interval zones (Eberle and Lillegraven 1998a). This issue was a matter of debate concerning the Pu2 and Pu3 interval zones because it was questioned whether one could distinguish these interval zones outside their type areas in the San Juan Basin (Archibald et al. 1987). In addition to Protungulatum, Pu1 interval zone localities of the Ferris Formation have yielded specimens referred to Mesodma, Peradectes, Cimolestes, Oxyprimus, Mimatuta, Maiorana, and Eoconodon.

Of the three states (Montana, Wyoming, Colorado) and one province (Saskatchewan) in which the Pu1 interval zone can be recognized, only local faunas in northern Wyoming (Mantua Lentil) and eastern Montana have been correlated to the Geomagnetic Polarity Time Scale (GPTS). In these areas, Pu1 local faunas lie in a reversed magnetozone that has been correlated to magnetic polarity chron C29r (Archibald et al. 1982; Butler et al. 1987; Swisher et al. 1993). The entire Pu1 interval zone may lie in magnetic polarity chron C29r because the oldest part of the *Ectoconus/Taeniolabis taoensis* Interval Zone (Pu2) in the San Juan Basin is contained in strata of normal polarity that are correlated to magnetic anomaly chron C29n (Butler and Lindsay 1985; Williamson and Lucas 1992). Also, Hunter et al. (1997) suggested that the mammalian assemblage from the Hiatt local fauna (Ludlow Formation, southeastern Montana), which they refer to the Pu2 interval zone, may occur in strata of reversed polarity, which they correlate with magnetic polarity chron C29r. If they are correct, then the entire Pu1 interval zone would indeed lie in chron C29r.

In eastern Montana, Pui local faunas have been correlated to lignites that contain volcanic units suitable for argon–argon dating (Swisher et al. 1993). Data presented by Swisher et al. (1993) indicate that the Pui interval zone was approximately 400,000 years in duration.

- First appearances: Ampliconus, Baioconodon, Catopsalis, Conacodon, Eoconodon, Hemithlaeus?, Mimatuta, Oxyacodon, Oxyclaenus, Peradectes, Procerberus, Protungulatum, Purgatorius?, and Tinuviel?
- Last appearances: Alostera?, Alphadon?, Batodon?, Cimolomys?, Didelphodon?, Essonodon?, Glasbius?, Gypsonictops?, Meniscoessus?, Pediomys?, and Turgidodon?
- Index fossils: Acheronodon, Auraria, Maiorana, and Oxyprimus
- Characteristic fossils: Cimexomys, Cimolestes, Mesodma, and Stygimys
- Taxa absent but known before and after Pui: *Cimolodon?*, *Kimbetohia*, *Neoplagiaulax?*, *Parectypodus*, and *Viridomys?*

Ectoconus/Taeniolabis taoensis Interval Zone (Pu2) We define the *Ectoconus/T. taoensis* Interval Zone to include faunas that occurred between the first appearance of *Ectoconus* and the first appearance of *T. taoensis*.

In 1892, Wortman recognized two faunal zones for Puercan assemblages in what are now called the Dena-zin and Alamo washes (see Osborn and Earle 1895; Sinclair and Granger 1914). These are the lower "Ectoconus zone" (= "Hemithlaeus zone" of Van Valen 1978) and the upper "Taeniolabis zone" (Sinclair and Granger 1914; Matthew 1937). Archibald et al. (1987) used these zones as the basis for the naming and characterization of the Ectoconus/Taeniolabis taoensis (Pu2) and the Taeniolabis taoensis/Periptychus (Pu3) interval zones. However, they did so with caution because faunal differences between the zones were slight and there was concern that the difference between the zones may have resulted more from ecological variation than from significant differences in age (Lindsay et al. 1981; Archibald et al. 1987). There was little doubt that the interval zones were superposed in De-na-zin and Alamo washes and

represented some difference in time, but the absence of the multituberculate Taeniolabis in the other two major collecting areas for the type Puercan fauna, the Kimbetoh and Betonnie-Tsosie arroyos, supported the view that the differences may have been ecological. Also, in strata located along the West Fork of Gallegos Canyon (another collecting area for Puercan mammals northwest of De-na-zin and Alamo washes; locality A in column 1 of figure 3.2), Lucas (1984) described a small assemblage of mammals that included Taeniolabis. However, stratigraphically below the fauna that included Taeniolabis, Lucas (1984) was unable to locate a mammalian assemblage referable to the Ectoconus/Taeniolabis taoensis Interval Zone (Pu2). These data presented Archibald et al. (1987) with a problem regarding the Puercan mammal age: the inability to clearly identify zones within the type Puercan mammal age of the San Juan Basin and then to extend this zonation beyond the limits of that basin. Also, paleomagnetic analysis adds little to differentiation of Pu2 and Pu3 interval zones in the San Juan Basin because both interval zones occur in strata of normal polarity that is correlated with magnetic chron C29n (Lindsay et al. 1981; Butler and Lindsay 1985; Williamson and Lucas 1992). Accordingly, Archibald et al. (1987) defined the Pu2 and Pu3 interval zones with the caveat that revision may be needed and that they should be used provisionally in other parts of the San Juan Basin and western North America.

Reanalysis of the Puercan sites and establishment of a local biostratigraphic zonation in the San Juan Basin (Williamson 1996) and the recent discovery of new Puercan local faunas from the Ferris Formation of Wyoming (Eberle and Lillegraven 1998a, 1998b) provide support for subdividing the middle and late parts of the Puercan mammal age into the Pu2 and Pu3 interval zones. Concerning the possibility that the "Ectoconus zone" or Pu2 interval zone (H-T zone of Williamson 1996) and the "Taeniolabis zone" or Pu3 interval zone (T-P zone of Williamson 1996) represented ecological differences rather than differences in time, Williamson (1996:54) argued that "there is no doubt that the two faunas are superposed and separated by a barren interval of approximately 25 meters in the De-na-zin Wash section" and that 25 m of sedimentation suggests that a significant interval of time elapsed between the deposition of the two faunas. Williamson (1996:54) also stated that "there are no significant facies changes between the two fossiliferous zones and therefore no direct evidence to indicate different environments," data that further support the biochronologic utility of the Pu2 and Pu3 interval zones.

The first record of superposed mammalian faunas referable to the Pu2 and Pu3 interval zones in an area outside the San Juan Basin comes from the type Ferris Formation in the Hanna Basin of Wyoming (Eberle and Lillegraven 1998a, 1998b). Preserved in a 540-m-thick section of the formation are mammalian assemblages indicating that the lowest stratigraphic occurrence of Taeniolabis taoensis is 240 m above the lowest stratigraphic occurrence of *Ectoconus* (similarly, the lowest stratigraphic occurrence of Ectoconus is 77 m above that of Protungulatum; Eberle and Lillegraven 1998a, 1998b). The Hanna Basin is the only area in North America in which all three Puercan interval zones are found in superposition. Thus mammalian faunas from the type Ferris Formation help to confirm the distinctiveness of the Pu2 and Pu3 interval zones outside the San Juan Basin and provide a unique reference section for the entire Puercan mammal age.

In the San Juan Basin, mammalian faunas that form the basis for the definition of the Pu2 interval zone are found in the Arroyo Chijuillita Member of the Nacimiento Formation, located in De-na-zin, Alamo, Kimbeto, and Betonnie-Tsosie washes (Williamson 1996). Based on a list of therian taxa and their biostratigraphic ranges provided by Williamson (1996), it should be noted that the Pu2 mammalian fauna is distinguished from the Pu₃ mammalian fauna primarily by species-level differences in ungulate genera. Three genera (the tillodont Schochia and the ungulates Platymastus and Hemithlaeus) have unique occurrences in the Pu2 interval zone, but Schochia and Platymastus are known only from their holotypes (Williamson 1996) and represent taxa with limited biochronologic utility. Thus detailed taxonomic comparisons of ungulate species are needed before biochronologic correlations to the Pu2 interval zone of the San Juan Basin from elsewhere in North America can be made with confidence.

In the Hanna Basin of Wyoming, 240 m of the Ferris Formation represent strata referred to the Pu2 interval zone by Eberle and Lillegraven (1998a, 1998b). The multituberculates *Ptilodus* and *Ectypodus* and the ungulates *Loxolophus, Mithrandir, Oxyacodon, Conacodon, Ectoconus, Periptychus*, and *Promioclaenus* are genera that appear in Pu2 strata from the Ferris Formation that are typical elsewhere of the Pu2 interval zone. A net result of these introductions is that, compared with the Pu1 interval zone, the Pu2 interval zone is characterized by more than two times more diversity of ungulate genera and by greater body size and dental specialization (Eberle and Lillegraven 1998a).

From the Denver Formation in the Denver Basin of eastern Colorado, Middleton (1983) described the mam-

malian assemblages found at the Corral Bluffs and West Bijou Creek-1 localities. These sparsely fossiliferous sites share some ungulate species in common with the Pu2 and Pu3 interval zones of the San Juan Basin, but the multituberculate *Taeniolabis* has not been recovered from either locality. Therefore Corral Bluffs or West Bijou Creek-1 cannot be assigned to the Pu2 or Pu3 interval zone with confidence.

The North Horn Formation contains the Gas Tank Local Fauna, named by Robison (1986) after the Gas Tank Hill locality (Van Valen 1978; = Flagstaff Peak Locality in Spieker 1960). The Gas Tank Local Fauna is composed of a series of widely separated localities grouped based on general stratigraphic position (distance in meters below the base of the overlying Flagstaff Peak Formation) and faunal similarity (Robison 1986). We suggest caution in grouping these localities and analyzing them as one local fauna because most sites referred to the Gas Tank Hill Local Fauna occur in areas where the strata have been slumped (see Robison 1986). Archibald et al. (1987) tentatively referred the Gas Tank Local Fauna to the Pu2 interval zone because it is lower stratigraphically than the Wagonroad Local Fauna, and the latter fauna contains Taeniolabis (see Gazin 1941; Tomida and Butler 1980). However, Williamson (1996) noted that of the five ungulate species the Gas Tank Local Fauna shares with Puercan faunas in the San Juan Basin, only Loxolophus pentacus shows a range limited to either the Pu2 or Pu3 interval zone, in this case the Pu2 interval zone. Also, Robison (1986) tentatively referred an incisor fragment from the Ferron Mountain Locality of the Gas Tank Local Fauna to cf. Taeniolabis taoensis. If this identification is correct, then at least one locality (Ferron Mountain) of the Gas Tank Local Fauna would be referable to the Pu3 interval zone. Therefore we tentatively follow Archibald et al. (1987) and refer the Gas Tank Local Fauna to the Pu2 interval zone, recognizing that much more work must be done to confirm this correlation.

From the lower part of the Ludlow Formation in southwestern North Dakota, Hunter (1999) reported a sparse mammalian assemblage from the Pita Flats locality. The presence of *Oxyacodon priscilla* at Pita Flats indicates a middle to late Puercan age or referral to the Pu2 or Pu3 interval zone (Hunter 1999).

In southeastern Montana near Glendive, Hunter et al. (1997) described the mammalian assemblage from the Hiatt Local Fauna located in the lower part of the Ludlow Member of the Fort Union Formation. Hunter et al. (1997) argued that the diverse assemblage of archaic ungulates in the Hiatt Local Fauna in conjunction with the absence of *Taeniolabis* suggests that the Hiatt Local Fauna is referable to the Pu2 interval zone. They also suggested that the Hiatt Local Fauna may occur in strata of reversed polarity that they correlated with magnetic polarity chron C29r. Because Pu2 faunas elsewhere are known only from strata of normal polarity correlated with magnetic chron C29n, if the Hiatt Local Fauna is indeed in strata of reversed polarity representing chron C29r, it could not be younger than Pu2.

In addition to the Hiatt Local Fauna, the only other place at which local faunas referred to the Pu2 interval zone have been correlated to the magnetic anomaly correlation scale occur in the San Juan Basin. These local faunas lie in strata of normal polarity correlated with magnetic anomaly chron C29n (Lindsay et al. 1981; Butler and Lindsay 1985; Williamson and Lucas 1992).

- First appearances: Anisonchus, Bubogonia, Carcinodon, Choeroclaenus, Chriacus, Desmatoclaenus, Ectoconus, Ectypodus, Ellipsodon, Eucosmodon, Haploconus, Ictidodopappus?, Litomylus, Loxolophus, Microcosmodon, Mimotricentes, Mithrandir, Onychodectes, Pandemonium, Periptychus, Promioclaenus, Ptilodus, Tiznatzinia, Wortmania, and Xyronomys
- Last appearances: *Alticonus, Ampliconus, Hemithlaeus,* and *Mimatuta*
- Index fossils: Alveugena, Platymastus, and Schochia
- Characteristic fossils: Baioconodon, Catopsalis, Cimexomys, Cimolestes, Conacodon, Eoconodon, Kimbetohia, Mesodma, Neoplagiaulax, Oxyacodon, Oxyclaenus, Parectypodus, Peradectes, Procerberus?, Protungulatum, Purgatorius, Stygimys, and Tinuviel
- Taxa absent but known before and after Pu2: *Cimolodon?* and *Viridomys?*

Taeniolabis taoensis/Periptychus carinidens Interval Zone (Pu3) We define the *T. taoensis/P. carinidens* Interval Zone to include faunas that occurred between the first appearance of *T. taoensis* and the first appearance of *P. carinidens*.

In the San Juan Basin, mammalian assemblages that comprise the type fauna of the Pu₃ interval zone (= T-Pinterval zone of Williamson 1996) are located in the Arroyo Chijuillita Member of the Nacimiento Formation in De-na-zin and Alamo washes and in the West Fork of Gallegos Canyon (Williamson 1996). Based on faunal data presented by Williamson (1996), the Pu₂ and Pu₃ interval zones in the San Juan Basin differ in the following ways. First, the tillodont *Schochia* and the ungulates *Hemithlaeus* and *Platymastus* are not present in Pu₃ faunas; *Hemithlaeus* is common in Pu₂ faunas, but *Platymastus* and *Schochia* are rare. Second, a number of ungulate species that occur in Pu2 did not persist into the Pu3 interval zone. Finally, the ungulates *Loxolophus pentacus, L. priscus,* and *Oxyclaenus antiquus* and the multituberculate *Taeniolabis taoensis* are index taxa for the Pu3 interval zone. Because the Pu2 and Pu3 interval zones are faunally similar, the fact that *Taeniolabis taoensis* is limited to the Pu3 interval zone in the San Juan Basin becomes, by default, a critical factor in assigning middle to late Puercan faunas elsewhere in North America to the Pu2 or Pu3 interval zone. Paleomagnetic correlations in the San Juan Basin offer little assistance in this regard because both the Pu2 and Pu3 interval zones are located in strata of normal polarity correlated to magnetic anomaly chron C29n (Lindsay et al. 1981; Butler and Lindsay 1985; Williamson and Lucas 1992).

The Wagonroad Local Fauna from the North Horn Formation in Utah was first described by Gazin (1941), with additions from Tomida and Butler (1980), Robison (1986), and Cifelli et al. (1995). The Wagonroad Local Fauna is small and shares only three species with Puercan faunas from the San Juan Basin (Williamson 1996), making a firm biochronologic correlation difficult. However, Gazin (1941:8) described a broken first lower molar from the Wagonroad Local Fauna and referred it only to the generic level (Taeniolabis) even though "in size and appearance the specimen closely resembles this portion of the m1 in Taeniolabis taoensis from the Puerco of New Mexico." Therefore, although the Wagonroad Local Fauna may contain Taeniolabis taoensis, better material is needed for confirmation. Paleomagnetic evidence indicates that strata containing the Wagonroad Local Fauna straddle a transition from normal to reversed polarity that is correlated with the transition from magnetic polarity chron C29n to C28r (Tomida and Butler 1980). Based on both biochronologic (presence of Taeniolabis) and paleomagnetic correlations (Pu3 in San Juan Basin is in C29n), we refer the Wagonroad Local Fauna to the Pu₃ interval zone.

In the section of the Ferris Formation assigned to the Pu3 interval zone (more than 200 m thick) based on the lowest stratigraphic occurrence of *Taeniolabis taoensis*, there is not as dramatic a difference in composition of mammalian assemblages between Pu2 and Pu3 as there is between Pu1 and Pu2. Also, the number of ungulate genera remains nearly constant between Pu2 and Pu3 (Eberle and Lillegraven 1998a). It is interesting to note that the only known occurrence of *Protoselene* in the Puercan mammal age is based on a dentary fragment referred to cf. *Protoselene* from the Pu3 interval zone in the Ferris Formation (Eberle and Lillegraven 1998a). As to the importance of the Ferris Formation to Puercan biochronology, we again stress that superposition of localities in the Ferris Formation yielding Pu2 and Pu3 mammalian assemblages strongly supports the reality of discrete Pu2 and Pu3 interval zones. This northward extension of the Pu2 and Pu3 interval zones from the San Juan Basin into southern Wyoming suggests that we may be able to recognize discrete Pu2 and Pu3 interval zones even further north (Canada and Montana), although the significant biogeographic provinciality evident in the late Puercan makes correlations into Canada and Montana very tentative.

Based on a well-preserved taeniolabidid dentary from the Bechtold Site, Ludlow Formation, southeastern Montana, Simmons (1987) described a second species of *Taeniolabis*, *T. lamberti*. The presence of at least one species of *Taeniolabis* distinct from *T. taoensis* outside the San Juan Basin does not necessarily indicate that this or other sites with this species (Garbani Local Fauna, discussed later in this chapter) are correlatives of the Pu₃ interval zone. However, in the absence of well-documented evidence showing that *Taeniolabis* occurs in a fauna referable to an interval zone other than Pu₃, we tentatively refer the Bechtold Site and others sites yielding *Taeniolabis* (see further discussion later in this chapter) to the Pu₃ interval zone.

The Purgatory Hill and Garbani local faunas from the Tullock Formation in northeastern Montana appear to be correlatives of the Pu3 interval zone. The Purgatory Hill Local Fauna was the first Puercan fauna in Montana to be discovered and was briefly described by Van Valen and Sloan (1965) and Van Valen (1978). Sloan (1970) assigned the Purgatory Hill Local Fauna a late Puercan age based in part on the presence of Taeniolabis (fragment of an M2). This specimen was described and referred to Taeniolabis by Simmons (1987). The Garbani channel complex is more fossiliferous than the Purgatory Hill site, and Simmons (1987) described seven isolated teeth of Taeniolabis from the Garbani channel complex, two of which she referred to Taeniolabis lamberti and the other five to Taeniolabis species. Although Clemens (2002) presented an updated list of the mammalian assemblages for both the Garbani and Purgatory Hill local faunas, in reality few taxa in either fauna have been thoroughly described (see Clemens 1974; Novacek 1977; Novacek and Clemens 1977; Archibald et al. 1983; Simmons 1987; Weil 1998), making comparisons to other faunas uncertain. This problem is exacerbated by the reality that a considerable level of biogeographic provinciality exists in the Puercan mammal age, especially between northern and southern faunas (Buckley 1994; Williamson 1996; Eberle and Lillegraven 1998a). Therefore we tentatively assign the Garbani and Purgatory Hill local faunas to the Pu3 interval zone, recognizing that our correlation is based primarily on the

occurrence of *Taeniolabis* in both faunas. In the absence of evidence to the contrary, we speculate that *Taeniolabis* has a biochronologic range limited to that of the Pu3 interval zone of the San Juan Basin. Both the Purgatory Hill and Garbani local faunas occur in strata of normal polarity correlated to magnetic anomaly chron C29n (Archibald et al. 1982; Swisher et al. 1993), which is consistent with a correlation to the Pu2 or Pu3 interval zone of the San Juan Basin.

The Rav W-1 and Croc Pot sites from the Ravenscrag Formation in southern Saskatchewan yield mammalian assemblages similar in composition to the Garbani and Purgatory Hill local faunas of eastern Montana and the Simpson Quarry from south central Montana. The fauna from the Rav W-1 site was described by Johnston (1980) and Johnston and Fox (1984), with updated lists provided by Fox (1990c, 1997). Johnston and Fox (1984) suggested that Rav W-1 is older than or occurs very early in the Hemithlaeus zone (Pu2 interval zone of Archibald et al. 1987), even though a species of Taeniolabis is present. They argued that the species of Taeniolabis from Rav W-1 (based on tooth fragments) and the Garbani Local Fauna (based on isolated teeth) are the same and that this species is more primitive than Taeniolabis taoensis from the type Puercan assemblage of the San Juan Basin. From her detailed analysis of Taeniolabis, Simmons (1987) noted that the ambiguous nature of dental characters and the limited material available for study make it impossible to determine whether Taeniolabis lamberti (Garbani and Bechtold sites), Taeniolabis sp. (Garbani, Purgatory Hill, and Rav W-1), or T. taoensis is more or less derived. Also, based on their interpretation of the stage of evolution of ungulate species, Johnston and Fox (1984) argued that some of the ungulate species at Rav W-1 are less derived than their generic counterparts from the Hemithlaeus zone (Pu2 interval zone) of the San Juan Basin. Later, Fox (1997:77) stated that the Rav W-1 mammals "correlate most closely with mid-Puercan (Pu2) faunas in the US, although species differences make comparisons with standard Puercan sequences of the San Juan Basin, New Mexico difficult." As with the Garbani and Purgatory Hill local faunas, correlation is limited by faunal provinciality, but we tentatively assign the Rav W-1 fauna to the Pu3 interval zone based on the presence of Taeniolabis. The mammalian fauna from the Croc Pot site is small and undescribed, but faunal lists provided by Fox (1990c, 1997) indicate that the site yields Taeniolabis taoensis, and its overall mammalian assemblage is similar to that of Rav W-1. Therefore we assign Croc Pot to the Pu3 interval zone. Magnetostratigraphic data are not available for the Rav W-1 and Croc Pot sites.

In a mostly unpublished dissertation, Buckley (1994) described a large mammalian assemblage from Simpson Quarry, located in the Bear Formation in the Crazy Mountains Basin of south-central Montana. The fauna from Simpson Quarry is most similar to that from Rav W-1 in Canada, but Simpson Quarry has not yielded Taeniolabis (see Buckley 1994). Taxonomic composition of the mammalian assemblage from Simpson Quarry also has close affinities to local faunas from Purgatory Hill and Garbani Quarry in Montana and the Croc Pot site in Canada. Taken together, these four sites or local faunas form a biogeographic province that differs from southern sites in the San Juan Basin and Utah (Buckley 1994). Because of the absence of Taeniolabis and the level of biogeographic provincialism between northern and southern middle-late Puercan faunas, we assign Simpson Quarry to an undifferentiated Pu2-Pu3 interval zone. Magnetostratigraphic analysis indicates that Simpson Quarry lies in strata of normal polarity correlated to magnetic anomaly chron C29n (Buckley 1994), which is consistent with a Pu2 or Pu3 interval zone assignment.

The Big Bend area of Texas may yield mammalian assemblages that are Puercan in age, but correlations are uncertain. In a mostly unpublished dissertation, Standhardt (1986) described small faunas from the Dogie, Glenn Eleven, and Tom's Top sites, located in the Javelina Member of the Tornillo Formation, and assigned them to the Puercan mammal age. The Javelina and Blacks Peak formations were reduced to member status in the Tornillo Formation by Schiebout et al. (1987). The taxa listed for each site by Standhardt (1986) show affinities to both the Puercan and Torrejonian mammal ages (Williamson 1996). Also, small sample sizes and fragmentary material make some identifications tenuous (see Williamson 1996). The three sites may be Puercan or Torrejonian. Tom's Top occurs in strata of reversed polarity that are tentatively correlated to magnetic polarity chron C28r (Standhardt 1986; Schiebout et al. 1987), which would support a late Puercan or early Torrejonian age for the site.

Magnetostratigraphic analysis of the Pu₃ interval zone in the San Juan Basin indicates that the Pu₃ interval zone occurs in strata of normal polarity interpreted as magnetic polarity chron C₂₉n. Because the Pu₂ interval zone also occurs in rocks of normal polarity correlated to magnetic polarity chron C₂₉n, magnetostratigraphic analysis offers no support for differentiating the Pu₂ and Pu₃ interval zones.

First appearances: Goniacodon, Haplaletes, Leptacodon?, Litaletes, Palaeictops, Prodiacodon, and Protoselene? Last appearances: Baioconodon, Bubogonia, Carcinodon, Choeroclaenus, Cimexomys, Cimolestes, Cimolodon?, Ectoconus, Eoconodon, Kimbetohia, Mithrandir, Onychodectes, Oxyacodon, Pandemonium, Procerberus, Protungulatum, Purgatorius, Tinuviel, Tiznatzinia, and Wortmania

Index fossils: Ravenictis and Taeniolabis

- Characteristic fossils: Anisonchus, Catopsalis, Chriacus, Conacodon, Desmatoclaenus, Ellipsodon, Eucosmodon, Haploconus, Loxolophus, Mesodma, Microcosmodon, Mimotricentes, Neoplagiaulax, Oxyclaenus, Parectypodus, Peradectes, Periptychus, Promioclaenus, and Stygimys
- Taxa absent but known before and after Pu3: *Ectypodus*, *Ictidopappus*?, *Litomylus*, *Ptilodus*, *Viridomys*?, and *Xyronomys*

TORREJONIAN MAMMAL AGE

Initially, the Torrejonian mammal age included only the *Pantolambda* zone of Osborn and Matthew (1909). Later, however, Sinclair and Granger (1914) recognized two faunal zones, a lower *Deltatherium* and an upper *Pantolambda* zone. The zones were questioned by Matthew (1937) and others, mainly because neither *Deltatherium* nor *Pantolambda* was abundant enough to warrant much confidence in their stratigraphic range.

Wood et al. (1941) defined the Puercan and Torrejonian NALMAs based on fossils from the "Puerco" and "Torrejon" formations in the San Juan Basin. Later, Simpson (1959) reported the presence of fossils of Torrejonian age from the type section of the Puerco Formation. Because the formations apparently were defined on flawed paleontologic and not lithologic criteria, the "Puerco" and "Torrejon" formations were abandoned and replaced by a redefined Nacimiento Formation (see Gardner 1910; Simpson 1959). But the concept of using the Puercan and Torrejonian faunas (within the redefined Nacimiento Formation) as reference assemblages for biochronologic units for part of the Puercan and Torrejonian mammal ages was retained (Archibald et al. 1987).

The concept of the Torrejonian mammal age has been substantially modified since Wood et al. (1941) with the inclusion of the Dragonian mammal age by Archibald et al. (1987). Wood et al. (1941) defined a Dragonian mammal age between the Puercan and Torrejonian mammal ages, based on the Dragon Local Fauna from the North Horn Formation of Utah. Because it was convincingly demonstrated that a Dragonian faunal correlative is present in the San Juan Basin (Tomida and Butler 1980; Tomida 1981), Archibald et al. (1987) recognized the tem-

poral equivalent to the Dragonian mammal age as the first interval zone in a redefined Torrejonian mammal age. Recent work in the Nacimiento and North Horn formations lends further support for inclusion of the Dragonian in the Torrejonian mammal age (see Williamson 1996; Lucas et al. 1997). Also, Williamson (1996:61) contends "that Gazin (1938, 1939, 1941), convinced of the intermediate age of the Dragonian fauna between known Puercan and Torrejonian faunas, was led to give taxonomic significance to any small difference in morphology." Therefore detailed reanalysis of the Dragon Local Fauna may result in synonymy of many species described by Gazin (1938, 1939, 1941) with those from other Puercan and Torrejonian sites (Williamson 1996). As a first step, a revised faunal list for the Dragon Local Fauna was provisionally provided by Williamson (1996, table 12), pending thorough revision.

Wood et al. (1941) recognized two correlatives of the Torrejonian mammal age: the "Lebo" and "Rock Bench." No correlatives were listed for the Dragonian mammal age. "Lebo" refers to the Lebo Member of the Fort Union Formation in Simpson's (1935a, 1937b) Crazy Mountain Field, Montana. (In present usage in the Crazy Mountains area, Lebo is elevated to formation status and Fort Union to group status.) Simpson's (1937b) "Lebo" is now considered to include both Torrejonian and Tiffanian local faunas. "Rock Bench" refers to the Rock Bench Quarry from the Fort Union Formation in the Bighorn Basin of Wyoming, a large quarry sample of Torrejonian age.

Archibald et al. (1987) listed the following as correlatives of the Torrejonian mammal age: Farrand Channel Local Fauna, Tullock Formation, northeastern Montana (Archibald 1982); Goler Formation, California (McKenna 1960; West 1976), now considered Tiffanian (McKenna and Lofgren in press); Porcupine Hills Formation, Alberta (Russell 1958; Krause 1978); and Fort Union Formation of Washakie Basin, Wyoming (Rigby 1980). Since publication of Archibald et al. (1987), a significant number of new Torrejonian localities or additions to existing localities have been reported from the Nacimiento Formation of New Mexico (Williamson 1996), Tornillo Formation of Texas (Standhardt 1986), North Horn Formation of Utah (Robison 1986), Hanna Formation of Wyoming (Secord 1998; Higgins 2000), Fort Union Formation of Wyoming (Hartman 1986; Leite 1992), Fort Union Group of the Crazy Mountains area of southcentral Montana (Hartman and Krause 1993; Buckley 1994), Fort Union Formation of the Clark's Fork area of south-central Montana (Butler et al. 1987), Fort Union Formation of southeast Montana (Hunter et al. 1997),

Ludlow Formation of North Dakota (Hunter 1999), and Coalspur Formation of Alberta, Canada (Fox 1990c).

PUERCAN-TORREJONIAN BOUNDARY

The beginning of the Torrejonian mammal age is recognized by appearance of the periptychid Periptychus carinidens. P. carinidens is a distinctive member of Torrejonian faunas, including the Dragon Local Fauna of Utah (see Williamson 1996 for discussion of synonymy of P. carinidens and Periptychus gilmorei) on which the Dragonian mammal age was based (Wood et al. 1941). Tomida and Butler (1980) established a magnetic polarity sequence in the North Horn Formation that indicated that the Dragon Local Fauna occurred in strata that span magnetic chron C28n and C27r. Also, Tomida (1981) described a small fauna from the San Juan Basin correlated to the upper part of magnetic chron C28n and base of chron C27r that yielded typical Torrejonian mammals. Because it was well documented that the Dragonian interval occurred in the San Juan Basin and yielded a Torrejonian mammalian assemblage (Tomida and Butler 1980; Tomida 1981), the Dragonian mammal age was assigned to the Torrejonian mammal age as the To1 interval zone (Archibald et al. 1987).

De-na-zin Wash is the only known area in the San Juan Basin in which the Pu2, Pu3, and To1 interval zones are in direct superposition (Williamson 1996). In De-na-zin Wash, P. carinidens is present 52.5 m above the Pu3 interval zone (see Section J in Williamson 1996). Sites correlated to the To1 interval zone also overlie Pu2 interval zone sites (by more than 70 m) in both Kimbeto and Betonnie-Tsosie washes (Lindsay et al. 1981; Williamson 1996). The highest stratigraphic records of Puercan mammals from the San Juan Basin occur in strata with normal polarity, interpreted as magnetic polarity chron C29n. The lowest records of *P. carinidens* in the San Juan Basin occur in the next higher normal polarity magnetozone, interpreted as magnetic polarity chron C28n. Therefore, a stratigraphic interval of more than 50 m, which entirely spans the duration of magnetic polarity chron C28r, separates Puercan and Torrejonian assemblages in the San Juan Basin.

DEFINITION AND CHARACTERIZATION

We follow Archibald et al. (1987) by defining the Torrejonian mammal age to include faunas that occur during the time between the first appearance of the periptychid condylarth *P. carinidens* and the first appearance of the plesiadapid primate *Plesiadapis*.

As mentioned previously, Tomida and Butler (1980) demonstrated that strata of the North Horn Formation yielding the Dragon Local Fauna, type fauna for Dragonian mammal age, correlate with a stratigraphic level in the San Juan Basin containing typical Torrejonian mammals (Tomida 1981). Tomida (1981) also showed that the Dragonian level in the San Juan Basin is faunally distinct and designated this interval as the Periptychus-Loxolophus chronozone. As discussed later in this chapter, our Periptychus carinidens/Protoselene opisthacus Interval Zone (To1) is equivalent to the Dragonian mammal age, Tomida's Periptychus-Loxolophus chronozone, and the To1 interval zone of Archibald et al. (1987), except for tentative inclusion of American Museum of Natural History (AMNH) locality 230 of Mesa de Cuba in our To1 interval zone.

There have been changes in the taxonomic characterization of the Torrejonian mammal age (in addition to inclusion of Dragonian mammal age) since publication of Wood et al. (1941). Of the taxa listed by Wood et al. (1941) as first appearances for the Torrejonian mammal age (including Dragonian), five are now known from the Puercan (*Periptychus, Catopsalis, Haploconus, Ptilodus,* and *Chriacus*), and *Didymictis* is now known to first occur in the Tiffanian mammal age. Similarly, in last appearances the only change is the probable occurrence of *Eucosmodon* in the Tiffanian mammal age. The index and characteristic fossils for the Torrejonian mammal age of Wood et al. (1941) have remained unchanged.

Based especially on the Kutz Canyon section in the San Juan Basin, Torrejonian faunas appear in rocks of normal polarity (interpreted as magnetic polarity chron C28n), continue upward in strata of reversed polarity, and are last known in superjacent layers of normal polarity (interpreted as magnetic polarity chron C27n by Lindsay et al. 1981; Butler and Lindsay 1985; Williamson and Lucas 1992; Williamson 1996). This is supported by new paleomagnetic data from the Tornillo Formation of Texas (Standhardt 1986; Schiebout et al. 1987); Fort Union Group, Crazy Mountains, and Fort Union Formation, Clark's Fork Basin, both south-central Montana (Butler et al. 1987; Buckley 1994); and Tullock Formation, eastern Montana (Swisher et al. 1993).

The faunal characterization of the Torrejonian mammal age is as follows.

First appearances: Acmeodon, Adunator, Anconodon, Aphronorus, Baiotomeus, Claenodon, Colpoclaenus, Coriphagus, Diacodon?, Dissacus, Elphidotarsius, Elpidophorus, Eudaemonema, Gelastops, Ignacius, Jepsenella, Krauseia, Litocherus, Mimetodon, Myrmecoboides, Neoclaenodon, Palaechthon, Palaeoryctes, Palenochtha, Paleotomus, Pantolambda, Pararyctes, Paromomys, Pentacodon, Phenacodus, Picrodus, Plesiolestes, Pronothodectes, Propalaeosinopa, Prothryptacodon, Protictis, Psittacotherium, Simpsonictis, Stilpnodon, Tetraclaenodon, and Unuchinia

- Last appearances: Ellipsodon, Goniacodon, Haploconus, Ictidopappus, Loxolophus, Oxyclaenus, Stygimys, Viridomys?, and Xyronomys
- Index fossils: Anasazia, Ankalagon, Avunculus, Conoryctella, Conoryctes, Deltatherium, Deuterogonodon, Draconodus, Dracontolestes, Escavadodon, Huerfanodon, Leptonysson, Microclaenodon, Mioclaenus, Mixodectes, Oxytomodon, Premnoides, Stelocyon, Swaindelphys, Triisodon, and Xanoclomys
- Characteristic fossils: Anisonchus, Catopsalis, Chriacus, Desmatoclaenus, Ectypodus, Eucosmodon, Haplaletes, Leptacodon, Litaletes, Litomylus, Mesodma, Mimotricentes, Neoplagiaulax, Palaeictops, Parectypodus, Peradectes, Periptychus, Prodiacodon, Promioclaenus, Protoselene, and Ptilodus
- Taxa absent but known before and after the Torrejonian: *Conacodon*? and *Microcosmodon*

ZONATION

Archibald et al. (1987) proposed three Torrejonian interval zones: the *Periptychus carinidens/Tetraclaenodon* Interval Zone (To1), the *Tetraclaenodon/Pantolambda* Interval Zone (To2), and the *Pantolambda/Plesiadapis praecursor* Interval Zone (To3). Their To1 interval zone was equivalent to both the *Periptychus–Loxolophus* chronozone of Tomida (1981) and the Dragonian mammal age of Wood et al. (1941). Their To2 interval zone was approximately equivalent to the *Deltatherium* zone of Osborn (1929) and the *Deltatherium* chronozone of Tomida (1981). Finally, their To3 interval zone was approximately equivalent to the *Pantolambda* zone of Osborn (1929) and the *Pantolambda* chronozone of Tomida (1981).

Recent collecting efforts in the San Juan Basin have resulted in downward extension of the stratigraphic ranges of *Tetraclaenodon* and *Pantolambda* (see Williamson 1996). *Tetraclaenodon* is now known from low in the section at Kutz Canyon from a horizon correlated to the Dragon Canyon Local Fauna, the type fauna for the Toi interval zone (Williamson 1996). A specimen of *Pantolambda* has been found low in the Kutz Canyon section approximately equivalent to a horizon that previously recorded the lowest stratigraphic occurrence of *Tetraclaenodon* (see Williamson 1996). Therefore, if *Tetraclaenodon* and *Pantolambda* were retained as defining taxa for the To₂ and To₃ interval zones in the San Juan Basin, the To₃ interval zone would include all localities formerly in To₂, and the To₂ interval zone would include a significant part of To₁.

Rather than expand the concepts of the Tetraclaenodon/Pantolambda Interval Zone (To2) and the Pantolambda/P. praecursor Interval Zone (To3), we redefine the interval zones for the Torrejonian mammal age. The Periptychus carinidens/Tetraclaenodon Interval Zone is renamed the P. carinidens/Protoselene opisthacus Interval Zone (To1), the Tetraclaenodon/Pantolambda Interval Zone is redefined as the Protoselene opisthacus/ Mixodectes pungens Interval Zone (To2), and the Pantolambda/P. praecursor Interval Zone is redefined as the M. pungens/P. praecursor Interval Zone (To3). In relation to the local zonation proposed for the San Juan Basin by Williamson (1996, figures 18 and 19), the To1, To2, and To3 interval zones correlate as follows: To1 is equal to Williamson's P–P zone (= Dragonian mammal age); To2 is equal to his combined P-E, E-A, A-P, and P-M zones (approximately equivalent to Deltatherium zone); and To₃ is equal to the M zone (= Pantolambda zone).

It is important to point out that *Protoselene opisthacus* and *M. pungens*, although common in the San Juan Basin at their defining horizons, are not ideal species to use for defining the To2 and To3 interval zones because their known geographic ranges are limited. However, we could not identify a more appropriate choice because taxa that are simultaneously common and geographically wide-spread are not available. Therefore the To2 and To3 interval zones may be difficult to distinguish outside the San Juan Basin based only on faunal correlations. Magnetostratigraphy appears to be helpful in correlating to the To2 and To3 interval zone is almost entirely within magnetic polarity chron C27r, and the To3 interval zone is almost entirely within magnetic polarity chron C970 (Williamson 1996).

In the San Juan Basin, the To1 interval zone is present in De-na-zin, Betonnie–Tsosie, and Kimbeto washes, Kutz Canyon (as "main body" of Nacimiento Formation) and perhaps Mesa de Cuba, from the Arroyo Chijullita Member of the Nacimiento Formation (Williamson 1996). Similarly, the To2 interval zone is present in Kutz and Gallegos canyons, the Betonnie–Tsosie, Kimbeto, Escavada, and Torrejon washes, and Mesa de Cuba–Mesa Portales from the Ojo Encino Member of the Nacimiento Formation (except for Kutz Canyon and Mesa de Cuba). The To3 interval zone is present in Torrejon and Escavada washes and Mesa Chijuilla, all from the Ojo Encino Member of the Nacimiento Formation (Williamson 1996). The appearance of *Plesiadapis praecursor* establishes the upper limit of the To3 interval zone and the beginning of the Tiffanian mammal age. Gingerich et al. (1983) noted the appearance of *Microcosmodon, Carpodaptes, Nannodectes, Ectocion,* and *Phenacodus* as well as *Plesiadapis* at the beginning of the Tiffanian. *Microcosmodon* has since been reported from the Puercan mammal age (Johnston and Fox 1984; Weil 1998), and *Phenacodus* is present in the Hanna Basin in strata interpreted to represent late phases of the Torrejonian mammal age (Higgins 2000). It is important to note that neither *Plesiadapis* nor a mammalian assemblage of early Tiffanian age is known from the Nacimiento Formation in the San Juan Basin. Consequently, the top of the To3 interval zone cannot be identified in the San Juan Basin.

Periptychus carinidens/Protoselene opisthacus Interval

Zone (To1) We define this interval zone to include faunas that occurred between the first appearance of *P. carinidens* and the first appearance of *P. opisthacus*. The Dragon Local Fauna of Utah has the best faunal representation of the To1 interval zone. It was described by Gazin (1938, 1939, 1941), with notable additions and revisions by Wilson (1956), MacIntyre (1966), Szalay (1969), West (1976), Tomida and Butler (1980), Robison (1986), Cifelli et al. (1995), and Williamson (1996). A revised faunal list and discussion were presented by Williamson (1996).

In addition to the Dragon Local Fauna, the To1 interval zone is documented in strata of the Nacimiento Formation of the San Juan Basin (Tomida 1981; Williamson 1996; Lucas et al. 1997), the Tullock Formation of eastern Montana (Archibald 1982; Clemens, pers. obs., 2000), and the Lebo Formation of south-central Montana (Hartman and Krause 1993, table 2).

A small and undescribed mammalian assemblage from the Farrand Channel (Mosquito Gulch Local Fauna) in the Tullock Formation of Montana contains Paromomys (Clemens, pers. obs., 2000), a distinctive Torrejonian to early Tiffanian taxon. Separated by approximately 25 m of strata, the Farrand Channel overlies the Garbani Channel, which yielded the Garbani Local Fauna, the mammalian assemblage we tentatively correlate to the Pu3 interval zone. Strata that contain the Farrand Channel are of reversed polarity, correlated with magnetic anomaly chron C28r (Swisher et al. 1993). The Farrand Channel is also bracketed by lignitic beds that bear volcanic crystal-rich partings suitable for dating. Two dated units (64.11 Ma below the channel, 63.90 Ma above) constrain the age of the channel filling (Swisher et al. 1993). These dates are consistent with correlation to magnetic anomaly chron C28r. Thus the Farrand Channel may be the

oldest known Torrejonian fauna in North America; Toi interval zone faunas in the Nacimiento and North Horn formations occur in strata correlated to magnetic anomaly chron C28n or the base of C27r (Tomida and Butler 1980; Lindsay et al. 1981; Butler and Lindsay 1985; Williamson and Lucas 1992; Williamson 1996).

From the lower part of the Lebo Formation in the Crazy Mountains Basin of south-central Montana are Simpson's (1937b) localities 9, 65, and 78. These sites have not been collected extensively, but they could be temporal equivalents of the Dragon Local Fauna (Sloan 1987).

From the Lebo Member of the Fort Union Formation in southeastern Montana is a sparse mammalian assemblage called the School Well Local Fauna that contains *Ptilodus, Litaletes, Periptychus,* and *Paromomys* (Hunter et al. 1997). The School Well Local Fauna probably is Torrejonian in age, but not enough information is available to firmly place it in a particular interval zone.

The To1 interval zone is not very fossiliferous in the San Juan Basin (Williamson 1996). As noted earlier, mammals assigned to the To1 interval zone have been found at sites superposed over localities yielding Puercan faunas in the De-na-zin, Kimbeto, and Betonnie-Tsosie washes (Lindsay et al. 1981; Tomida 1981; Williamson 1996). However, those Puercan and Torrejonian assemblages are separated by a wide stratigraphic interval. In Kutz Canyon and Mesa de Cuba, faunas of the To1 interval zone also are present, but they are not underlain by known Puercan sites. However, they are overlain by faunas referable to the To2 interval zone (Williamson 1996). Where sampling has been done, sites representing the To1 interval zone in the San Juan Basin occur in strata with normal polarity (Tomida 1981), interpreted as magnetic polarity chron C28n (Williamson and Lucas 1992; Williamson 1996). Combined with paleomagnetic correlations described previously from Montana and Utah, the To interval zone is interpreted to correlate with part of magnetic polarity chron C28r, the entirety of magnetic polarity chron C28n, and the lowermost part of magnetic polarity chron C27r (Tomida and Butler 1980; Butler and Lindsay 1985; Williamson and Lucas 1992; Swisher et al. 1993; Williamson 1996).

First appearances: Acmeodon, Aphronorus, Conoryctella, Mioclaenus, Palaechthon, Paromomys, Plesiolestes, Protictis, Tetraclaenodon, and Triisodon

- Last appearances: Oxyclaenus and Viridomys?
- Index fossils: Draconodus, Dracontolestes, and Oxytomodon
- Characteristic fossils: Anisonchus, Catopsalis, Chriacus, Desmatoclaenus, Eucosmodon, Goniacodon, Haplo-

conus, Litaletes, Litomylus, Loxolophus, Mimotricentes, Parectypodus, Periptychus, Promioclaenus, Protoselene, and Ptilodus

Taxa absent but known before and after To1: Conacodon?, Ectypodus, Ellipsodon, Haplaletes, Ictidopappus?, Leptacodon?, Mesodma, Microcosmodon, Neoplagiaulax, Palaeictops, Peradectes, Prodiacodon, Stygimys, and Xyronomys

Protoselene opisthacus/Mixodectes pungens Interval Zone (To2) We define this interval zone to include faunas that occurred between the first appearance of P. opisthacus and the first appearance of M. pungens. In the San Juan Basin, the To2 interval zone is better represented in abundance of fossils and localities than the To1 interval zone. The To2 interval zone as defined here includes, in ascending stratigraphic order, the P-E, E-A, A-P, and P-M biostratigraphic zones of Williamson (1996). Inclusion of the uppermost of these local San Juan Basin zones (i.e., the P-M zone) in the To2 interval zone is a departure from Archibald et al. (1987). They included this local zone in the To3 interval zone. As a result of this change, sites from the head of Kimbeto Wash (including AMNH locality 8 and Kansas University [KU] locality 9, "Little Pocket") and the south end of Kutz Canyon (including AMNH 1482 and 2658 and University of Arizona Laboratory of Paleontology [UALP] 7650) are now assigned to the To2 interval zone. The To3 interval zone thus becomes limited to the stratigraphic interval equivalent to the Pantolambda zone of Osborn (1929), including the richly fossiliferous Tsentas Microsite (New Mexico Museum of Natural History [NMMNH] locality L-312). Also, some sites previously assigned to the To3 interval zone are now correlated with the redefined To2 interval zone (discussed later in this chapter).

The To2 interval zone is well represented in Kutz Canyon, San Juan Basin, New Mexico (Williamson 1996). In Kutz Canyon this interval zone is superposed on the To1 interval zone. The To2 interval zone is overlain by the To3 interval zone in Torrejon and Escavada washes (Williamson 1996). Based on paleomagnetic correlations (Williamson 1996, figure 9), the To2 interval zone correlates closely with nearly the entire span of magnetic polarity chron C27r. This is important to note because the redefined To3 interval zone in the San Juan Basin correlates with nearly the entire span of magnetic polarity chron C27n.

Other diverse and well-known local faunas in the To2 interval zone are those from Gidley and Silberling quarries (Simpson 1937b; Rose 1981a) in the Crazy Mountains Basin, Montana; Rock Bench Quarry (Jepsen 1930, 1940; Rose 1981a) in the Bighorn Basin, Wyoming; and Swain Quarry (Rigby 1980) in the Washakie Basin, Wyoming. Williamson (1996) tentatively correlated the mammalian assemblages from the Swain, Gidley, and Rock Bench quarries to his P-M zone in the San Juan Basin. As indicated previously, we recognize Williamson's (1996) P-M zone as the highest stratigraphic interval in the San Juan Basin that is within the redefined To2 interval zone. Thus we tentatively assign the Gidley, Silberling, Rock Bench, and Swain guarries to the To2 interval zone (faunas from Gidley and Silberling quarries are similar; see Simpson 1937b and Rose 1981a). Rock Bench and Silberling quarries both occur in strata of reversed polarity correlated to magnetic polarity chron C27r (Butler et al. 1987). This is consistent with paleomagnetic results from the San Juan Basin in that faunas assigned to the To2 interval zone there occur in rocks of reversed polarity, also correlated to magnetic anomaly chron C27r (Williamson and Lucas 1992; Williamson 1996).

Rigby (1980) indicated the presence, based on isolated teeth, of the hyaenodontid *Prolimnocyon* in the mammalian sample from the Swain Quarry. This occurrence would greatly extend the first record of North American hyaenodontids from the Wasatchian into the Torrejonian mammal age. Pending further documentation, we omit this questionable record from our To2 fauna list.

Hunter (1999) reported the presence of two identifiable taxa (the taeniodont *Conoryctella* and the mesonychid *Dissacus*) from the Brown Ranch localities in the upper part of the Ludlow Formation of North Dakota. The co-occurrence of these taxa indicates that the Brown Ranch localities probably are referable to the To2 interval zone.

The Black Peaks Member of the Tornillo Formation of Texas yielded a small mammalian fauna at locality Texas Memorial Museum (TMM) 40147 (The Middle Peak– Alligator Alley) that shows strong Torrejonian affinities (Standhardt 1986; Williamson 1996). Paleomagnetic analysis of strata containing TMM 40147 indicates that the locality occurs in rocks that probably are of reversed polarity (Rapp et al. 1983; Standhardt 1986). If so, this might indicate a correlation with magnetic polarity chron C27r. Therefore we tentatively correlate TMM 40147 to the To2 interval zone.

A summary of magnetostratigraphic data for the To2 interval zone based mainly on analysis of the Nacimiento Formation in the San Juan Basin (see Williamson 1996 for summary), with additions by Butler et al. (1987) from Wyoming and Montana, indicates that the To2 interval zone occurs in reversely magnetized strata correlated with magnetic polarity chron C27r.

- First appearances: Adunator, Anconodon, Ankalagon, Avunculus, Claenodon, Colpoclaenus?, Conoryctes, Coriphagus, Deuterogonodon, Diacodon?, Dissacus, Elphidotarsius, Eudaemonema, Gelastops, Ignacius, Jepsenella, Microclaenodon, Mixodectes, Myrmecoboides, Palaeoryctes, Palenochtha, Paleotomus, Pantolambda, Pentacodon, Picrodus, Pronothodectes, Propalaeosinopa, Prothryptacodon, Psittacotherium, Simpsonictis, Stilpnodon, and Unuchinia
- Last appearances: Conoryctella, Ellipsodon, Ictidopappus, Stygimys, Triisodon, and Xyronomys
- Index fossils: *Deltatherium*, *Huerfanodon*, *Leptonysson*, and *Xanoclomys*
- Characteristic fossils: Acmeodon, Anisonchus, Aphronorus, Catopsalis, Chriacus, Ectypodus, Eucosmodon, Goniacodon, Haplaletes, Haploconus, Leptacodon?, Litaletes, Litomylus, Loxolophus, Mesodma?, Mimotricentes, Mioclaenus, Neoplagiaulax, Palaechthon, Palaeictops, Parectypodus, Paromomys, Peradectes, Periptychus, Plesiolestes, Prodiacodon, Promioclaenus, Protictis, Protoselene, Ptilodus, and Tetraclaenodon
- Taxa absent but known before and after To2: *Conacodon?*, *Desmatoclaenus* and *Microcosmodon*

Mixodectes pungens/Plesiadapis praecursor Interval Zone (To3) We define this interval zone to include faunas that occurred between the first appearance of *M. pungens* and the first appearance of *P. praecursor*.

The To₃ interval zone is found only in the eastern part of the San Juan Basin from the Ojo Encino Member of the Nacimiento Formation in Escavada and Torrejon washes and at Mesa Chijuilla, but these areas are richly fossiliferous. The best representation of To₃ faunas actually is from the type Torrejonian at the head of Torreon Wash. This area was collected in the 1890s by J. Wortman and W. Granger for the American Museum of Natural History (= AMNH locality 10). Many other institutions have collected from these strata over the last hundred years. Tsentas (1981) reported a productive screenwashing site from the To₃ interval zone in the type area that subsequently yielded small mammals not previously recorded from this interval zone (Williamson 1996, table 2).

Two faunas from Alberta that might belong in the To3 interval zone are the Calgary 2E Local Fauna (L. Russell 1958; D. Russell 1967; Krause 1978; Fox 1990c) from the Porcupine Hills Formation and the Diss Local Fauna from the Coalspur Formation (Fox 1990c). The small mammal fauna from the Calgary 2E Local Fauna includes *Tetraclaenodon, Claenodon, Proticitis, Pronothodectes,* and the multituberculates *Baiotomeus, Neoplagiaulax,* Anconodon, Euscosmodon, and Catopsalis (see Fox 1990c). The Diss Local Fauna is also small and includes *Pararyctes, Propalaeosinopa, Aphronorus, Colpoclaenus, Promioclaenus, Simpsonictis, Palaechthon,* and the multituberculates *Ptilodus, Baiotomeus, Mimetodon, Parectypodus,* and *Neoplagiaulax* (see Fox 1990c). The presence of *Baiotomeus* in both local faunas and *Pararyctes* in the Diss Local Fauna suggests an early Tiffanian age. However, most taxa in these two local faunas have strong Torrejonian affinities. We tentatively suggest an assignment of the Diss and Calgary 2E local faunas to the To3 interval zone.

A series of localities near Cub Creek in the Clark's Fork Basin of south-central Montana shows superposition of early Tiffanian (Ti1) over late Torrejonian (To3) sites in a measured section that has undergone magnetostratigraphic analysis (Butler et al. 1987). Here, a site (Cub Creek 2) referable to the To3 interval zone occurs in strata of normal polarity and is overlain by strata containing sites (Cub Creek 1, Cub Creek 3, Eagle Quarry) in rocks of reversed polarity that yield early Tiffanian mammals. Thus Cub Creek 2 is correlated with magnetic polarity chron C27n and the other three sites with magnetic polarity chron C26r (Butler et al. 1987). Until recently, this was the only section in North America known to have early Tiffanian faunas in superposition above a late Torrejonian site. However, biostratigraphic analysis of sections spanning the Torrejonian-Tiffanian boundary in the Bighorn and Hanna basins of Wyoming by Hartman (1986) and Higgins (2000), respectively, allow further refinement of this important biochronologic boundary (see "Torrejonian-Tiffanian Boundary" later in this chapter for further discussion).

Other sites containing faunas that might be referable to the To₃ interval zone are the Medicine Rocks 1–Mehling Site in southeastern Montana, Donnybrook and the Lloyd and Hares sites in North Dakota, and a series of localities in the Washakie Basin, Wyoming (Winterfeld 1982).

In general, the To3 interval zone is dominated by *Ptilodus, Mimotricentes,* and *Promioclaenus.* Primates, especially *Palaechthon* and *Paromomys,* may be dominant in northern faunas, whereas *Tetraclaenodon, Periptychus,* and *Mixodectes* may be dominant in southern faunas. Plesiadapid and carpolestid primates show strong affinity for northern latitudes. In contrast, the mixodectids are more common in southern latitudes in the time represented by the To3 interval zone (Archibald et al. 1987).

It has not been possible to identify a biochronologic basis or magnetostratigraphic limit for the Torrejonian–Tiffanian boundary in the San Juan Basin; definitive Tiffanian taxa such as *Plesiadapis* have not been recovered from the Nacimiento Formation. Therefore the top of the To₃ interval zone in the San Juan Basin remains biochronologically unconstrained.

A summary of magnetostratigraphic data for the To3 interval zone, based largely on work in the San Juan Basin (see Williamson 1996), shows that the To3 interval zone occurs in normally magnetized strata correlated with magnetic polarity chron C27n.

- First appearances: Baiotomeus, Elpidophorus, Krauseia, Litocherus, Mimetodon, Neoclaenodon, Pararyctes, and Phenacodus
- Last appearances: Ankalagon, Avunculus, Conoryctes, Deuterogonodon, Goniacodon, Haploconus, Loxolophus, Microclaenodon, Mioclaenus, and Mixodectes
- Index fossils: Anasazia, Escavadodon, Premnoides, Stelocyon, and Swaindelphys
- Characteristic fossils: Acmeodon, Adunator, Anconodon, Anisonchus, Aphronorus, Catopsalis, Chriacus, Claenodon, Colpoclaenus, Coriphagus, Diacodon?, Dissacus, Ectypodus, Elphidotarsius, Eucosmodon, Eudaemonema, Gelastops, Haplaletes, Ignacius, Jepsenella, Leptacodon, Litaletes, Litomylus, Mesodma, Mimotricentes, Myrmecoboides, Neoplagiaulax, Palaechthon, Palaeictops?, Palaeoryctes, Palenochtha, Paleotomus, Pantolambda, Parectypodus, Paromomys, Pentacodon, Peradectes, Periptychus, Picrodus, Plesiolestes, Prodiacodon, Promioclaenus, Pronothodectes, Propalaeosinopa, Prothryptacodon, Protictis, Protoselene, Psittacotherium, Ptilodus, and Tetraclaenodon
- Taxa absent but known before and after To3: Conacodon?, Desmatoclaenus, Microcosmodon, Simpsonictis, Stilpnodon?, and Unuchinia

TIFFANIAN MAMMAL AGE

Tiffany refers to a small settlement in southern Colorado; Walter Granger (1917) first used the term to refer to strata and their contained faunas in the northern San Juan Basin. The "Tiffany beds" are now assigned to the Animas Formation, which intertongues with the Nacimiento and San Jose formations to the south. The Tiffany beds probably are equivalent to part of the Cuba Mesa Sandstone member, the unfossiliferous basal unit of the San Jose Formation. However, definite stratigraphic placement of these beds laterally between the underlying Nacimiento Formation and overlying San

Jose Formation has not been demonstrated (Archibald et al. 1987).

The first collection of fossil mammals reported from the Tiffany beds was made by Wegemann (1917). Later that same year Granger (1917) presented a more detailed treatment of the Tiffany beds and their mammalian fauna and named the principal locality the Mason Quarry or Mason Pocket. Granger (1917) also suggested that the Tiffany mammalian assemblage was intermediate in evolutionary grade between "Torrejon" and "Wasatch" faunas and that it might be correlative with the Clark's Fork fauna of Wyoming, which he tentatively interpreted as early Eocene in age. The Tiffany Local Fauna from Mason Pocket and specimens from sites nearby were described by Simpson (1935c, 1935d, 1935e), and few additions or modifications have appeared since then.

In the 1920s and 1930s, additional mammalian assemblages were discovered that resembled the Tiffany fauna. These included Erickson's Landing and Red Deer from the Paskapoo Formation and Cochrane II from the Porcupine Hills Formation of Alberta (Simpson 1927; Russell 1929), a series of localities from the Fort Union Formation (= Polecat Bench Formation) in Wyoming (Jepsen 1930, 1940), and another series of localities from the Crazy Mountain field in Montana (Simpson 1936, 1937a, 1937b). These sites demonstrated that Tiffany faunas were late Paleocene in age and were younger than Torrejon faunas and older than Clark's Fork faunas (Simpson 1933).

Wood et al. (1941) named the Tiffanian land mammal age based on the fauna from the Tiffany beds of Colorado. Its two principal correlatives were Bear Creek and Silver Coulee. These refer to Bear Creek Local Fauna, Fort Union Formation, Montana (Simpson 1928, 1929a, 1929c; Jepsen 1937), and Silver Coulee Local Fauna, Fort Union Formation, Wyoming (Jepsen 1930, 1940). Although the faunas discovered in the Silver Coulee beds confirm the Tiffanian mammal age assigned to them by Wood et al. (1941), the Bear Creek Local Fauna has since been determined to be of Clarkforkian age (Rose 1981a).

Archibald et al. (1987) provided an updated characterization and zonation of the Tiffanian mammal age and discussed the many Tiffanian faunas discovered and described since the publication by Wood et al. (1941). These faunas were from the Paskapoo and Ravenscrag formations, Alberta and Saskatchewan (Russell 1967; Krishtalka 1973; Krause 1977, 1978); Fort Union Formation, central Montana (Gingerich et al. 1983); Tongue River Formation, eastern Montana (Wolberg 1979); Tongue River and Sentinel Butte formations, North Dakota (Holtzman 1978); Fort Union Formation, Clark's Fork and Bighorn basins, northern Wyoming (Gingerich 1976; Rose 1981a); Hoback Formation, Hoback Basin, Wyoming (Dorr 1952, 1958, 1978); the "sandstone and shale sequence," Togwotee Pass area, Wyoming (McKenna 1980); Shotgun Member, Fort Union Formation, Wind River Basin, Wyoming (Patterson and McGrew 1962; Gazin 1971; Krishtalka et al. 1975); Fort Union Group, Bison Basin, Wyoming (Gazin 1956a); Chappo Member, Wasatch Formation, Wyoming (Dorr and Gingerich 1980); Evanston Formation, Fossil Basin, Wyoming (Gazin 1956b, 1969); and Black Peaks Formation, Big Bend area, Texas (Schiebout 1974).

Since the publication by Archibald et al. (1987), additional Tiffanian faunas have been reported or previous ones have been described more completely. This applies to faunas from the Hanna Formation, Carbon and Hanna basins, south-central Wyoming (Secord 1998; Higgins 2000); Fort Union Formation, southern Bighorn Basin, central Wyoming (Hartman 1986; Leite 1992); Wasatch Formation, Wyoming (Gunnell 1994), Fort Union Formation, Crazy Mountains Basin, Montana (Hartman and Krause 1993); Fort Union Formation, Powder River Basin, Montana (Robinson and Honey 1987); Sentinel Butte and Tongue River formations, Williston Basin, North Dakota (Erickson 1991, 1999; Hartman and Kihm 1991, 1995, 1999; Hunter 1999); Paskapoo Formation, Alberta (Fox 1990c); Goler Formation, California (Lofgren et al. 1999; McKenna and Lofgren in press); and Williamsburg Formation, South Carolina (Schoch 1998).

TORREJONIAN-TIFFANIAN BOUNDARY

When Archibald et al. (1987) was published, the only continuously exposed sections of strata that documented superposition of Tiffanian over Torrejonian faunal assemblages were in the Clark's Fork Basin (at Cub Creek) in south-central Montana and the northern Bighorn Basin (at Polecat Bench) in northern Wyoming. As mentioned previously, strata that yield Eagle Quarry, Cub Creek 1, and Cub Creek 3 (all Ti1) overlie strata that yield the Cub Creek 2 locality (To3), and this sequence of localities begins in strata of normal polarity and continues up into those of reversed polarity correlated with magnetic polarity chron C27n and C26r, respectively (Butler et al. 1987).

This situation has changed: Since 1987 a series of mammalian assemblages from the southern Bighorn and Hanna basins in Wyoming have been reported that span the Torrejonian–Tiffanian boundary (Hartman 1986; Higgins 2000). Also, sites in the Carbon Basin adjacent to the Hanna Basin contain mammalian faunas that are either latest Torrejonian or earliest Tiffanian in age (Secord 1998).

In the southern Bighorn Basin near Cedar Mountain, 185–300 m above the base of the Fort Union Formation is a series of localities that yield late Torrejonian mammals. In direct superposition are strata 300–338 m above the base of the formation that yield early Tiffanian mammals, including *Plesiadapis praecursor* and *Nannodectes intermedius*. Hartman (1986:51) noted that although *Plesiadapis* is the FAD of the Tiffanian mammal age, early Tiffanian faunas at Cedar Mountain that contain *Plesiadapis* have a "strong Torrejonian element, with the transition to the Tiffanian marked only by appearance of the two plesiadapids indicative of the earliest Tiffanian."

A similar situation exists in the Carbon Basin, where the Grayson Ridge and Halfway Hill faunas yield mammalian assemblages with affinities to both the Torrejonian and Tiffanian mammal ages (Secord 1998). Because of the small sample sizes from Grayson Ridge and Halfway Hill, Secord (1998:135) argued that although "these faunas are close in age to the Torrejonian–Tiffanian boundary," a confident assignment to the latest Torrejonian or earliest Tiffanian mammal age is not warranted based on the available data. However, the presence of *Ectocion* in the Grayson Ridge Fauna and *Thryptacodon* in the Halfway Hill Fauna, taxa both limited to the Tiffanian elsewhere, would suggest an early Tiffanian (Tii) age.

In the Hanna Basin, an excellent faunal record of the transition from Torrejonian to Tiffanian faunas is available. Unique structural and depositional conditions in south-central Wyoming during Paleocene time resulted in deposition of the Hanna Formation, a rock unit more than 2 miles thick. Age of the formation ranges from Torrejonian at its base to early Wasatchian at its erosional top (Lillegraven and Snoke 1996). Lower reaches of the Hanna Formation in the Hanna Basin's northeastern corner exhibit a richly fossiliferous, 550-m-thick interval yielding latest Torrejonian (To3) through middle Tiffanian (Ti3) mammalian assemblages. The fossils represent The Breaks Local Fauna, described from 136 recorded localities by Higgins (2000). Minimally, the local fauna is composed of 72 mammalian species, identified at least to generic levels using data from 57 sites. A 55-m-thick interval, placed centrally in stratigraphic limits of the local fauna, has yielded an assemblage of species that ordinarily would be considered characteristic of latest Torrejonian (To3) or earliest Tiffanian (Ti1) age. Because of the grand thickness and richly fossiliferous nature of this section, it shows, for the first time, a clear picture of the nature of faunal change at the Torrejonian-Tiffanian boundary.

78 Donald L. Lofgren, Jason A. Lillegraven, William A. Clemens, Philip D. Gingerich, and Thomas E. Williamson

The zone of overlap in The Breaks Local Fauna documents first appearances of two species of plesiadapids (Nannodectes intermedius and Plesiadapis praecursor), traditional index taxa for recognizing advent of the Tiffanian mammal age. Additionally, the zone of overlap documents persistence, presumably as evolutionary relicts, of 14 species considered typical of Torrejonian time (Krauseia clemensi, Ectypodus szalayi, Gelastops joni, Paleotomus milleri, Aphronorous ratatoski, Litaletes disjunctus, Anisonchus sectorius, Tetraclaenodon puercensis, Prodiacodon puercensis, Mimotricentes subtrigonus, Palaechthon alticuspis, Palaechthon nacimienti, Palenochtha minor, and Paramomys depressidens). Indeed, were it not for presence of the plesiadapids, age of the zone of overlap probably would be identified as Torrejonian. This raises concern about accuracy of age control in stratigraphic sections elsewhere, supposedly representing latest Torrejonian time, in which plesiadapids may have been rare or absent. With this caveat in mind, we continue to use the first appearance of Plesiadapis in defining the advent of the Tiffanian mammal age. We believe that Plesiadapis is an appropriate taxon for this purpose because Plesiadapis has traditionally served as a taxon marking the beginning of the Tiffanian mammal age (Wood et al. 1941; Archibald et al. 1987); Plesiadapis is common and widespread, at least in northern faunas; and it has not been confidently documented that Plesiadapis occurs in strata of Torrejonian age (although this is somewhat circular because the presence of Plesiadapis in a transitional fauna of uncertain age, by definition, indicates a Tiffanian age for the fauna). Discovery of Plesiadapis in an unquestionably Torrejonian fauna (such as one in the Torrejonian interval of the Nacimiento Formation from the San Juan Basin) or in strata of normal polarity correlated to magnetic polarity chron C27n would be powerful evidence of Torrejonian occurrence of this genus.

As interpreted from Paleocene mammalian faunas in the Hanna Basin, important paleogeographic modifications occurred in western North America between Puercan and Tiffanian time. For example, Eberle and Lillegraven (1998b) reported that Puercan assemblages of the Hanna Basin had much greater taxonomic affinities with contemporaneous mammalian faunas to the south than to the north. Just the opposite became the case during late Torrejonian and early Tiffanian time (Higgins 2000). Such major alterations of distributional ranges may well reflect continental climatic change in the earlier half of the Paleocene.

Archibald et al. (1987) noted that all genera first appearing at the beginning of the Tiffanian mammal age

were plausibly derived from genera present in North America during the Torrejonian mammal age. Therefore, the boundary between the Torrejonian and the Tiffanian mammal ages probably was a product of intracontinental evolution and local dispersal. This is in contrast to the situation between the Tiffanian and the Clarkforkian mammal ages, which was marked by immigrations of new genera from Asia (Archibald et al. 1987). The immigrants represented new families, and even orders, on the North American continent.

DEFINITION AND CHARACTERIZATION

We define the Tiffanian mammal age to include faunas that occurred between the first appearance of the plesiadapid primate *Plesiadapis* and the first appearance of Rodentia.

Wood et al. (1941) listed the following taxa as making their first appearance in the Tiffanian mammal age: Palaeosinopa, Phenacodus, Plesiadapis, "Probathyopsis," Rodentia, and Thryptacodon. Based on present knowledge, Palaeosinopa, Plesiadapis, "Probathyopsis" (included in Prodinoceras by McKenna and Bell 1997), and Thryptacodon still occur first in the Tiffanian, whereas Phenacodus is now known from late Torrejonian rocks in the Hanna Basin of Wyoming (Higgins 2000); the Rodentia did not appear until the Clarkforkian mammal age. Four of the five genera noted as last appearances for the Tiffanian mammal age (Tetraclaenodon, Anisonchus, Pantolambda, and Claenodon) retain this distinction, whereas Leptacodon is questionably reported from the Clarkforkian mammal age. Wood et al. (1941) listed Barylambda, "Bathyopsoides," "Labidolemur," Phenacodus grangeri, "Sparactolambda," and Titanoides as index fossils for the Tiffanian mammal age. "Sparactolambda" is now considered a synonym of Titanoides, "Bathyopsoides" a synonym of Prodinoceras, and "Labidolemur" a synonym of Apatemys (see McKenna and Bell 1997). Of the other index fossils listed by Wood et al. (1941), only Titanoides and Phenacodus grangeri are limited to the Tiffanian; Barylambda is known from the Clarkforkian mammal age. Ectypodus was listed as the only characteristic fossil for the Tiffanian, and this designation remains valid.

Paleomagnetic sections have been developed in Clark's Fork and Bighorn basins, northern Wyoming (Butler et al. 1980, 1981) in conjunction with fossil localities ranging from the Ti2 lineage zone through Cf3 acme zone. Therefore these paleomagnetic sections make up one of the most comprehensive for Paleocene terrestrial strata in North America. Although not all of the fossiliferous parts of these strata were amenable to magnetostratigraphic analysis, the available part extended from within magnetic polarity chron C26r through C24r and included the Paleocene–Eocene boundary. In these basins Tiffanian faunas extend from magnetic polarity chron C26r into C25n (Archibald et al. 1987).

Rapp et al. (1983) presented a paleomagnetic sequence for the Black Peaks Member of the Tornillo Formation. The lower part of the Black Peaks Member, which includes Ray's Bonebed (TMM 40536–37, a locality correlated to the Ti3 lineage zone), occurs in strata of reversed polarity. Joe's Bone Bed (TMM 41365–66), a locality correlated with the Ti5 lineage zone, occurred in the overlying, reversed magnetozone. Rapp et al. (1983) and Schiebout et al. (1987) correlated these reversed magnetozones containing Joe's Bonebed (Ti5) with magnetic polarity chron C25r and Ray's Bonebed (Ti3) with magnetic polarity chron C26r, both of which are consistent with the paleomagnetic correlation of Tiffanian lineage zones in the Clark's Fork Basin (Butler et al. 1981).

To summarize, we place the Torrejonian-Tiffanian boundary at or near the boundary of magnetic polarity chrons C27n and C26r. The To3 interval zone is correlated with magnetic polarity chron C27n, the younger part of magnetic polarity chron C27r, and the older part of C26r. The Ti1 and Ti2 lineage zones are correlated with most of magnetic polarity chron C26r. The Ti3 lineage zone is correlated with younger parts of magnetic polarity chron C26r and part of C26n. The Ti4 lineage zone is correlated with most of magnetic polarity chron C26n and the beginning of chron C25r. The Ti5 lineage zone is correlated with most of magnetic polarity chron C25r and the earliest part of chron C25n. The Ti6 interval subzone of the Ti6-Cf1 lineage zone is correlated with part of magnetic polarity chron C25n. These data indicate that the Tiffanian mammal age began during magnetic polarity chron C26r and ended in magnetic polarity chron C25n.

Paleomagnetic samples also were analyzed from strata that yielded the type Tiffanian mammal age in southern Colorado, including Mason Pocket (Butler et al. 1981). The strata sampled were of reversed polarity, correlated to magnetic polarity chron C25r based on faunal correlation to mammalian assemblages in the Clark's Fork and Bighorn basins (Butler et al. 1981).

Characterization of the Tiffanian mammal age is as follows.

First appearances: Aletodon, Anacodon, Apatemys, Arctostylops, Barylambda, Carpolestes, Chiromyoides, Cyriacotherium, Didymictis, Dillerlemur, Dipsalodon, Ectocion, Ectoganus, Entomolestes, Esthonyx?, Haplolambda, Lambertocyon, Limaconyssus, Micromomys, Neoliotomus, Oxyaena, Palaeosinopa, Phenacodaptes, Phenacolemur?, Plesiadapis, Princetonia, Prochetodon, Prodinoceras, Thryptacodon, Thylacaelurus?, Titanoides, and Viverravus

- Last appearances: Acmeodon, Anconodon, Anisonchus, Aphronorus, Baiotomeus, Catopsalis, Claenodon, Colpoclaenus, Conacodon?, Coriphagus, Desmatoclaenus, Elphidotarsius, Elpidophorus, Eucosmodon?, Eudaemonema, Gelastops, Haplaletes, Jepsenella, Krauseia, Litaletes, Litocherus, Litomylus, Mesodma, Mimetodon, Mimotricentes, Myrmecoboides, Neoclaenodon, Neoplagiaulax, Palaechthon, Palenochtha, Paleotomus, Pantolambda, Pararyctes, Paromomys, Pentacodon, Periptychus, Picrodus, Plesiolestes, Promioclaenus, Pronothodectes, Propalaeosinopa, Prothryptacodon, Protictis, Protoselene, Psittacotherium, Ptilodus, Simpsonictis, Stilpnodon?, Tetraclaenodon, and Unuchinia
- Index fossils: Aaptoryctes, Amelotabes, Bisonalveus, Caenolambda, Carpocristes, Carpodaptes, Carpomegodon, Cedrocherus, Copecion, Dorraletes, Fractinus, Ignatiolambda, Liotomus, Litolestes, Melaniella, Mentoclaenodon, Mingotherium, Nannodectes, Navajovius, Pentacosmodon, Pristinictis, Propalaeanodon, Raphictis, Saxonella, Tytthaena, Utemylus, Xenacodon, and Zanycteris
- Characteristic fossils: Adunator, Chriacus, Diacodon, Dissacus, Ectypodus, Ignacius, Leptacodon, Microcosmodon, Palaeictops, Palaeoryctes, Parectypodus, Peradectes, Phenacodus, and Prodiacodon
- Taxa absent but known before and after the Tiffanian: none

ZONATION

The large number of mammalian faunas belonging to the Tiffanian mammal age and the fact that many of them are located in separate depositional basins has made it difficult to determine the relative ages of localities and their contained faunas. Archibald et al. (1987) formalized the methods used to place Tiffanian localities in successive biostratigraphic zones or faunally equivalent biochronologic zones. We follow Archibald et al. (1987) and subdivide the Tiffanian mammal age into five lineage zones (Ti1–Ti5) and one interval subzone (Ti6, part of a sixth lineage zone, Ti6–Cf1) based on apparently nonoverlapping species of the primate *Plesiadapis* that have been argued to represent a single evolving lineage (Gingerich 1976). *Plesiadapis* is one of the most abundant and most widely distributed genera of late Paleocene

mammals, at least in northerly realms of the Western Interior, and is a suitable taxon for lineage-based zonation. The five lineage zones and one interval subzone of the Tiffanian that we recognize are *Plesiadapis praecursor/P*. anceps Lineage Zone (Ti1), P. anceps/P. rex Lineage Zone (Ti2), P. rex/P. churchilli Lineage Zone (Ti3), P. churchilli/P. simonsi Lineage Zone (Ti4), P. simonsi/P. gingerichi Lineage Zone (Ti5), and P. gingerichi/Rodentia Interval Subzone (Ti6) of the P. gingerichi/P. cookei Lineage Zone (Ti6-Cf1). The first three lineage zones are represented by faunas from the Crazy Mountains Basin, Montana (Simpson 1937a; Gingerich 1976). The second through fifth lineage zones and the sixth interval subzone are represented by faunas from the Clark's Fork and Bighorn basins, Wyoming (Gingerich 1976, 2000; Gingerich et al. 1980).

Plesiadapis praecursor/P. anceps Lineage Zone (Ti1) We define the *P. praecursor/P. anceps* Lineage Zone to include faunas that occurred between the first appearance of *P. praecursor* and the first appearance of *P. anceps.*

As noted by Archibald et al. (1987), earliest Tiffanian faunas were known from central Alberta to probably southern Texas, but the zone was one of the least well known for the Tiffanian mammal age; samples from many Ti1 localities were either small or only partially described. This statement is still valid concerning Cochrane I in central Alberta (Russell 1958; Fox 1990c), Little Muddy Creek in the Fossil Basin of southwestern Wyoming (Gazin 1969), Bangtail Locality in the western Crazy Mountains Basin of southcentral Montana (Gingerich et al. 1983), and Schiebout– Reeves Quarry in the Big Bend area of Texas (Schiebout 1974; Rapp et al. 1983; Schiebout et al. 1987).

Two of the largest and potentially most important collections from the Ti1 lineage zone, those from Keefer Hill in the Wind River Basin of Wyoming and Cochrane II from central Alberta, remain largely undescribed. Only preliminary faunal lists have been published for the Cochrane II (Fox 1990c) and Keefer Hill local faunas (Keefer 1961; D. Russell 1967), and some taxa cited in these preliminary lists are new records for the Ti1 lineage zone. We include most in table 3.2, which lists temporal ranges of North American genera of Paleocene mammals. Pending descriptions of specimens, we exclude *Oxyprimus*? and *Acheronodon* reported from Cochrane II because these undocumented records would drastically alter the temporal ranges of these genera, now both known elsewhere from the Pu1 interval zone only.

In the eastern Crazy Mountains Basin are the Douglass, Glennie, and Bingo localities. The mammalian assemblage from the Douglass Quarry was described by Krause and Gingerich (1983), but extensive collections have been made since then. These collections, as well as those made from the Glennie and recently discovered Bingo locality, remain undescribed (Hartman and Krause 1993). These three quarries are especially important because they are located low in the Melville Formation. Stratigraphically, they occur above the Gidley and Silberling quarries (To3 interval zone) in the upper Lebo Formation and stratigraphically below Scarritt Quarry (Ti2 lineage zone) in the Melville Formation (Simpson 1937b; Krause and Gingerich 1983; Hartman and Krause 1993). Although no faunal list was presented, Hartman and Krause (1993) suggested that the mammalian assemblage from the Bingo Quarry appears to be correlative to the Bangtail Locality (Til lineage zone) in the western Crazy Mountains Basin, which was described by Gingerich et al. (1983).

Robinson and Honey (1987) described a diverse new vertebrate fauna, including 21 mammalian species, from Newell's Nook (U.S. Geological Survey D-2003), Tongue River Member of the Fort Union Formation in the northern Powder River Basin of Montana. No specimens referable to *Plesiadapis* were reported. However, the mammalian assemblage does contain *Anconodon, Acmeodon, Nannodectes, Ectocion,* and *Anisonchus,* all taxa for which known temporal ranges overlap in the Til lineage zone.

As mentioned earlier in the discussion of the Torrejonian–Tiffanian boundary, new earliest Tiffanian (Ti1) localities from Wyoming have been reported from the southern Bighorn Basin (Hartman 1986), the Hanna Basin (Higgins 2000), and probably the Carbon Basin (Secord 1998). Also, Cub Creek 1, Cub Creek 3, and Eagle Quarry from the Clark's Fork Basin in southern Montana yield sparse faunas referred to the Ti1 lineage zone.

The Douglass Quarry, Cub Creek 1, Cub Creek 3, Eagle Quarry, and probably Schiebout–Reeves Quarry all occur in strata of reversed polarity correlated with magnetic polarity chron C26r (Rapp et al. 1983; Schiebout et al. 1987; Butler et al. 1987). Thus, based on present knowledge, the Ti1 lineage zone is constrained within the older part of magnetic polarity chron C26r.

- First appearances: Bisonalveus, Carpodaptes, Ectocion, Limaconyssus, Nannodectes, Navajovius, Plesiadapis, Thryptacodon, Thylacaelurus?, and Titanoides
- Last appearances: Anisonchus, Coriphagus, Eucosmodon?, Jepsenella, Krauseia, Litaletes, Palenochtha, Pantolambda, Pentacodon, Plesiolestes, Pronothodectes, Prothryptacodon, and Tetraclaenodon
- Index fossils: Fractinus, Liotomus, Nannodectes intermedius, Plesiadapis praecursor, and Pristinictis

- Characteristic fossils: Acmeodon, Adunator, Anconodon, Aphronorus, Baiotomeus, Catopsalis, Chriacus, Claenodon, Colpoclaenus, Desmatoclaenus, Diacodon?, Dissacus, Ectypodus, Elphidotarsius, Elpidophorus, Eudaemonema, Gelastops, Haplaletes, Ignacius, Leptacodon, Litocherus, Litomylus, Mesodma, Microcosmodon, Mimetodon, Mimotricentes, Myrmecoboides, Neoclaenodon, Neoplagiaulax, Palaechthon, Palaeoryctes, Paleotomus, Pararyctes, Parectypodus, Paromomys, Peradectes, Periptychus, Phenacodus, Picrodus, Prodiacodon?, Promioclaenus, Propalaeosinopa, Protictis, Protoselene, Psittacotherium, Ptilodus, and Simpsonictis
- Taxa absent but known before and after Ti1: *Conacodon*?, *Palaeictops*, *Stilpnodon*?, and *Unuchinia*

Plesiadapis anceps/Plesiadapis rex Lineage Zone (Ti2) We define the *P. anceps/P. rex* Lineage Zone to include faunas that occurred between the first appearance of *P. anceps* and the first appearance of *P. rex*.

Localities referred to the Ti2 lineage zone are known only from Montana and Wyoming and possibly Canada and California. Like the Ti1 lineage zone, the Ti2 lineage zone is not well known. Faunal studies on Scarritt Quarry from the Crazy Mountains Basin of southcentral Montana (Simpson 1936, 1937a) and Saddle Locality from the Bison Basin of south-central Wyoming (Gazin 1956b) are the only published descriptions available for taxa occurring in the Ti2 lineage zone, and both local faunas are small. An updated faunal list for Scarritt Quarry was presented by Rose (1981a), and the sample appears to be biased in favor of small mammals (Rose 1981a, 1981b).

Much smaller collections of mammals from the Ti2 lineage zone are known from University of Michigan (UM) locality 263 in the Polecat Bench section, Bighorn Basin, Wyoming; the Tongue River Formation of North Dakota (Hunter 1999); and several localities (White Site, 7-Up Butte, Highway Blowout) in the Medicine Rocks area of southeastern Montana.

Fox (1990c) provided lists of taxa from two sites, Aaron's Locality and Hand Hills West lower level, from the Paskapoo Formation of Alberta that may be referable to the Ti2 lineage zone. Aaron's Locality contains *Bisonalveus, Ignacius, Elphidotarsius,* and *Ptilodus,* and the fauna at Hand Hills West lower level includes *Neoplagiaulax, Elphidotarsius, Picrodus,* and *Pararyctes.* Not enough faunal data are available to determine whether these sites are Ti1 or Ti2 in age (Fox 1990c).

The Goler Formation of California contains two mammalian assemblages, the Laudate Local Fauna and that from the Edentulous Jaw Site. Both are apparently Tiffanian in age because both sites yield Plesiadapis (see Lofgren et al. 1999; McKenna and Lofgren in press). The Laudate Local Fauna had yielded Microcosmodon?, Neoliotomus?, Neoplagiaulax, Mesodma?, Ptilodus, Paromomys, Conacodon, and Dissacus and was tentatively assigned a late Torrejonian or early Tiffanian age (McKenna 1955, 1960; McKenna et al. 1987; Lofgren et al. 1999). Recently, a specimen of a smaller species of Plesiadapis was recovered, which indicates that the site probably is early Tiffanian in age (McKenna and Lofgren in press). The small fauna from the Edentulous Jaw Site may be a correlative of the Ti2 lineage zone. A small to medium-sized species of Plesiadapis occurs at the Edentulous Jaw Site (Lofgren et al. 1999) that shows many similarities in size and morphology (Lofgren unpubl. data) to Plesiadapis anceps. Thus correlation to the Ti2 lineage zone is plausible, pending the results of further analysis of screenwashed samples from this site.

The Hanna Basin of Wyoming is the only other area that has yielded sites referable to the Ti2 lineage zone. These sites are part of a series of localities that make up The Breaks Local Fauna of Higgins (2000), which is late Torrejonian (To3) through mid-Tiffanian (Ti3) in age.

Ti2 lineage zone sites that have undergone paleomagnetic analysis are Scarritt Quarry in the Crazy Mountains Basin of Montana and localities in the Clark's Fork Basin of Wyoming. The strata that contain all these sites are of reversed polarity and are correlated to magnetic polarity chron C26r (Butler et al. 1981, 1987).

First appearances: Caenolambda, Mentoclaenodon, Neoliotomus?, and Palaeosinopa

Last appearances: Anconodon, Desmatoclaenus, Neoclaenodon, and Simpsonictis?

Index fossils: Plesiadapis anceps and Nannodectes gazini

- Characteristic fossils: Bisonalveus, Carpodaptes, Chriacus, Claenodon, Conacodon?, Dissacus, Ectocion, Ectypodus, Elpidophorus, Haplaletes, Ignacius, Leptacodon, Litocherus, Litomylus, Mesodma, Microcosmodon, Mimotricentes, Nannodectes, Neoplagiaulax, Paleotomus, Pararyctes, Paromomys?, Peradectes, Phenacodus, Picrodus, Plesiadapis, Prodiacodon, Promioclaenus, Propaleosinopa, Protictis, Protoselene, Ptilodus, Thryptacodon, Titanoides, and Unuchinia
- Taxa absent but known before and after Ti2: Acmeodon, Adunator, Aphronorus, Baiotomeus, Catopsalis, Colpoclaenus, Diacodon?, Elphidotarsius, Eudaemonema, Gelastops, Limaconyssus, Mimetodon, Myrmecoboides, Navajovius, Palaechthon, Palaeictops, Palaeoryctes, Parectypodus, Periptychus, Psittacotherium, Stilpnodon?, and Thylacaelurus?

82 Donald L. Lofgren, Jason A. Lillegraven, William A. Clemens, Philip D. Gingerich, and Thomas E. Williamson

Plesiadapis rex/Plesiadapis churchilli Lineage Zone (**Ti3**) We define the *P. rex/P. churchilli* Lineage Zone to include faunas that occurred between the first appearance of *P. rex* and the first appearance of *P. churchilli*.

The Ti₃ lineage zone is much better represented than the Ti1 and Ti2 lineage zones. Fifty percent more genera and localities are known from the Ti3 lineage zone than from Ti1 or Ti2 (Archibald et al. 1987). Cedar Point Quarry, in the Bighorn Basin of northwestern Wyoming, contains the largest sample, numbering almost 2000 specimens. Available papers describe several taxonomic groups such as adapisoricids (Krishtalka 1976a; Gingerich 1983), nyctitheriids (Krishtalka 1976b), apatemyids (West 1973), plesiadapids (Gingerich 1976), carpolestids (Rose 1975), arctocyonids (Van Valen 1978), phenacodontids (West 1971, 1976; Thewissen 1990), carnivores (Gingerich and Winkler 1985), creodonts (Gingerich 1980b), pantodonts (Simons 1960), and microsyopoidea (Gunnell 1989). Rose (1981a) presented a preliminary list of the Cedar Point Quarry fauna and the relative abundances of taxa in the sample, which was dominated by P. rex and Ptilodus.

Smaller samples that have received descriptive treatment are Ray's Bonebed from the Big Bend area of Texas (Schiebout 1974; Standhardt 1986; Schiebout et al. 1987); the Ledge, Saddle Annex, and West End sites in the Bison Basin of Wyoming (Gazin 1956b); the Brisbane and White's River Basin Survey Site from the Williston Basin of North Dakota (Holtzman 1978; Hartman and Kihm 1991, 1995); the Chappo Type Locality from the Green River Basin of southwest Wyoming (Dorr and Gingerich 1980; Gunnell 1994); the Battle Mountain locality from the Hoback Basin of southwest Wyoming (Dorr 1958); and the Police Point Local Fauna from southeast Alberta (Krishtalka 1973).

Other important sites representing the Ti3 lineage zone include Simpson's Locality 13 (Simpson 1937b) in the Crazy Mountains Basin of south-central Montana, a site that occurs in strata of reversed polarity correlated with magnetic polarity chron C26r (Butler et al. 1987); The Breaks Local Fauna from the Hanna Basin (Higgins 2000) and perhaps the Sand Creek fauna (two taxa) from the Carbon Basin (Secord 1998), both of south-central Wyoming; and a series of sites from the Paskapoo Formation in Alberta (Fox 1983, 1984a–1984d, 1990c; Webb 1995). Preliminary faunal lists provided by Fox (1990c) from these sites (Hand Hills West, upper level; Blindman River localities DW-1, DW-2, DW-3, Mel's Place; Burbank; Joffre Bridge localities) indicate that a diverse middle Tiffanian fauna is present in this area of Alberta. Specimens from the DW-2 site are especially noteworthy because of their exceptional preservation and completeness (Fox 1990c).

Of the many Ti3 sites, only Ray's Bonebed, Simpson Locality 13, and localities in the Clark's Fork Basin have undergone paleomagnetic analysis. Results indicate that these sites occur in strata of both reversed and normal polarity correlated magnetic polarity chron C26r and C26n (Butler et al. 1981; Rapp et al. 1983; Schiebout et al. 1987; Butler et al. 1987).

- First appearances: Aletodon, Apatemys, Barylambda, Carpocristes, Chiromyoides, Cyriacotherium, Dorraletes, Lambertocyon, Litolestes, Micromomys, Prochetodon, Raphictis, and Zanycteris
- Last appearances: Acmeodon, Aphronorus, Baiotomeus, Bisonalveus, Caenolambda, Colpoclaenus, Conacodon?, Elphidotarsius, Eudaemonema, Gelastops, Mentoclaenodon, Palaechthon, Paromomys?, Promioclaenus, Protoselene, and Stilpnodon?
- Index fossils: Cedrocherus, Chiromyoides minor, Copecion, Melaniella, Nannodectes simpsoni, Plesiadapis rex, Saxonella, and Tytthaena
- Characteristic fossils: Adunator, Carpodaptes, Chriacus, Claenodon, Dissacus, Ectocion, Ectypodus, Elpidophorus, Haplaletes, Ignacius, Leptacodon, Litocherus, Litomylus, Mesodma, Microcosmodon, Mimetodon, Mimotricentes, Myrmecoboides, Nannodectes, Navajovius, Neoliotomus?, Neoplagiaulax, Palaeoryctes, Palaeosinopa, Paleotomus, Pararyctes, Parectypodus, Peradectes, Periptychus, Phenacodus, Picrodus, Plesiadapis, Prodiacodon, Propalaeosinopa, Protictis, Psittacotherium, Ptilodus, Thryptacodon, Titanoides, and Unuchinia
- Taxa absent but known before and after Ti3: *Catopsalis*, *Diacodon?*, *Limaconyssus*, *Palaeictops*, and *Thylacaelurus*?

Plesiadapis churchilli/Plesiadapis simonsi Lineage Zone (**Ti4**) We define the *P. churchilli/P. simonsi* Lineage Zone to include faunas that occurred between the first appearance of *P. churchilli* and the first appearance of *P. simonsi*.

The type Tiffanian fauna from the Mason Pocket site of southwestern Colorado lies in the Ti4 lineage zone and was described in detail by Simpson (1935c, 1935d, 1935e). Paleomagnetic analysis of strata containing Mason Pocket exhibit reversed polarity, and the rocks are correlated with magnetic polarity chron C25r based on faunal correlation to mammalian assemblages in the Clark's Fork and Bighorn basins (Butler et al. 1981).

The largest sample (exceeding 5000 specimens) of Ti4 lineage zone mammals is from the Roche Percée localities in southeastern Saskatchewan. Thus far, only multituberculates (Krause 1977), primates (Krause 1978), and a pantodont (Rose and Krause 1982) have been described from the Roche Percée Local Fauna.

Also from Canada is a series of sites referred to the Ti4 lineage zone from the Paskapoo Formation. The Crestomere School and Canyon Ski Quarry sites have yet to be fully described, although a preliminary faunal list was provided by Fox (1990c). Swan Hills Site 1 is the most northerly Tiffanian and North American Paleocene fossil mammal locality known (Archibald et al. 1987), and its fauna has been described in some detail (L. Russell 1967; Krishtalka 1973; Krause 1978; Gingerich 1986; Fox 1990c).

Wolberg (1979) presented preliminary faunal lists for the Olive and Circle local faunas of eastern Montana. Included in Wolberg's list from the Olive site are several taxa that otherwise are unknown from the Ti4 lineage zone (e.g., *Nyctitherium, Protentomodon*, cf. *Purgatorius*). They have not been included as first or last appearances in the lists in this chapter pending publication of full descriptions and analyses.

In the Bighorn Basin are several Ti4 lineage zone localities of interest (Airport, Witter Quarry, Divide Quarry) because they can be placed in stratigraphic relationship to sites that yield mammalian assemblages representative of the Ti3 or Ti5 lineage zones (Archibald et al. 1987).

Mammalian assemblages from other Ti4 lineage zone localities include a series of sites in the Rock Springs uplift of southwestern Wyoming (Winterfeld 1982), Malcolm's Locality in the Wind River Basin of central Wyoming (Krishtalka et al. 1975), and a series of localities in the Williston Basin of central North Dakota (Holtzman 1978; Erickson 1991, 1999; Hartman and Kihm 1991, 1995, 1999). The Wannagan Creek Local Fauna is of special interest because the preliminary faunal list includes cf. *Phenacolemur, Entomolestes* sp., and *Leptictis* sp. (see Erickson 1991, 1999). All three taxa represent significant range extensions. Pending description of specimens, we tentatively include *Phenacolemur* and *Entomolestes* in our faunal characterization for the Ti4 lineage zone.

Paleomagnetic analyses of strata yielding mammals representing the Ti4 lineage zone from southern Colorado and the Clark's Fork Basin of Wyoming indicate that these rocks are of reversed and normal polarity correlated with magnetic polarity chrons C26n and C25r (Butler et al. 1981).

First appearances: *Anacodon, Entomolestes, Haplolambda, Ignatiolambda, Phenacodaptes, and Phenacolemur?*

Last appearances: Catopsalis, Elpidophorus, Litomylus, Mesodma, Pararyctes, Periptychus, Raphictis, and Zanycteris

- Index fossils: Amelotabes, Carpomegodon, Chiromyoides caesor, Nannodectes gidleyi, Plesiadapis churchilli, Utemylus, and Xenacodon
- Characteristic fossils: Adunator, Aletodon, Apatemys, Barylambda, Carpocristes, Carpodaptes, Chiromyoides, Chriacus, Claenodon, Cyriacotherium, Dissacus, Ectocion, Ectypodus, Haplaletes, Ignacius, Lambertocyon, Leptacodon, Litocherus, Litolestes, Microcosmodon, Micromomys, Mimetodon, Mimotricentes, Nannodectes, Navajovius, Neoplagiaulax, Palaeictops, Palaeoryctes, Palaeosinopa, Peradectes, Phenacodus, Plesiadapis, Prochetodon, Propalaeosinopa, Protictis, Ptilodus, Thryptacodon, Titanoides, and Unuchinia
- Taxa absent but known before and after Ti4: Diacodon?, Dorraletes, Limaconyssus, Myrmecoboides, Neoliotomus?, Paleotomus, Parectypodus, Picrodus, Prodiacodon, Psittacotherium?, and Thylacaelurus?

Plesiadapis simonsi/**Plesiadapis gingerichi** Lineage **Zone (Ti5)** We define the *P. simonsi*/*P. gingerichi* Lineage Zone to include faunas that occurred between the first appearance of *P. simonsi* and the first appearance of *P. gingerichi*.

Most Ti5 lineage zone localities are from the Clark's Fork and Bighorn basins. Of these, the mammalian fauna from Princeton Quarry is the best known because the fauna was examined in detail by Rose (1981a, 1981b). Rose (1981a) noted that there may be a significant size bias in the sample because the fauna is dominated by smaller taxa (*Phenacodaptes, Plesiadapis*), whereas larger forms are rare or absent.

Small collections of Ti5 lineage zone mammals have been described from the Bayfield area, northern San Juan Basin, Colorado (Simpson 1935c, 1935d, 1935e); various localities at the Rock Springs uplift, Wyoming (Winterfeld 1982); the *Titanoides* Locality, Bison Basin, Wyoming (Gazin 1956b); the Dell Creek Quarry, Hoback Basin, Wyoming (Dorr 1952, 1958, 1978); and Joe's Bonebed, Big Bend area, Texas (Schiebout 1974; Standhardt 1986; Schiebout et al. 1987).

Recently, Schoch (1985, 1998) reported a sparse but unique occurrence of Paleocene land mammals from the East Coast of North America (Williamsburg Formation, South Carolina) consisting of three identifiable specimens referred to *Mingotherium*, *Ectoganus*, and *Phenacodus grangeri*. *Mingotherium* is a genus of uncertain affinity for which the temporal range is unknown. However, *Ectoganus* occurs in strata elsewhere from the Ti5 lineage zone through the Clarkforkian Mammal Age (Archibald et al. 1987), and *P. grangeri* is known from the Ti1 to Ti5 lineage zones (Thewissen 84 Donald L. Lofgren, Jason A. Lillegraven, William A. Clemens, Philip D. Gingerich, and Thomas E. Williamson

1990). Therefore we tentatively assign this fauna to the Ti5 lineage zone.

Strata that contain Joe's Bonebed and Ti5 sites in the Clark's Fork Basin are of reversed and normal polarity correlated with magnetic polarity chron C25r and C25n (Butler et al. 1981; Rapp et al. 1983; Schiebout et al. 1987).

- First appearances: Arctostylops, Carpolestes, Didymictis, Dillerlemur, Dipsalodon, Ectoganus, Oxyaena, Princetonia, Prodinoceras, and Viverravus
- Last appearances: Carpocristes, Carpodaptes, Claenodon, Dorraletes, Haplaletes, Ignatiolambda, Litocherus, Litolestes, Mimetodon, Myrmecoboides, Nannodectes, Navajovius, Neoplagiaulax, Paleotomus, Picrodus, Propalaeosinopa, Protictis, Psittacotherium?, Ptilodus, and Unuchinia
- Index fossils: Aaptoryctes, Chiromyoides potior, Mingotherium, Pentacosmodon, Plesiadapis fodinatus, Plesiadapis simonsi, and Propalaeanodon
- Characteristic fossils: Adunator, Aletodon, Anacodon, Barylambda, Chiromyoides, Chriacus, Cyriacotherium, Diacodon, Dissacus, Ectocion, Ectypodus, Haplolambda, Ignacius, Lambertocyon, Leptacodon, Microcosmodon, Micromomys, Mimotricentes, Neoliotomus, Palaeictops, Palaeoryctes, Palaeosinopa, Parectypodus, Peradectes, Phenacodaptes, Phenacodus, Plesiadapis, Prochetodon, Prodiacodon, Thryptacodon, and Titanoides
- Taxa absent but known before and after Ti5: *Apatemys, Entomolestes, Limaconyssus, Phenacolemur?,* and *Thylacaelurus?*

Plesiadapis gingerichi/Rodentia Interval Subzone (Ti6) of the *P. gingerichi*/*P. cookei* Lineage Zone (Ti6–Cf1) *P. gingerichi* was described by Rose (1981a), who interpreted it to be phylogenetically and temporally intermediate between *P. simonsi* (latest Tiffanian, Ti5) and *P. cookei* (middle Clarkforkian, Cf2). Following Rose (1981a) and Archibald et al. (1987), we define the *P. gingerichi*/*P. cookei* Lineage Zone to include faunas that occurred between the first appearance of *P. gingerichi* and the first appearance of *P. cookei*.

The Ti6–Cf1 lineage zone as first defined by Rose (1980, 1981a) was interpreted to straddle the Tiffanian– Clarkforkian boundary (Archibald et al. 1987). To specify this relationship, Archibald et al. (1987) subdivided the lineage zone into two interval subzones. The end of the Ti6 interval subzone and commencement of the Cf1 interval subzone equaled the Tiffanian–Clarkforkian boundary (as well as first appearance of the Rodentia). Thus Archibald et al. (1987) defined the first interval subzone, the *P. gingerichi*/Rodentia Interval Subzone (Ti6), to include faunas that occurred between the first appearance of *P. gingerichi* and first appearance of the Rodentia. The purpose in recognizing two interval subzones in the Ti6–Cfi lineage zone was to highlight that the lineage zone straddles the Tiffanian–Clarkforkian boundary (Archibald et al. 1987). We accept and follow this reasoning.

The Ti6 interval subzone has been recognized with certainty only in the Clark's Fork Basin (and perhaps the Wind River Basin) of Wyoming, and the subzone is poorly known (Archibald et al. 1987). The long list of genera given here for taxa absent but known before and after Ti6 is evidence of this fact. Several other faunas that may be referable to the Ti6 interval subzone are discussed later in this chapter under the Cf1 interval subzone.

Sites referred to the Ti6 interval subzone from the Clark's Fork Basin occur in strata of normal polarity correlated to magnetic polarity chron C25n (Butler et al. 1981).

First appearances: Esthonyx?, P. gingerichi, and Plesiadapis dubius

Last appearances: *Mimotricentes*

Index fossils: none

- Characteristic fossils: Adunator, Carpolestes, Chiromyoides, Cyriacotherium, Didymictis, Dillerlemur, Dipsalodon?, Dissacus, Ectocion, Ectoganus, Leptacodon, Neoliotomus, Oxyaena, Palaeosinopa, Phenacodus, Plesiadapis, Prodinoceras, and Prochetodon
- Taxa absent but known before and after Ti6: Aletodon, Anacodon, Apatemys, Arctostylops, Barylambda, Chriacus, Diacodon?, Ectypodus, Entomolestes, Haplolambda, Ignacius, Lambertocyon, Limaconyssus, Microcosmodon, Micromomys, Palaeictops, Palaeoryctes, Parectypodus, Peradectes, Phenacodaptes, Phenacolemur?, Princetonia, Prodiacodon, Thryptacodon, Thylacaelurus?, Titanoides?, and Viverravus

CLARKFORKIAN MAMMAL AGE

Granger (1914) applied the term *Clark Fork* to a stratigraphic interval at the southwestern end of Polecat Bench in the Clark's Fork Basin of northwestern Wyoming. Fossils in this "Clark Fork fauna" were described by Matthew (1915a, 1915b, 1915c), Granger (1915), Jepsen (1930, 1940), and Simpson (1929b, 1937c). Wood et al. (1941:9) formally proposed the Clarkforkian as a North American provincial age, "based on the Clark Fork member (and faunal zone) of the Polecat Bench Formation"; they selected Granger's locality near Polecat Bench as the type locality. Also, Wood et al. (1941) considered the Clarkforkian as the youngest of the Paleocene provincial ages.

Because of the small collections, inadequate stratigraphic documentation, and other factors, there was initial skepticism about legitimacy of the Clarkforkian mammal age. Eventually, that skepticism culminated in rejection by R. Wood (1967) of the Clarkforkian as a valid mammal age. Nevertheless, collecting in the Clark's Fork Basin in the 1970s and 1980s yielded thousands of specimens that clearly reaffirmed the recognizability of a distinctive Clarkforkian fauna (Gingerich and Rose 1977; Rose 1978, 1980, 1981a). In addition, study of these collections indicated that Clarkforkian assemblages in the type area are not limited to the Fort Union Formation (= Polecat Bench Formation) but occur primarily in lower parts of the overlying Willwood Formation (Archibald et al. 1987).

Wood et al. (1941) did not recognize any faunal correlatives elsewhere of the Clarkforkian mammal age. Later, however, correlatives of this age were recognized and discussed by Rose (1981a). These faunas occur in the following formations: Fort Union and Willwood formations, Clark's Fork and Bighorn basins, northern Wyoming and southern Montana (Sinclair and Granger 1912; Simpson 1928, 1929a, 1929c; Jepsen 1937; Van Houten 1944; Van Valen and Sloan 1966; Gingerich and Rose 1979); "lower variegated sequence," Togwotee Pass area, northwestern Wyoming (McKenna 1972, 1980); Chappo Member, Wasatch Formation, Hoback Basin, western Wyoming (Dorr 1952, 1958, 1978; Dorr and Steidtmann 1970; Dorr et al. 1977) and Green River Basin, southwestern Wyoming (Gazin 1942, 1956a; Dorr and Gingerich 1980); Fort Union Formation, Washakie Basin, south-central Wyoming (Rose 1981a); Debeque Formation, Piceance Creek Basin, northwestern Colorado (Patterson 1933, 1936, 1937, 1939, 1949; Patterson and Simons 1958; Patterson and West 1973; Kihm 1984); and possibly localities in the Tornillo Formation, Big Bend area, southwestern Texas (Schiebout 1974; Schiebout et al. 1987). Rose (1981a) provided stratigraphic sections, descriptions, and ranges of Clarkforkian mammals from the type area and a discussion of most of the Clarkforkian assemblages listed here.

TIFFANIAN-CLARKFORKIAN BOUNDARY

In the Clark's Fork Basin, the beginning of the Clarkforkian mammal age can be recognized by the first occurrence of the orders Rodentia and Tillodontia (*Esthonyx*) and the genera *Haplomylus* (Condylarthra) and *Coryphodon* (Pantodonta). It was appearance of the Rodentia, however, that was used to define the beginning of this mammal age (Gingerich and Gunnell 1979; Rose 1980, 1981a; Archibald et al. 1987). All of these first appearances seem to represent immigrants, and discoveries in Paleocene strata of China suggest that rodents and tillodonts may have originated in Asia (Wang 1975; Zhou et al. 1977; Gingerich 1980a; Zhang 1980; Dawson et al. 1984). The first occurrence of any of these four immigrants is a good indication of the beginning of the Clarkforkian mammal age, but none is common in early parts of this mammal age (Rose 1981a; Archibald et al. 1987).

Wood et al. (1941) listed the Tiffanian as the oldest record of Rodentia. However, this was based on the occurrence of rodents at Bear Creek, Montana (Jepsen 1937), a locality that is now considered to be of Clarkforkian age (Van Valen and Sloan 1966; Sloan 1970; Rose 1975, 1977, 1981a; Gingerich 1976).

Exposures yielding the type Clarkforkian fauna in vicinity of the Polecat Bench–Clark's Fork Basin occur in an interval about 470 m thick in the upper Fort Union and lower Willwood formations. The earliest Clarkforkian faunas are found about 350 m above the level of the late Tiffanian Princeton Quarry. The only Clarkforkian faunas known outside the Clark's Fork Basin that may overlie Tiffanian faunas and thus include the Tiffanian– Clarkforkian boundary are from strata preserved in the Togwotee Pass area and the Hoback Basin, both in western Wyoming. However, collections from these strata do not permit precise location of the Tiffanian–Clarkforkian boundary (Archibald et al. 1987).

DEFINITION AND CHARACTERIZATION

Archibald et al. (1987), using Rose's (1980, 1981a) study of the mammalian fauna from the area of the type Clarkforkian, defined the Clarkforkian mammal age to include faunas that occurred between the first appearance of the Rodentia and the first appearance of the Artiodactyla.

Wood et al. (1941) listed cf. *Coryphodon, Ectocion, Esthonyx,* and *Oxyaena* as first appearing in the Clarkforkian mammal age. Indeed, *Coryphodon* and perhaps *Esthonyx* (there is a questionable occurrence in the Ti6 interval subzone) are now known to appear for the first time in the Clarkforkian. However, *Ectocion* and *Oxyaena* have been recorded subsequently from Tiffanian faunas. Wood et al. (1941) also listed *Carpolestes* and *Plesiadapis* as having last appearances in the Clarkforkian mammal age. The final appearance of *Carpolestes* is still known from Clarkforkian strata, but a single specimen of *Plesiadapis dubius* was reported from an early Wasatchian fauna (Rose and Bown 1982). Wood et al. (1941) listed *Plesiadapis cookei* as the only index fossil for the Clarkforkian mammal age, and this assignment remains valid. Characteristic fossils listed by Wood et al. (1941) for this mammal age (i.e., *Didymictis, Ectypodus, Phenacodus, "Probathyopsis,*" and *Thryptacodon*) remain valid in that sense, although McKenna and Bell (1997) synonymized "*Probathyopsis*" with *Prodinoceras*.

In their update of Wood et al. (1941), Archibald et al. (1987) commented on the following aspects of Clarkforkian faunas. First, common index fossils of the Clarkforkian include Plesiadapis cookei, Carpolestes nigridens, Aletodon gunnelli, Apheliscus nitidus, Haplomylus simpsoni, Dissacus praenuntius, Esthonyx xenicus, Esthonyx ancylion, and Acritoparamys atavus, and all occur in at least one Clarkforkian fauna outside the Clark's Fork Basin in addition to the type Clarkforkian fauna. Second, the most common taxa of the Clarkforkian mammal age are phenacodontid condylarths (Ectocion osbornianus, Phenacodus primaevus, and Phenacodus vortmani), which together constitute about 50 percent of individuals at most levels in the Clark's Fork Basin (Rose 1981a, 1981b). Third, Ectocion is the most common taxon at most localities. Finally, phenacodontids persist into Wasatchian time but exhibit a dramatic decline in abundance at the Clarkforkian–Wasatchian boundary.

Magnetostratigraphic sections have been developed in the Clark's Fork and Bighorn basins, northern Wyoming (Butler et al. 1980, 1981), and these sections encompass all three zones recognized by Rose (1981a) for the type Clarkforkian fauna and part of the next younger, Wasatchian fauna. These data indicate that Clarkforkian faunas extend from magnetic polarity chron C25n into C24r.

The characterization of the Clarkforkian mammal age is as follows.

- First appearances: Acritoparamys, Apatosciuravus, Apheliscus, Arctodontomys, Chalicomomys, Coryphodon, Dipsalidictides, Franimys, Haplomylus, Hyopsodus, Icaronycteris?, Leipsanolestes, Meniscotherium, Microparamys, Mimoperadectes?, Niptomomys, Palaeanodon, Paramys, Plagioctenodon, Plagiomene, Pontifactor?, Reithroparamys, Tinimomys, Uintacyon, and Worlandia
- Last appearances: Adunator, Aletodon, Anacodon, Arctostylops, Carpolestes, Chiromyoides, Cyriacotherium, Dipsalodon, Haplolambda, Lambertocyon, Limaconyssus, Microcosmodon, Palaeoryctes, Phenacodaptes, Prochetodon, and Titanoides?
- Index fossils: Acidomomys, Acritoparamys atavus, Alagomys, Aletodon gunnelli, Apheliscus nitidus, Carpolestes nigridens, Ceutholestes, Dissacus praenuntius, Esthonyx ancylion, Esthonyx xenicus, Haplomylus simp-

soni, Palaeonictis, Planetetherium, Plesiadapis cookei, Protentomodon, Thelysia, and Wyonycteris

- Characteristic fossils: Apatemys, Barylambda, Chriacus, Diacodon?, Didymictis, Dillerlemur, Dissacus, Ectocion, Ectoganus, Ectypodus, Esthonyx, Ignacius, Leptacodon, Neoliotomus, Oxyaena, Palaeosinopa, Parectypodus, Peradectes, Phenacodus, Phenacolemur, Plesiadapis, Princetonia, Prodiacodon, Prodinoceras, Thryptacodon, and Viverravus
- Taxa absent but known before and after the Clarkforkian: Entomolestes, Micromomys, Palaeictops, and Thylacaelurus?

ZONATION

Archibald et al. (1987) subdivided the Clarkforkian mammal age into one subzone and two zones based on work by Rose (1980, 1981a) in the Clark's Fork Basin. The first subzone in the Clarkforkian mammal age, the Rodentia/*Plesiadapis cookei* Interval Subzone (Cf1), is the second of two interval subzones in the *P. gingerichi/P. cookei* Lineage Zone (Ti6–Cf1). As mentioned previously, the Ti6–Cf1 lineage zone, as defined by Rose (1980, 1981a), straddles the Tiffanian–Clarkforkian boundary, and Archibald et al. (1987) recognized two interval subzones within it. The Ti6 interval subzone corresponds to the Tiffanian part of the Ti6–Cf1 lineage zone, and the Cf1 interval subzone corresponds to its Clarkforkian part.

The second Clarkforkian zone, the *Plesiadapis cookei* Lineage Zone (Cf2), bears only the name of the species defining the beginning of the zone; the third Clarkforkian zone is not based on the first appearance of a single taxon and therefore is neither a lineage zone nor an interval zone (Archibald et al. 1987). This third zone, the *Phenacodus/Ectocion* Acme Zone (Cf3), is based on the simultaneous abundance of the phenacodontid condylarths *Phenacodus* and *Ectocion* (Archibald et al. 1987).

Recognition of this zonation in strata of the Clark's Fork Basin was augmented by use of species of *Phenacolemur* and *Esthonyx* (see Rose 1981a; Archibald et al. 1987). *Esthonyx xenicus* occurs in the Ti6–Cf1 lineage zone and through the lowest 30 m of strata bearing faunas referable to the Cf2 lineage zone. *Esthonyx ancylion* continues above the 30-m level in strata bearing faunas of the Cf2 lineage zone into about the lowest 20 m of strata with faunas assigned to the Cf3 acme zone. *Esthonyx grangeri* continues through the remainder of the Cf3 acme zone into the Wasatchian mammal age. *Phenacolemur pagei* first appears in the later part of the Tiffanian mammal age and continues into the Clarkforkian mammal age, coexisting with *E. xenicus* and *E. ancylion. Phenacolemur praecox* follows *P. pagei* and, as does *E. grangeri*, continues into the Wasatchian mammal age. Archibald et al. (1987) indicated that although species of *Esthonyx* and *Phenacolemur* may be useful in recognition of Clarkforkian zones, these two genera constitute evolving lineages that are somewhat arbitrarily divided into species.

Rodentia/*Plesiadapis cookei* Interval Subzone (Cf1) of the *P. gingerichi*/*P. cookei* Lineage Zone (Ti6–Cf1) We follow Archibald et al. (1987) and define the Rodentia/*P. cookei* Interval Subzone to include faunas that occurred between the first appearance of the Rodentia and the first appearance of *P. cookei*.

The Cf1 interval subzone can be recognized with certainty only in the Clark's Fork Basin (Archibald et al. 1987). The only other local faunas (in addition to those from the type area in the Clark's Fork Basin) that are referred to this interval subzone are Bear Creek, some sites in the Bighorn Basin, perhaps a site in the Togwotee Pass area west of the Wind River Basin (Archibald et al. 1987), and probably the Big Multi Quarry in the Washakie Basin of southwestern Wyoming (Wilf et al. 1998). The Big Multi Quarry is especially important because it has yielded a large and diverse assemblage (Rose 1981a; Wilf et al. 1998, table 3) and it records the only known Clarkforkian occurrence of the rodent Alagomys (Dawson and Beard 1996). The Big Multi Quarry was previously assigned to the Cf2 lineage zone (Archibald et al. 1987). However, a correlation with the Cf1 interval subzone is now advocated by Wilf et al. (1998) based on additional samples collected from the site beginning in 1992.

Based on paleomagnetic correlations provided by Butler et al. (1981) from the Clark's Fork Basin, the Cf1 interval subzone begins in strata of normal polarity and continues up into those of reversed polarity correlated to magnetic polarity chrons C25n and C24r.

- First appearances: Acritoparamys, Apatosciuravus, Apheliscus, Arctodontomys, Ceutholestes, Chalicomomys, Coryphodon, Dipsalidictides, Haplomylus, Leipsanolestes, Palaeanodon, Paramys, Plagioctenodon, Planetetherium, Tinimomys, and Wyonycteris
- Last appearances: Haplolambda, Lambertocyon, Phenacodaptes, Plesiadapis gingerichi, and Titanoides?
- Index fossils: Alagomys and Protentomodon
- Characteristic fossils: Adunator, Aletodon, Apatemys, Barylambda, Carpolestes, Chiromyoides, Chriacus, Cyriacotherium, Didymictis, Dillerlemur, Dissacus, Ectocion, Ectoganus, Ectypodus, Esthonyx, Ignacius, Leptacodon, Limaconyssus, Microcosmodon, Neoliotomus, Oxyaena, Palaeoryctes, Palaeosinopa, Parectypodus, Per-

adectes, Phenacodus, Phenacolemur, Plesiadapis, Prochetodon, Prodinoceras, Thryptacodon, and Viverravus Taxa absent but known before and after Cf1: Anacodon, Arctostylops, Diacodon?, Dipsalodon, Entomolestes, Micromomys, Palaeictops, Princetonia, Prodiacodon, and Thylacaelurus?

Plesiadapis cookei Lineage Zone (Cf2) *P. cookei* is limited to the middle of the Clarkforkian mammal age. Its appearance marks the beginning of the lineage zone bearing its name, and it is common in this interval. The species disappears abruptly in the Clark's Fork Basin section (and apparently elsewhere), and its absence is characteristic of the succeeding Cf3 acme zone (Rose 1981a). Based on these data, Archibald et al. (1987) defined this lineage zone to include faunas that occurred between the first and last appearances of *P. cookei*. We follow their usage.

Of the three Clarkforkian zones, the Cf2 lineage zone can be recognized over the widest geographic area. In the Clark's Fork Basin section, local faunas referable to the Cf2 lineage zone occur in the middle 200 m of strata containing Clarkforkian faunas (Archibald et al. 1987). Another series of major Cf2 interval zone sites is located in the Bighorn Basin, and these are the Rough Gulch, Foster Gulch, and Ries localities. Rough Gulch and Foster Gulch have yielded P. cookei, the index taxon for the Cf2 lineage zone (Archibald et al. 1987). One of the largest and most diverse Clarkforkian assemblages outside the Clark's Fork or Bighorn basins occurs in the Togwotee Pass area in northwestern Wyoming (Rose 1981a), where P. cookei also has been recovered. The local fauna from Buckman Hollow of the Green River Basin, Wyoming, is another site that yields a mammalian assemblage referable to the Cf2 lineage zone based on many diagnostic taxa including P. cookei (Gazin 1942, 1956c; Archibald et al. 1987). Other areas that might contain Clarkforkian local faunas that might be referable to the Cf2 lineage zone are the Hoback and Wind River basins of Wyoming and the Piceance Creek Basin of Colorado (Kihm 1984).

Paleomagnetic correlations indicate that the Cf2 lineage zone occurs entirely in magnetic polarity chron C24r (Butler et al. 1981).

- First appearances: Aletodon gunnelli, Esthonyx ancylion, Franimys, Microparamys, Niptomomys, Plagiomene, Pontifactor?, Reithroparamys, Uintacyon, and Worlandia
- Last appearances: Anacodon, Chiromyoides, Esthonyx xenicus, Microcosmodon, and Planetetherium?
- Index fossils: Acidomomys, Chiromyoides major, Plesiadapis cookei, and Thelysia

- Characteristic fossils: Adunator, Aletodon, Apatemys, Apatosciuravus, Apheliscus, Arctodontomys, Arctostylops, Barylambda, Carpolestes, Chriacus?, Coryphodon, Cyriacotherium, Diacodon?, Didymictis, Dillerlemur, Dipsalidictides, Dipsalodon, Dissacus, Ectocion, Ectoganus, Ectypodus, Esthonyx, Haplomylus, Ignacius, Leipsanolestes, Leptacodon, Neoliotomus, Oxyaena, Palaeanodon, Palaeoryctes, Palaeosinopa, Paramys, Parectypodus, Peradectes, Phenacodus, Phenacolemur, Plagioctenodon?, Plesiadapis, Princetonia, Prochetodon, Prodiacodon?, Prodinoceras, Thryptacodon, Tinimomys, and Viverravus
- Taxa absent but known before and after Cf2: Acritoparamys, Ceutholestes, Chalicomomys, Entomolestes, Limaconyssus, Micromomys, Palaeictops, Thylacaelurus?, and Wyonycteris

Phenacodus–Ectocion Acme Zone (Cf3) The beginning of the Cf3 acme zone occurs immediately after the last appearance of *Plesiadapis cookei* (Rose 1981a; Archibald et al. 1987). It can be recognized further by the evolutionary first occurrence of *Esthonyx grangeri* and *Phenacolemur praecox*, which make their appearances during but not at the beginning of the zone (Rose 1981a). Archibald et al. (1987) did not offer a formal definition of this zone but noted that the end of the zone is marked by the appearance of Artiodactyla. Other taxa common in the Cf3 acme zone are *Ectocion, Phenacodus, Prodinoceras*, and *Didymictis* (Archibald et al. 1987).

Outside the Clark's Fork and Bighorn basins, no assemblages can be referred with certainty to the Cf3 acme zone (Archibald et al. 1987). The "cf. Late Clarkforkian Local Fauna" from the Piceance Creek Basin of Colorado described by Kihm (1984) may be referable to the Cf3 acme zone because it includes *Phenacolemur* sp. near *P. praecox.*

Paleomagnetic correlations indicate that the Cf3 acme zone occurs entirely within magnetic polarity chron C24r (Butler et al. 1981).

- First appearances: *Esthonyx grangeri*, *Hyopsodus*, *Icaronycteris?*, *Meniscotherium*, *Mimoperadectes?*, and *Phenacolemur praecox*
- Last appearances: Adunator, Aletodon, Apheliscus nitidus, Arctostylops, Carpolestes, Ceutholestes, Cyriacotherium, Dipsalodon?, Dissacus praenuntius, Esthonyx ancylion, Haplomylus simpsoni, Limaconyssus, Palaeoryctes, Prochetodon, and Wyonycteris

Index fossils: Palaeonictis

Characteristic fossils: Apatemys, Apatosciuravus, Apheliscus, Arctodontomys, Barylambda?, Chriacus?, Coryphodon, Didymictis, Dillerlemur, Dipsalidictides, Dissacus, Ectocion, Ectoganus, Ectypodus, Esthonyx, Haplomylus, Ignacius, Leipsanolestes, Leptacodon, Microparamys, Niptomomys, Oxyaena, Palaeanodon, Palaeosinopa, Paramys, Peradectes, Phenacodus, Phenacolemur, Plagiomene, Plesiadapis, Prodiacodon?, Prodinoceras, Thryptacodon, Uintacyon, Viverravus, and Worlandia

Taxa absent but known before and after Cf3: Acritoparamys, Chalicomomys, Diacodon?, Entomolestes, Franimys, Micromomys, Neoliotomus, Palaeictops, Parectypodus, Plagioctenodon, Pontifactor?, Princetonia, Reithroparamys, Thylacaelurus?, and Tinimomys

INTERCONTINENTAL CORRELATIONS

Intercontinental correlations are important in assessing global distribution patterns of mammals, centers of origin for major taxonomic groups, and dispersal events. These sorts of information also provide useful global contexts to questions of detailed correlation of biological and geologic happenings in North America itself. Therefore we briefly discuss Paleocene mammalian assemblages from other continents. We review their proposed correlations to the succession of mammal ages from North America.

EUROPEAN PALEOCENE FAUNAS

Mammalian faunas of earliest Paleocene age are not known from Europe. The sparse mammalian assemblage from Hainin in Belgium appears to be Danian in age and is the oldest known European Paleocene fauna (Russell et al. 1982). The Hainin Local Fauna includes endemic elements mixed with taxa of North American Torrejonian affinity (Vianey-Liaud 1979). There may have been some mammalian dispersal between Europe and North America in the early Paleocene (Savage and Russell 1983). If so, however, it was minor in terms of number of taxa (Woodburne and Swisher 1995).

The next younger Paleocene assemblages in Europe appear to be those from a fissure-fill at the Walbeck site in Germany and the Campo locality in Spain. Based on stage of evolution, the Walbeck assemblage may be a temporal equivalent of the early Tiffanian (Savage and Russell 1983). The Campo locality yields a sparse assemblage of Paleocene mammals (Tambareau et al. 1992) associated with marine fossils that indicate a Thanetian age (Gheerbrant et al. 1997). The Campo assemblage is interpreted to be slightly older than the Walbeck assemblage (Gheerbrant et al. 1997). However, magnetostratigraphic analysis of rocks containing the Campo locality indicate that the site lies close to the boundary between magnetic polarity chrons C26n and
C25r, a paleomagnetic interval that correlates to the Ti4 lineage zone in North America (Gheerbrant et al. 1997).

The Cernaysian mammal age was proposed by Savage and Russell (1983) for a series of mammalian assemblages that occurs in sites located primarily in the Paris Basin of France. There is consensus on a late Paleocene (Thanetian) age assignment for the Cernay faunas (Berggren and Aubry 1998; Lucas 1998), younger than Campo and Walbeck. Cernaysian mammal faunas lack the large herbivores (e.g., pantodonts and uintatheres) present in presumably temporally equivalent assemblages from North America. Cernaysian assemblages show some taxonomic resemblance to late Paleocene North American faunas, but this may principally reflect inherited vestiges from preceding faunas rather than solid evidence of dispersals (Savage and Russell 1983).

The Cernay Conglomerate (type Cernaysian) is overlain by the Argile Plastique, which yields a dramatically different assemblage of mammals of Sparnacian age (Savage and Russell 1983). European Sparnacian faunas are similar to North American Wasatchian faunas, and therefore the Cernaysian is certainly older than Wasatchian. Younger Cernaysian faunas probably are a temporal equivalent of the Ti6–Cf1 lineage zone based on comparisons of lineages of plesiadapids (Rose 1981a; Gingerich 1976; Gingerich and Rose 1977). However, Wing (1984) suggested that Cernaysian faunas correlate with later Tiffanian rather than early Clarkforkian faunas. Lucas (1998), in further contrast, considers the Cernaysian to be correlative with the Clarkforkian.

Recently, a sparse mammalian assemblage was reported from the "Calcaires de Rona," Transylvania, Romania (Gheerbrant et al. 1999). The fauna, which includes an incisor fragment referred to Rodentia, is the oldest mammalian assemblage known from eastern Europe. Based on preliminary analysis, the fauna may be a Clarkforkian equivalent (Gheerbrant et al. 1999). Another small assemblage of mammals recently reported from Spain may also be a Clarkforkian equivalent (Lopez-Martinez and Pelaez-Campomanes 1998).

THE PALEOCENE-EOCENE BOUNDARY

The Paleocene–Eocene boundary has long been controversial because of the paucity of biostratigraphic sections spanning the boundary and ambiguity in original definition of the nonmarine Paleocene in conjunction with the marine Eocene sections. The Paleocene Epoch was named by Schimper (1874) for a distinctive terrestrial flora that held plants then considered to have both a Cretaceous and an Eocene aspect. Schimper's Paleocene floras came from rocks in the Paris Basin, different strata of which now are assigned to the Thanetian, Sparnacian, and Cuisian ages. At about the same time, Gervais (1873) reported a distinctive assemblage of terrestrial vertebrates, also then thought to exhibit Cretaceous and Eocene aspects, from the Cernay Conglomerate in the Paris Basin. Later, Gervais (1877) described more specimens from the Paris Basin including *Plesiadapis tricuspidens* and proposed a new faunal interval between those characteristic of the Cretaceous and Eocene.

Paleocene and early Eocene mammals have been studied intensively in Europe since the time of Gervais. The Cernay fauna (and Cernaysian mammal age) is accepted as late Paleocene, whereas Sparnacian faunas are generally regarded as early Eocene. Sparnacian faunas differ from those of the Paleocene in having the modern, cosmopolitan orders Perissodactyla, Artiodactyla, and Primates, along with representatives of the Hyaenodontidae. There are several problems with study of Paleocene-Eocene vertebrate faunas in Europe. Many samples come from isolated exposures, there are few thick stratigraphic sections, and deposition near sea level means that substantial hiatuses are common (Pomerol 1989; Dashzeveg 1988; Hooker 1998). These uncertainties are compounded by the fact that the Paleocene-Eocene boundary is currently placed at two different stratigraphic levels separated by approximately 1 m.y. (Berggren and Aubry 1998; Aubry et al. 1999). One level, based on micropaleontology, is the base of the Ypresian Stage (narrowly interpreted to exclude Sparnacian strata), which corresponds approximately to the NP9/NP10 (calcareous nannofossil) and P5/P6 (planktonic foraminiferal) zonal boundaries. The second is the base of the Sparnacian Stage, which corresponds to major turnover in mammalian assemblages. Although the latter is based mainly on fossil mammals, it may correlate approximately with the P4/P5 zonal boundary (Aubry et al. 1999).

The zone of uncertainly between the two stratigraphic levels apparently occurs in magnetic polarity chron C24r (see figure 1 in Berggren et al. 1995 and figure 2.2 in Berggren and Aubry 1998). A highly significant negative carbon isotope excursion is associated with "type" ("lower") Sparnacian mammals in the Paris Basin and with global extinction or turnover of benthic foraminiferans in marine sections (Hooker 1998; Berggren and Aubry 1998; Steurbaut et al. 1999 and references therein). Documentation of a carbon isotope excursion associated with latest Clarkforkian and Wasatchian mammals (Koch et al. 1992; Bowen et al. 2001; Bains et al. 2003) is seen more clearly in Wyoming than in association with Sparnacian mammals of Europe. A carbon isotope excursion associated with earliest Bumbanian mammals has recently been identified in Asia (Bowen et al. 2002; Ting et al. 2003). Assuming that these various carbon isotope excursions represent the same event recognizable on a global scale, they provide a geochemical means of correlating nonmarine and marine rocks between continents and marine basins.

The North American record of vertebrate change across the Paleocene-Eocene boundary is more continuous and more complete than in Europe. Indeed, the former may eventually hold a reference nonmarine global stratotype section and point (GSSP) for the series boundary (Lucas 1998). In the Clark's Fork and northern Bighorn basins of Wyoming, a stratigraphic section about 2300 m thick spans much of late Paleocene (Tiffanian and Clarkforkian mammal ages) and early Eocene (Wasatchian) time. Recent work in that area has concentrated on Wasatchian biostratigraphy and faunal change (Gingerich 1989, 1991; Clyde and Gingerich 1998). As in Europe, Plesiadapis is present in North American Paleocene faunas. Rodents, tillodonts, Haplomylus, and Coryphodon appear at or near the beginning of the Clarkforkian, and perissodactyls, artiodactyls, primates (including Cantius), and hyaenodontids appear at the beginning of the Wasatchian. Late Paleocene mammals tend to be endemic on the northern continents. In contrast, Wasatchian mammals in North America are part of a Holarctic assemblage that appears at or near the beginning of Eocene time in Europe (Hooker 1998) and central Asia (Meng and McKenna 1998).

Therefore, the presumed boundary between Paleocene and Eocene time is sharply distinct on all three northern continents. In North America, the age of the Clarkforkian-Wasatchian faunal turnover is constrained in two ways. Paleomagnetic stratigraphy has been studied in two nearby areas by Butler et al. (1981, 1987) and Clyde et al. (1994). The early Wasatchian falls in chron C24r. Interpolation using the numerical calibration of Cande and Kent (1995) places the base of the Wasatchian near or slightly before 55.0 Ma. Carbon isotope stratigraphy has been studied by Koch et al. (1992, 1995), and the negative carbon isotope excursion interpreted as correlative with extinction of benthic foraminifera falls in the earliest parts of the Wasatchian. The beginning of the carbon isotope excursion occurs at approximately 54.95 Ma, with the event lasting 120–220 k.y. (Norris and Rohl 1999; Rohl et al. 2000). Thus major mammalian turnovers at the Cernaysian-Sparnacian and Clarkforkian-Wasatchian boundaries appear to coincide with two other major events, a benthic foraminiferal extinction and a carbon isotope excursion. Although agreement on final placement of the Paleocene-Eocene boundary remains unresolved, the International Geological Correlation Programme (IGCP) Paleocene–Eocene boundary working group formally voted recently that the boundary will be linked to the carbon isotope excursion (Luterbacher et al. 2000).

In any event, the North American record of mammalian evolution across the Paleocene–Eocene boundary is exceptionally complete, and it corroborates the sharp distinction of Paleocene and Eocene mammalian faunas first discovered in Europe. A major dispersal of mammals occurred between Europe and North America in the latest Paleocene or earliest Eocene. Wasatchian and Sparnacian mammalian assemblages of the two continents are very similar, more so than during any other time of the Cenozoic (Savage and Russell 1983). Dispersal was aided by sea level lowstands in a time of high sea level (Haq et al. 1987; Woodburne and Swisher 1995). The route probably was via a corridor between Greenland, Spitzbergen, and adjacent land masses (McKenna 1975, 1983).

ASIAN PALEOCENE FAUNAS

In recent years, the number of depositional basins reported from China and Mongolia that yield Paleocene mammals has increased significantly. The total now stands at 12 in China and 2 in Mongolia (Wang et al. 1998; Ting 1998). In tandem with the increased knowledge of Paleocene mammalian assemblages from China and Mongolia, three Asian land mammal ages-the Shanghuan, Nongshanian, and Gashatan-have now been formally named and defined (Ting 1998). The names Shanghuan and Nongshanian were first proposed by Li and Ting (1983), but they were not defined. Romer (1966) proposed the term Gashatan, which was later defined by Szalay and McKenna (1971). In defining the Shanghuan, Nongshanian, and Gashatan, Ting (1998) uses a system similar to that used for NALMAs, in which biochronologic units are defined by successive appearances of unrelated taxa.

In contrast to those from North America, Paleocene mammalian assemblages from Asia were dominated by anagalids, pantodonts, and, to a lesser extent, mesonychids (Wang et al. 1998; see tables 1–3 and figures 4–6 in Ting 1998). Also, no species and only a few genera (*Dissacus, Prodinoceras, Coryphodon,* and perhaps *Oxyaena*) are shared between North America and Asia in strata of undoubted Paleocene age (Wang et al. 1998; Ting 1998). Thus Asian Paleocene mammalian assemblages display endemism, especially before the late Paleocene. As a result, proposed correlations between Asian and North American mammal ages remain tentative. The Shanghuan Asian land mammal age was defined by Ting (1998) to include the time between appearance of the Pantodonta, represented by *Bemalambda*, and the first appearance of the Arctostylopida, represented by *Asiostylops*. Ting (1998) also subdivided the Shanghuan into two interval zones, the *Bemalambda* and *Archaeolambda* interval zones.

Correlation between the Shanghuan mammal age and those of the North American Paleocene have been based on comparisons of stage of evolution using taxa that are largely endemic. Thus Shanghuan assemblages (*sensu* Li and Ting 1983) and the Shanghuan land mammal age as defined by Ting (1998) have been regarded variously as correlative to the Tiffanian (Savage and Russell 1983), Torrejonian (Ting 1998), Torrejonian and latter part of the Puercan (Zhou et al. 1977; Li and Ting 1983; Sloan 1987; Mateer and Chen 1992; Russell et al. 1993), Puercan and all but the latter part of the Torrejonian (Wang et al. 1998), and Puercan (Lucas and Williamson 1995).

Paleomagnetic correlations and radiometric dating techniques are helpful in assessing correlations between Asia and North America. Paleomagnetic data from the Nanxiong Basin suggest that the Shanghuan spans the latter part of polarity chron C29r through C27r (Zhao et al. 1991). Also, paleomagnetic data from the Shanyang Basin indicate that Bemalambda occurs in rocks of reversed polarity correlated with chron C27r (Xue et al. 1994, 1996). Magnetic polarity correlations in North America indicate that the interval from the latter part of C29r through C27r spans the Puercan and most of the Torrejonian. Also, magnetic polarity chron C27r would be approximately correlative to the To2 interval zone (see figure 3.2). The only radiometric date associated with rocks yielding Paleocene mammals in China comes from the Xinzhou Basin. There, intrusive basaltic rocks thought to be younger than beds bearing Paleocene mammals yield a date of 61.63 ± 0.92 (Wang et al. 1998), which is consistent with correlation to chron C27r or the Torrejonian mammal age (figure 3.2; see also Berggren et al. 1995; Cande and Kent 1995).

Lucas and Williamson (1995) argue that the sudden appearance in North America, the lack of older North American close relatives, and the presence of older, more primitive Shanghuan relatives in China supports an Asian origin and immigration of Paleocene mammalian groups. Specifically, they suggest dispersal to North America of Carnivora, Mesonychia, Pantodonta, and Tillodontia at about the beginning of Torrejonian time. However, the presence of an earlier and possibly more plesiomorphic carnivoran (*Ravenictis krausei*) from the Puercan of Saskatchewan (Fox and Youzwyshyn 1994) might suggest a North American origin for the Carnivora. The Nongshanian Asian land mammal age was defined by Ting (1998) to include the time between the first appearance of the Arctostylopida, represented by *Asiostylops*, and the first appearance of Rodentia, represented by *Tribosphenomys*. Ting (1998) subdivided the Nongshanian into the *Asiostylops* and *Sinostylops* interval zones. Dinocerata and the families Phenacolophidae and Ernanodontidae (Edentata?) made their first appearance in Asia during the Nongshanian (Ting 1998).

Paleomagnetic and radiometric data are not available from strata that yield mammalian assemblages assigned to the Nongshanian mammal age. Correlations between Asia and North America for the Nongshanian are very uncertain, therefore, because they are based on comparisons between faunas that are largely endemic. First occurrences of the orders Arctostylopida and Dinocerata in both the Nongshanian and the Tiffanian (Ti5 lineage zone) nevertheless suggest correlation between the Tiffanian and the Nongshanian (Ting 1998). A strong sea level lowstand in the medial Tiffanian (Woodburne and Swisher 1995) may have contributed to the presumed exchange of these taxa between Asia and North America. Beard and Dawson (1999) correlated the Nongshanian with the late Torrejonian and the first half of the Tiffanian. Similarly, Wang et al. (1998) correlated the Nongshanian with the late Torrejonian through middle Tiffanian (To3-Ti4). They based their correlation on the conclusion by Cifelli et al. (1989) that the Nongshanian arctostylopids (Bothriostylops and Sinostylops) are more primitive than the Tiffanian (Ti5) Arctostylops. Also, Ernanodon, the supposed edentate from China, known from both the Nongshanian and Gashatan mammal ages, could suggest a faunal tie to South America, presumably via North America during the middle to late Paleocene.

The Gashatan Asian land mammal age was defined by Ting (1998) to include the time between the appearance of Rodentia, represented by *Tribosphenomys*, and the first appearance of Perissodactyla, represented by *Orientolophus*. In contrast to the Shanghuan and Nongshanian mammal ages, subdivision of the Gashatan mammal age into interval zones was not proposed.

Archibald et al. (1987) used the first occurrence of Rodentia in North America to define the beginning of the Clarkforkian mammal age, a definition that we follow in this update. Tillodontia (minus *Deltatherium*) and *Coryphodon* also apparently occurred synchronously with Rodentia in the earliest Clarkforkian (Archibald et al. 1987), and these first occurrences in North America may reflect dispersals from Asia across Beringia or the Euramerican corridor (Krause and Maas 1990; Woodburne and Swisher 1995). 92 Donald L. Lofgren, Jason A. Lillegraven, William A. Clemens, Philip D. Gingerich, and Thomas E. Williamson

Ting (1998) correlated the Gashatan with the Clarkforkian mammal age in North America based mainly on the first occurrences of Rodentia and the pantodont family Coryphodontidae in both the Gashatan and Clarkforkian ages. In contrast, Wang et al. (1998) tentatively correlated the Gashatan with the late Tiffanian through Clarkforkian based on similarities between Asian and North American arctostylopids and dinoceratans. Beard (1998) and Beard and Dawson (1999) argued that dispersal of mammals rarely coincides precisely with their phylogenetic origin. They reasoned further that the beginnings of the Gashatan and Bumbanian mammal ages probably are older than the Clarkforkian and Wasatchian, respectively. Recognition of a carbon isotope excursion in the earliest Bumbanian confirms that the Gashatan-Bumbanian boundary coincides closely with both the Clarkforkian-Wasatchian and Paleocene-Eocene boundaries (Bowen et al. 2002; Ting et al. 2003).

AFRICAN PALEOCENE FAUNAS

The only known mammalian faunas of Paleocene age from all of Africa are from the Ouarzazate and Ouled Abdoun basins of Morocco. Mammals from the Ouarzazate Basin were first reported by Cappetta et al. (1978). The assemblage from the Ouarzazate Basin is diverse, including palaeoryctids, adapisoriculids, ?creodonts, carnivores, condylarths, todralestids, and an omomyid primate (Sige et al. 1990; Sudre et al. 1993; Gheerbrant 1991, 1992, 1994, 1995). Fossils of these taxa were recovered primarily from two localities in the Jbel Guersif Formation: Adrar Mgorn 1 and Ihadjamene (Gheerbrant et al. 1993). The Jbel Guersif Formation is thought to be Thanetian based on chondrichthyians (Cappetta et al. 1987). Thanetian is considered late Paleocene in age (Berggren et al. 1995). Paleomagnetic study of the Jbel Guersif Formation in the vicinity of Adrar Mgorn 1 indicates that the site occurs in rocks of reversed polarity that reasonably could be correlated either to magnetic polarity chron C25r or C24r (Gheerbrant et al. 1998b). Compared with correlations of magnetic polarity chrons with mammal ages in North America, Adrar Mgorn 1 would correlate with late phases of the Tiffanian if C25r is correct or Clarkforkian if C24r is correct.

Before the late 1990s, the phosphates of the Ouled Abdoun Basin yielded two mammalian specimens, both of which were identified as *Phosphatherium*, interpreted to be the oldest known proboscidean(Gheerbrant et al. 1996, 1998a). The locality from which the specimens were derived was unknown, but analysis of matrix from the specimens confirmed its phosphatic nature. Foraminifera and tiny chondrichthyian teeth from the matrix also indicated a Thanetian age (Gheerbrant et al. 1996, 1998a). However, additional specimens of *Phosphatherium* were recently collected from strata in the Ouled Abdoun Basin that have been reported as Ypresian or early Eocene in age (Gheerbrant et al. 2001).

Paleocene faunal comparisons between North America and Africa are limited by endemism, but there is some relationship at the familial level (palaeoryctids), and the genera *Cimolestes* and *Palaeoryctes* are found on both continents (Gheerbrant et al. 1998b). In North America, *Cimolestes* is known from the Lancian and Puercan, and *Palaeoryctes* is known from the mid-Torrejonian to late Clarkforkian. The antiquity of cimolestids in North America suggests a dispersal event between North America and Africa, probably via Europe, in the early Paleocene (Gheerbrant 1990).

SOUTH AMERICAN PALEOCENE FAUNAS

Paleocene mammalian assemblages from South America are large, diverse, and dominated by endemic types of marsupials, leptictids, notoungulates, litopterns, and condylarths, along with lesser numbers of trigonostylopoids, astrapotheres, xenungulates, and xenarthrans. One species each of an enigmatic multituberculate-like gondwanathere (Krause et al. 1997; Pascual et al. 1999), a pantodont (de Muizon and Marshall 1992), and a monotreme (Pascual et al. 1992) also are present. The South American Paleocene fauna is distinctly different from those of probable Campanian-Maastrichtian age (the Los Alamitos and La Colonia local faunas of Argentina; see Bonaparte 1990; Pascual et al. 2000). These Late Cretaceous mammalian faunas are composed of a variety of nontherian mammals, a faunal assemblage dubbed the "Gondwanan Stage" by Pascual (see Pascual et al. 2000 and references therein). During an interval after the last records of the "Gondwanan Stage," which has been estimated to be approximately 10 m.y. (Pascual 1998), most of these Gondwanan nontherian lineages became extinct. For the most part, South American Paleocene mammalian faunas are made up of immigrants or descendants of immigrants from Laurasian continents (Luo et al. 2001).

Paleocene mammalian assemblages are known from four main areas of South America: Laguna Umayo, southeastern Peru; the Andean Basin of northwest Argentina and southern Bolivia (includes Tiupampa and Tres Cruces); Itaborai, southeastern Brazil; and the San Jorge Basin of southern Argentina (includes the Rio Chico and Punta Peligro faunas). Marshall and Sempere (1993) reviewed the Cenozoic land mammal record of South America and recognized three South American land mammal ages: the Tiupampian (early but not earliest Paleocene), including the faunas from Laguna Umayo and Tiupampa; the Itaboraian (middle? Paleocene to early Eocene?), including the fissure fill faunas from Itaborai; and the Riochican (late Paleocene), including faunas from the Rio Chico Formation. Marshall and Sempere (1993) also noted the lack of geochronologic control for the Itaborai faunas, which Savage and Russell (1983) included in the Riochican age.

More recently, Marshall et al. (1997) proposed a refined zonation for Paleocene land mammal faunas of South America, suggested that all these faunas are of late Paleocene age, and identified two mid- to late Paleocene interchange events between North and South America. Their refined zonation and new correlation were based on revised calibration of the Paleocene mammalian local faunas from the southern Andean Basin using regional stratigraphy and magnetostratigraphy (Sempere et al. 1997) along with reassessment of the ages of local faunas from the San Jorge Basin and Itaborai. Marshall et al. (1997) recognized a single Riochican South America land mammal age (spanning 60.0-55.5 Ma) with four subages. Listed chronologically, they are the Peligrian (based on sparse faunas from Tres Cruces in the Andean Basin and Punta Peligro in the San Jorge Basin), Tiupampian, Itaboraian, and Riochican (sensu stricto). Marshall et al. (1997) did not propose a definition or characterization of their Riochican age or any of its four subages. This reassessment by Marshall et al. (1997), which suggests that no known mammalian assemblage from South America predates 60 Ma, is a radical departure. Earlier interpretations of faunal data from Tiupampa suggested an age of approximately 64-63 Ma, if correlations to North American faunas are accurate (Van Valen 1988; Williamson 1996).

To provide a structure for evaluating these conflicting interpretations, we will discuss South American Paleocene mammal faunas and their correlation to NALMAs in the context of their four main geographic areas (Laguna Umayo, Andean Basin, Itaborai, and San Jorge Basin). The new calibration of Paleocene mammalian faunas from the Andean Basin, reassessment of the age of other local faunas, and the refined zonation for Paleocene land mammal faunas of South America proposed by Sempere et al. (1997) and Marshall et al. (1997) will be addressed where appropriate.

The Laguna Umayo Local Fauna described by Sige (1972) is from a red bed succession (Umayo Formation) exposed near Lake Titicaca in southeastern Peru. More

recently, Crochet and Sige (1993) reported another mammalian assemblage from the Umayo Formation that was recovered about 200 m stratigraphically higher than the Laguna Umayo Local Fauna. The magnetostratigraphic section of the Umayo Formation is entirely of reversed polarity (Sige et al. in prep., cited in Marshall et al. 1997), so correlation to the GPTS is difficult. Various correlations to magnetic polarity chrons (C29r, C28r, C27r, or C26r) are possible, and egg shells of dinosaurs or large ground birds are associated with the mammals (see Marshall et al. 1997 for discussion). Therefore reasonable age assignments for the mammalian assemblages from the Umayo Formation based on available data vary from Late Cretaceous to late Paleocene.

The Andean Basin of northwestern Argentina and southern Bolivia yields the Tiupampa Local Fauna, one of the best-known Paleocene mammalian assemblages in South America. The Tiupampa Local Fauna from the Santa Lucia Formation of south-central Bolivia includes a large and diverse assemblage of mammals. It includes several groups of marsupials and members of the placental orders Pantodonta, Leptictida, Condylarthra, and Notoungulata (de Muizon and Marshall 1992; Marshall et al. 1997). This fauna was originally assigned a Late Cretaceous age, but later it was considered to represent the early Paleocene (de Muizon and Marshall 1992; Marshall and Sempere 1993 and references therein).

The Tiupampa Local Fauna includes two mioclaenids, *Tiuclaenus* and *Molinodus*, along with the only known South American pantodont, *Alcidedorbignya*. The mioclaenids represent a distinct stock (Williamson 1996) and have been assigned to an endemic subfamily, Kollpaniinae (de Muizon and Cifelli 2000). Currently, the oldest records of mioclaenids in North America (five genera) are from the Pu2 interval zone. The contemporaneous appearances of such diverse genera strongly suggests an earlier radiation of the group in an as yet unsampled area outside the Western Interior of North America.

The South American pantodont *Alcidedorbignya* may be more primitive than the earliest known North American pantodonts. The presence of primitive molar characters in several Asian taxa and their absence in North and South American pantodonts points to an Asiatic origin for the group (de Muizon and Marshall 1992). Also, de Muizon and Marshall (1992) suggested that presence of *Alcidedorbignya* in South America in the early Paleocene requires a Maastrichtian (Late Cretaceous) or older, Asia to South America, via North America, dispersal route for pantodonts. However, the earliest North American pantodont is *Pantolambda intermedium* from the To2 interval zone in the San Juan Basin (Williamson 1996). Therefore presence of *Alcidedorbignya*, as well as *Tiuclaenus* and *Molinodus*, in the Tiupampa Local Fauna suggests a pre-Torrejonian age for dispersal of primitive ungulates from North America to South America and a dispersal of Pantodonta to South America from Asia predating the San Juan Basin occurrence (To2) in North America. Similarly, based on comparison of the fauna of placental mammals from Tiupampa with those from the Paleocene of North America, Van Valen (1988) correlated the Tiupampa Local Fauna to the late Puercan or early Torrejonian (approximately 64–63 Ma).

Recent stratigraphic and magnetostratigraphic correlations proposed by Sempere et al. (1997) indicate that the section of the Santa Lucia Formation containing the Tiupampa Local Fauna is of reversed polarity, which they correlate to magnetic polarity chron C26r or about 59 Ma. Based on this interpretation, the Tiupampa Local Fauna would be about mid-Tiffanian in age and thus much younger than previously thought. However, the magnetostratigraphic correlation proposed by Sempere et al. (1997) for the Tiupampa Local Fauna depends heavily on the accuracy of their correlation of the magnetostratigraphic sequence at La Palca (which includes the El Molino Formation and the overlying Santa Lucia Formation) to the GPTS. It is important to note that the La Palca magnetostratigraphic section is complicated and records many geomagnetic polarity reversals (see figure 10 in Sempere et al. 1997). A single radioisotopic date $(72.1 \pm$ 0.5 Ma) from the lower part of the El Molino Formation is used to correlate the lower part of the paleomagnetic section to the GPTS (Sempere et al. 1997). Radioisotopic data are not available for the Santa Lucia Formation. With this degree of uncertainty in correlation to the GPTS, more than one interpretation is plausible. Thus the reversed polarity section of the Santa Lucia Formation at Tiupampa might correlate with magnetic polarity chron C28r or perhaps C27r. Either chron would be more in agreement with the faunal correlations proposed by Van Valen (1988) and Williamson (1996).

At Sao Jose de Itaborai, inland from Rio De Janeiro, Brazil, a large and diverse assemblage of mammals was collected from marl fills in karst cavities that developed in limestones of the Sao Jose de Itaborai Formation (Savage and Russell 1983 and references therein). Based on the Itaborai fauna, an Itaboraian mammal age was proposed by Paula Couto (1952), but it was later placed in the Riochican mammal age (Savage and Russell 1983). Recently, Marshall et al. (1997) proposed that karst formation and infilling at Itaborai coincided with the large sea level lowstand between 58.5 and 56.5 Ma recognized by Haq et al. (1987). This sea level lowstand would correlate approximately with the late Paleocene (late Tiffanian) interval of dispersal advocated by Gingerich (1985), in which representatives of the Dinocerata, Notoungulata (represented by Arctostylopidae), and Edentata dispersed from South America to North America. Because of its fissure fill provenance, the mammalian assemblage from Itaborai remains unconstrained geochronologically.

The last area of South America known to yield Paleocene mammals is the San Jorge Basin, located in southern Argentina. There, a succession of mudstone and sandstone beds, which yields a diverse and endemic assemblage of mammals, is referred to the Rio Chico Formation. The Rio Chico Formation probably is no older than late Paleocene. It is superposed on the marine Salamanca Formation, which has been correlated with the Dano-Montian Stage of Europe based on foraminiferans (Loeblich and Tappan 1957; Savage and Russell 1983). The age of the Itaborai fauna was approximately correlated with mammalian assemblages from the Rio Chico Formation. Together, they were considered to represent the Riochican mammal age of late Paleocene age (Simpson 1940; Savage and Russell 1983).

The mammalian assemblages from the Rio Chico Formation occur near the Atlantic coast, and Marshall et al. (1997) attempted to correlate lithologic changes with transgressive-regressive cycles proposed by Haq et al. (1987). Marshall et al. (1997) identified several guide levels in the detailed sections provided by Simpson (1935b) and Feruglio (1949). Combining these guide levels and lithologic changes with paleomagnetic data from Cerro Redondo (Marshall et al. 1981) and other stratigraphic sections, Marshall et al. (1997) developed a tentative correlation of mammal-bearing sections of the Rio Chico Formation (see figure 6 and table 2 in Marshall et al. 1997). They were able to distinguish at least four distinct ages of mammalian assemblages in the Rio Chico Formation. The oldest assemblage, containing South America's only known occurrence of Monotremata, Monotrematum (Pascual et al. 1992), comes from the Banco Negro Inferior at Punta Peligro, which Marshall et al. (1997) dated at approximately 60 Ma. The fauna from the Banco Negro Inferior and that from Tres Cruces in the Andean Basin form the Peligrian subage (Marshall et al. 1997). The lower mammal-bearing levels at Bajo de la Palangana and Cerro Redondo are interpreted to have been deposited about 59 Ma. They are considered approximate equivalents of the Tiupampa fauna from the Andean Basin. These three faunas form the Tiupampian subage (Marshall et al. 1997). The remainder of the mammalian assemblages from the Rio Chico Formation are referred to the Itaboraian or Riochican subages, interpreted to range from 58.0 to 56.0 Ma (Marshall et al. 1997).

In summary, based on similarity of faunas, there appear to have been two distinct intervals of dispersal between North and South America. The older occurred in the early Paleocene, perhaps during the late Puercan or early Torrejonian. Faunal data from Tiupampa and Puercan and early Torrejonian sites in North America suggest a connection between the continents in the early Paleocene (de Muizon and Marshall 1992; Van Valen 1988; Williamson 1996). However, recent biostratigraphic and geochronologic correlations proposed by Sempere et al. (1997) and Marshall et al. (1997) suggest that the Tiupampa Local Fauna is significantly younger than the early Paleocene. The second interval of dispersal was during the late Paleocene, probably in the late Tiffanian (Gingerich 1985; Marshall et al. 1997). Unlike the earlier interval, proposed geochronologic correlations between the Americas indicate that the late Tiffanian faunas of North America are approximate time equivalents of the Itaboraian and Riochican subages of the Riochican mammal age of Marshall et al. (1997) or the Riochican mammal age of Savage and Russell (1983).

SUGGESTIONS FOR FUTURE RESEARCH

With the publications by Wood et al. (1941) and Archibald et al. (1987), North American land mammal ages have become widely accepted biochronologic units. However, this does not mean that these mammal ages could ever replace a detailed chronostratigraphic framework for continental strata deposited in North America during the Paleocene; definitions and characterizations of mammal ages and zones still rely heavily on faunal data. Is a truly chronostratigraphic framework of stages based on tighter stratigraphic control of mammalian faunas possible for the North American Paleocene? Yes, but this will entail continued emphasis on developing detailed biostratigraphic and stratigraphic fieldwork coupled with reanalysis of previously published biostratigraphic data from a number of well-studied basins in western North America. That is, we must continue to gather additional faunal data from local sections with determinable superpositional relationships, interpret the data in terms of biogeographic provinces, and then correlate to other faunal provinces based on comparison of detailed faunal successions. Research in each area must be followed by refinement of correlation within and between provinces through use of magnetostratigraphy. Finally, temporal calibration using radioisotopes must be applied if possible. Further refinement of the Puercan through Clarkforkian mammal ages and development of greater solidity of the chronostratigraphic framework is desirable and should be a high priority for future research.

To aid in developing a firmer chronostratigraphic framework, in concert with additional biostratigraphic data, sampling rocks associated with mammalian faunas for magnetostratigraphic and radioisotopic analysis should be emphasized. Only one Lancian to early Torrejonian sequence of rocks (encompassing the upper Hell Creek and Tullock formations in eastern Montana) has undergone all three (biostratigraphic, magnetostratigraphic, and radioisotopic) primary types of analyses (Swisher et al. 1993; Clemens 2002). In fact, the radioisotopic dates from Montana are among the few associated with Paleocene mammalian faunas in North America. Granted, the paucity of available data is partially a factor of the rarity in many Paleocene basins of rocks suitable for isotopic analysis. But some areas known to have Paleocene mammals and volcanic units suitable for dating remain unsampled. For the time being, magnetostratigraphy remains a primary method of providing independent checks on faunal correlation for mammal-bearing sections throughout western North America. Wherever possible, additional paleomagnetic data should be obtained from mammalbearing rocks.

Finally, the available record of Paleocene mammalian faunas is geographically concentrated in northern and midcontinental Rocky Mountain states, from the San Juan Basin of New Mexico north to Alberta, Canada. Significant faunal provinciality is evident in comparisons between mammalian assemblages from New Mexico and Montana to southern Canada (for example, see the discussion of Pu2 and Pu3 interval zones). Wyoming shows varying intermediacies, with greater affinities to the south during the Puercan and greater northward affinities during the late Torrejonian and early Tiffanian. Therefore additional faunal data are needed throughout all latitudes of the North American continent to fully assess temporally shifting patterns of faunal distribution. Although Paleocene nonmarine rocks that yield mammals are known from southwest Texas and southern California, faunal data available from these areas are sparse. Also, Mexico has yet to yield Paleocene mammals. But because Cretaceous and Eocene mammals are known from that country, it is only a matter of time until Paleocene mammals are discovered. The same can be said for Alaska because nonmarine strata of proba96 Donald L. Lofgren, Jason A. Lillegraven, William A. Clemens, Philip D. Gingerich, and Thomas E. Williamson

ble Paleocene age are exposed along the banks of some of the major rivers on its North Slope.

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Paleocene Biochronology: The Puercan Through Clarkforkian Land Mammal Ages 97

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4

Wasatchian Through Duchesnean Biochronology

• HE PREVIOUS EDITION of this chapter (Krishtalka et al. 1987) assembled much information about the areal distribution and biochronology of the continental rocks and faunas representing the Wasatchian through Duchesnean North American land mammal ages (NAL-MAs). That edition detailed the history of the classification of terrestrial rocks, particularly of western North America, and included some information on radioisotopic and paleomagnetic determinations. This revision concentrates on the inclusion of new data and includes expanded information concerning Mexico and Canada. We introduce new information about radioisotopic ages and paleomagnetic correlations. Wherever possible, we include data from unpublished sources and do not repeat data already cited in detail. The bibliography is as inclusive as possible. We stress field information.

Recently the definition of the Paleocene-Eocene boundary has been reviewed and is still under discussion (Aubry 1996, 1998, 2000; Berggren and Aubry 1998; Gingerich 1989, 2000; Gunnell 1998b; Koch et al. 1992). A recommendation has been put forward to locate the lower boundary of the Eocene at the negative carbon isotope excursion (CIE) in chron C24r (Koch et al. 1992; Gingerich 2001), at the beginning of the Wasatchian land mammal age (LMA) in North America. The base of the Wasatchian is marked by a major vertebrate faunal immigration event including the widespread dispersal in the Northern Hemisphere of the orders Artiodactyla, Perissodactyla, and Primates, as well as hyaenodontid Creodonta. The ultimate location of the Paleocene-Eocene boundary is in some sense irrelevant to the goals of this chapter (but see "Geochronology" later in this chapter), Peter Robinson, Gregg F. Gunnell, Stephen L. Walsh, William C. Clyde, John E. Storer, Richard K. Stucky, David J. Froehlich, Ismael Ferrusquia-Villafranca, and Malcolm C. McKenna

which is refinement of Wasatchian through Duchesnean biochronology. This biochronologic framework will remain unaffected by the ultimate placement of the Paleocene–Eocene boundary, which may be placed at the Dababiya section in Egypt (Aubry 2001). It is clear that most of the Wasatchian and all of the Bridgerian through Duchesnean will be recognized as representing the Eocene and contingent on the final position of the Global Stratotype Section and Point (GSSP), all of the Wasatchian may ultimately be included in the Eocene. The Chadronian LMA is considered latest Eocene (Swisher and Prothero 1990) but is addressed in the following chapter.

The prior edition of this chapter pointed out that the terminology for the NALMA discussed was based on formational names and that the resulting confusion of the differences between what is contained in a rock unit and what is contained in a temporal unit with essentially the same name is regrettable, even though the temporal boundaries are flexible (Wilson 1975). This situation has not changed significantly for the LMAs in the intervening years, although there has been much more precision in the methods of collecting and recording data, and subdivisional terminology has helped. That the inconsistencies of the Wood committee (Wood et al. 1941) remain is obvious, but they are recognized as such. Many assemblages have been studied since the publication of the Wood committee report. Faunal sequences in several of these show that the age boundaries are not, need not be, and probably should not be synchronous with lithostratigraphic boundaries. For example, in several subunits of the Greater Green River Basin, Bridgerian mammals have

been recovered from rocks referred to the upper part of the Cathedral Bluffs Tongue of the Wasatch Formation, and Uintan mammals have been recovered from beds high in the Bridger Formation (Evanoff et al. 1994). Most of the lower part of the Duchesne River Formation is Uintan in age, whereas some of the lower part and the upper part are Duchesnean (Gazin 1955; Clark et al. 1967; Tedford 1970). Table 4.1 lists the more significant Wasatchian through Duchesnean fossil mammal localities relevant to this chapter.

The four NALMAs discussed here are based on mammalian fossil assemblages (figure 4.1) from two Rocky Mountain basins: the western Green River Basin (Wasatchian and Bridgerian) and the Uinta Basin (Uintan and Duchesnean). This terminology has been correlated outward from these two basins and is used throughout North America. The term Wasatchian is derived from the Wasatch Formation and its faunas in the Greater Green River and Fossil basins; all of the Wasatchian subages are actually derived from the faunal content of the Willwood and Wind River Formations (Sandcouleean, Graybullian, Lysitean, and Lostcabinian). The term Bridgerian is taken from the Bridger Formation of the Greater Green River Basin, and two of its accepted subage names are based on lithologic members of that formation, a situation that has to change, as will be shown later in this chapter.

Gingerich (1989, 2001) and his coworkers have developed a terminology for the subdivision of the Wasatchian (biochrons Wao to Wa7) that has been modified for other NALMAs, such as biochrons Bro–Br3 (Gunnell 1998a; Gunnell and Yarborough 2000). This terminology will be used and expanded here to include a revised subdivision of the Uintan; the Duchesnean is not subdivided here.

HISTORY OF TERMINOLOGY

We present here an abridged version of historical terminology. See Krishtalka et al. (1987) and references therein for more detailed accounts.

WASATCH FORMATION AND WASATCHIAN LMA

Hayden (1869) gave the name *Wasatch Group* to a reddish fluvial sequence and was derived from Wasatch Station in Weber Canyon, Summit County, Utah. This type locality (as cited by Veatch 1907) includes sediments from two separate basins, the southwestern part of the Greater Green River Basin (Carter, Wyoming, located in the Bridger Basin of authors) and the southern part of the Fossil Basin (Wasatch Station). Cope (1877, 1882) extended the usage of Wasatch beds to the San Juan Basin in New Mexico and the Bighorn Basin in northwestern Wyoming, identifying the rocks as the *Coryphodon* zone. Hayden (1878) similarly referred sedimentary rocks in the Wind River Basin of central Wyoming to the Wasatch Formation.

The informal name *Gray Bull beds* was proposed (Granger 1914) for the lower part of the Bighorn Basin sequence. Granger (1914) extended the Lost Cabin beds (or *Lambdotherium* level) into the Bighorn Basin and referred rocks between the *Lambdotherium*-bearing deposits and the Gray Bull beds to the Lysite beds. The Lysite and Lost Cabin beds had initially been recognized as distinct units by Granger (1910), and the two names were proposed as formations by Sinclair and Granger (1911). A geologically older stratum, the Sand Coulee beds, was recognized in the Bighorn Basin by Granger (1914).

Lithostratigraphic terminology has been standardized in Wyoming basins. Wasatchian rocks of the Wind River Basin are represented in part by the Wind River Formation and include the Lysite and Lostcabin members. Temporally, the Wind River Formation spans the late Wasatchian to early Bridgerian time, with three faunal levels: Lysitean, Lostcabinian, and Gardnerbuttean. The "Big Horn Wasatch" was formalized by Van Houten (1944) as the Willwood Formation. The Willwood Formation is conformable in most places on rocks variously referred to the Fort Union Formation and is subdivided lithologically, in the southern part of the basin, into the Elk Creek and Sand Creek facies (Bown 1979b). The term Wasatch Formation unfortunately is still used for the upper Paleocene and lower Eocene sediments of the Powder River Basin, although this basin is physically separated from the Greater Green River Basin by both the Wind River and Hanna basins.

Veatch (1907) subdivided Hayden's Wasatch into three formations: Almy at the base, Fowkes disconformably overlying it, and Knight at the top. The type localities of these formations are all in the Fossil Basin. In 1960, the U.S. Geological Survey standardized usage of Wasatch Formation across the entire Green River Basin area, including the Washakie Basin and Great Divide Basin (*sensu* Love 1961; now all included in the Greater Green River Basin). Oriel (1962) advocated elimination of Veatch's formations altogether in favor of a broad usage of the Wasatch Formation. Veatch's Fowkes Formation is now known to be Bridgerian in age (Nelson 1973, 1979).

Roehler (1992a–1992c) points out that the eastern (Great Divide, Washakie, and Sand Wash) and western parts

TABLE 4.1 Wasatchian Through Duchesnean Fossil Localities in North America

- 1. Sand Coulee beds, Willwood Formation, Bighorn Basin (Wa0-Wa2)
- 2. "Wasatch" Formation, Powder River Basin (Wa0-Wa3)
- 3. Lower variegated beds, Togwotee Pass (Wa1)
- 4. Red Hot L.F., Tuscahoma Formation, Lauderdale County, Mississippi (Wa1)
- 5. Four Mile area, Wasatch Formation, Washakie–Sand Wash Basin divide, eastern Greater Green River Basin (Wa1–Wa2)
- 6. Wasatch and Pass Peak formations, Hoback Basin (Wa1-Wa5)
- 7. DeBeque Formation, Shire Member, Piceance Creek Basin (Wa2–Wa7)
- 8. Indian Meadows Formation, northwest Wind River Basin (Wa2–Wa3)
- 9. Wasatch Formation, Northern Washakie Basin (Wa3-Wa7)
- Raven Ridge, Colton Formation, eastern Uinta Basin (Wa2–Wa7)
- 11. Golden Valley Formation, North Dakota (Wa3)
- 12. Bashi Formation, Lauderdale County, Mississippi (Wa3)
- Las Lomas de Tetas de Cabra Formation, Baja California (Wa3? and later?)
- 14. "Cuchara" Formation, Raton Basin (Wa3?)
- Gray Bull beds, Willwood Formation, Bighorn Basin (Wa3–Wa5)
- Cooper Creek area, "Wind River" Formation, Laramie Basin (Wa3–Wa5)
- 17. Fisher/Sullivan Site, Nanjemoy Formation, Virginia (Wa3–Wa5)
- 18. San Jose Formation, San Juan Basin (Wa5–Wa6)
- Main Body, Wasatch Formation, eastern Greater Green River Basin including Dad L.F. (Wa5–Wa7)
- 20. Lower Huerfano Formation, Raton Basin (Wa5–Br0)
- 21. Lysite Member, Wind River Formation, Wind River Basin (Wa6)
- 22. Lysite beds, Willwood Formation, Bighorn Basin (Wa6)
- Morena Boulevard L.F., unnamed formation, southern California (Wa5–Wa6)
- 24. Cerrillos L.F., Galisteo Formation, New Mexico (Wa5?–Wa6?)
- 25. Book Cliffs area, Colton Formation, southern Uinta Basin (Wa6–Wa7)
- 26. Wasatch Formation, Fossil Basin (Wa6–Wa7)
- 27. LaBarge area, Wasatch Formation, western Greater Green River Basin (Wa6–Wa7)
- North and South Fork localities, Willwood and Aycross formations, Bighorn Basin (Wa6–Br2)
- 29. Hannold Hill Formation, Big Bend National Park, Texas (Wa7)
- 30. Lost Cabin beds, Willwood Formation, Bighorn Basin (Wa7)
- Hatchetigbee Bluff L.F., Hatchetigbee Formation, Wilcox Group, Washington County, Alabama (Wa7–Br0)
- 32. Niland Tongue, Wasatch Formation, northeastern Greater Green River Basin (Wa7)
- Lost Cabin Member, Wind River Formation, northern Wind River Basin (Wa7–Br1a)
- 34. Farisita Formation, Raton Basin (Wa7–Br1a)
- 35. Locality L-41, Aycross Formation, Togwotee Pass (Wa7-Br1a)
- Raven Ridge, Green River Formation, eastern Uinta Basin (Wa7–Br2)

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- Ellesmere and Axel Heiberg Islands, Eureka Sound Group, Nunavut Territory, Canada (Wa–Br)
- 38. Sage Creek Formation, Sage Creek Basin, Montana (Br0–Br3)
- 39. Aycross Formation, northwestern Wind River Basin (Br1b–Br2)
- 40. Upper Huerfano Formation, Raton Basin (Br1a)
- Cathedral Bluffs Tongue, Wasatch Formation, Greater Green River Basin (Wa7–Br1a)
- 42. Lower Blacks Fork "Member" (Bridger A), Bridger Formation, southwestern Greater Green River Basin (Br1b)
- Powder Wash locality, Green River Formation, Raven Ridge, Uinta Basin (Br1b?)
- 44. Middle Bridgerian beds, northwest Green River Basin (Br2)
- 45. Upper Blacks Fork "Member" (Bridger B), Bridger Formation, southwestern Greater Green River Basin (Br2)
- 46. Aycross Formation, southern Absaroka Range, Bighorn Basin (Br2)
- 47. Localities 17 and 18, Wagon Bed Formation, northern Wind River Basin (Br2)
- 48. Elderberry Canyon L.F., Sheep Pass Formation, Nevada (Br2)
- 49. Hart Mine Formation, New Mexico (Br3)
- 50. Princeton Locality, British Columbia (Br2?)
- 51. Togwotee Summit, Aycross Formation, Togwotee Pass (Br2?)
- 52. Swami's Point L.F., Delmar Formation, southern California (Br2)
- 53. Tatman Formation, Bighorn Basin (Wa7-Br2)
- 54. Kinney Rim Member, Washakie Formation, eastern Greater Green River Basin (Br3)
- Twin Buttes "Member," Bridger Formation, western Greater Green River Basin (Br2–Br3)
- 56. Tabernacle Butte, Upper Bridger Formation, western Greater Green River Basin (Br3)
- 57. Fowkes Formation, Fossil Basin, Wyoming and Utah (Br3)
- 58. Nut Bed, Clarno Formation, Oregon (Br3)
- 59. Lower Adobe Town Member, Washakie Formation, eastern Green River Basin (Br3)
- Black's Beach L.F., Scripps Formation, southern California (Br3–Ui1)
- 61. Marfil, Conglomerado Rojo de Guanajuato, Guanajuato, Mexico (Br–Ui)
- 62. Little Stave Creek L.F., Gosport Sand, Claiborne Group, Clarke County, Alabama (Wa?, Br–Ui)
- 63. Washakie Formation, Sand Wash Basin, eastern Greater Green River Basin (Br3–Ui2)
- 64. Jackson Group, St. Francis County, Arkansas (Br-Ch?)
- Junction localities, Agua Fria area, Devil's Graveyard Formation, west Texas (Ui1)
- 66. Bridger E, Turtle Bluffs Member, Bridger Formation, southwestern Greater Green River Basin (Ui1)
- 67. Canoe assemblage A, Canoe Formation and Big Bend lateral equivalent, Devil's Graveyard Formation, west Texas (Ui1?)
- Bone Bed A, Tepee Trail Formation, East Fork River, Wind River Basin (Ui1–Ui2)
- Middle Adobe Town Member, Washakie Formation, eastern Greater Green River Basin (Ui1–Ui2)
- 70. Beaver Divide, Wagon Bed Formation, southern Wind River Basin (Ui2)

TABLE 4.1 (continued)

- 71. Owl Creek area, Wiggins Formation, Absaroka Mountains (Ui2)
- 72. Uinta B1 and B2, Wagonhound Member, Uinta Formation, Uinta Basin (Ui2)
- 73. Friars L.F., Friars Formation, southern California (Ui1–Ui2)
- 74. Member B, Santiago Formation, southern California (Ui1–Ui2)
- 75. Lower Member, Stadium Conglomerate, southern California (Ui2)
- Locality 1, Wagon Bed Formation, northern Wind River Basin (Ui2)
- 77. Upper Adobe Town Member, Washakie Formation, greater Green River Basin (Ui2–Ui3)
- Whistler Squat Quarry, Devil's Graveyard Formation, west Texas (Ui1–Ui2)
- 79. Myton Member, Uinta Formation, Uinta Basin (Ui3)
- 80. Unnamed L.F., Sespe Formation, southern California (Ui3)
- Tapo Canyon and Brea Canyon localities, Sespe Formation, southern California (Ui3)
- 82. Canoe assemblage B, Canoe Formation, West Texas (Ui3)
- 83. Chisos Formation, west Texas (Ui3)
- Stonecrest L.F., Upper Member, Stadium Conglomerate, southern California (Ui3)
- 85. Serendipity L.F., Devil's Graveyard Formation, west Texas (Ui3)
- Lake Casa Blanca L.F., Laredo Formation, Webb County, Texas (Ui3)
- 87. Candelaria L.F., Colmena Tuff, west Texas (Ui3)
- Swift Current Creek beds, Cypress Hills Formation, Saskatchewan (Ui3)
- Mission Valley L.F., Mission Valley Formation, southern California (Ui3)
- 90. Eastview L.F., Lower and Miramar Sandstone members, Pomerado Conglomerate, southern California (Ui3)
- 91. "Randlett Fauna," Brennan Basin Member, Duchesne River Formation, Uinta Basin (Ui3)
- 92. Localities 5, 6, and 7, Hendry Ranch Member, Wagon Bed Formation, northern Wind River Basin (Ui3)
- 93. Douglass Draw and Hough Draw L.F., "Dell Beds," Montana (Ui3)
- 94. Upper Assemblage, Pomerado Conglomerate, southern California (Du–Ch)

- 95. Lower Member C, Santiago Formation, southern California (Ui3)
- 96. Laguna Riviera and Camp San Onofre L.F., upper Member C of the Santiago Formation, southern California (Ui3–Du)
- 97. Strathern/Hartman Ranch L.F., Sespe Formation, southern California (Ui3–Du)
- Geodetic Hills, Axel Heiberg Island, Eureka Sound Group, Nunavut Territory, Canada (Ui–Du)
- 99. Skyline Channels L.F., Devil's Graveyard Formation, west Texas (Du)
- 100. Porvenir L.F., Chambers Tuff, west Texas (Du)
- 101. Cotter Channel, Devil's Graveyard Formation, west Texas (Du)
- 102. Green River Formation, central Utah (Du)
- 103. Dry Gulch Creek Member, Duchesne River Formation, Uinta Basin (Du)
- 104. LaPoint Member, Duchesne River Formation, Uinta Basin, Utah (Du)
- 105. Pearson Ranch/Simi Valley Landfill L.F., Sespe Formation, southern California (Du)
- Bonita L.F., "Sweetwater" Formation, southern California (Ui3–Du)
- 107. Shoddy Springs L.F., Climbing Arrow Formation, Montana (Du)
- 108. Localities Wood, Rodent, and 20, Hendry Ranch Member, Wagon Bed Formation, northern Wind River Basin (Du)
- 109. Antelope Creek L.F., Slim Buttes Formation, South Dakota (Du)
- 110. Hancock Quarry, Clarno Formation, Oregon (Du)
- 111. Tonque L.F., Galisteo Formation, New Mexico (Du)
- 112. Baca and Cub Mountain formations, New Mexico (Du)
- 113. Carthage Coal Field, Baca Formation, New Mexico (Du)
- 114. Windmill Hill locality, New Mexico (Du)
- 115. Turtle Basin L.F., "Brian Head Formation," Sevier Plateau, Utah (Du)
- 116. Flathead Valley, Kishenehn Formation, British Columbia, Canada (Du–Ch)
- 117. Lac Pelletier, lower and upper faunas, Saskatchewan, Canada (Du–Ch)
- 118. Diamond O L.F., Climbing Arrow Formation, Montana (?Du-?Ch)

Biochronologic zone range in parentheses: Br, Bridgerian; Ch, Chadronian; Du, Duchesnean; Ui, Uintan; Wa, Wasatchian. L.F., Local Fauna. The locality numbers appear in figures 4.1–4.7.

(Green River Basin) of the major southwestern Wyoming basin are really parts of a Greater Green River Basin in which much of the middle part of the basin is divided by the structurally younger Rock Springs Uplift. The uplift does not cut the basin fully in half, and the units can be traced around the uplift on the northern side. The two sides of the basin have similar depositional histories. Physical correlation of the rock units between the Greater Green River Basin and other basins such as the Uinta and Piceance Creek basins to the south is much less easily accomplished, despite the superficial similarity of the rock units.

Granger (1914) divided Cope's (1877) "Wahsatch" in the San Juan Basin of New Mexico into lower Almagre beds and upper Largo beds, basing the difference on the presence of *Meniscotherium* in the Largo (Lucas 1977 has since reported it from the Almagre). Simpson (1948) concluded that the Almagre and Largo should be regarded as facies of a single formation, the San Jose Formation. Re-



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FIGURE 4.1 Map of the main Wasatchian through Duchesnean fossil mammal sites in western North America; localities are listed in table 4.1.

cent work indicates that most of the faunas of the San Jose Formation are Lysitean (Wa6) in age, based primarily on the distribution of the temporally limited taxon *Xenicohippus*. The presence of a large paromomyid in the fauna (Smith and Lucas 1991, locality 20) indicates either that rocks as old as Wa2 may be in the San Jose Formation (Robinson and Ivy 1994) or that large paromomyids survived much later in the Wasatchian as stated by Smith and Lucas (1991:35). Some of the San Jose Formation is Wa5 (upper Graybullian) in age.

There has been a general recognition that although the Wasatchian age sediments of each of the intermontane basins have certain similarities, the history of each basin is distinct and the geologic formations are separate sedimentologic entities. Other areas in which Wasatchian time is represented include the Hoback Basin of central western Wyoming; the Togwotee Pass area southeast of Yellowstone National Park; the Powder River Basin; the Williston Basin, Golden Valley Formation, in south-central North Dakota; the Laramie Basin of southeastern Wyoming; the Piceance Creek Basin of western Colorado; the Raton Basin of south-central Colorado; the Tuscahoma and Bashi formations in Mississippi; Hannold Hill Formation of west Texas; the Lomas las Tetas de Cabra Formation of Baja California; Axel Heiberg and Ellesmere Islands in Canada; and the Talkeetna Mountains in Alaska.

BRIDGER FORMATION AND BRIDGERIAN LMA

The Bridgerian age of Wood et al. (1941) is based on the time of deposition and the faunas of Bridger A-D. The Bridger Formation was named by Hayden (1869) as the Bridger Group, with the type area at Church Buttes Station, Wyoming. Matthew (1909) published a comprehensive Bridger stratigraphy, dividing the formation into five alphabetically designated zones (A–E) demarcated by laterally extensive white marker beds and further subdivided (B, B, etc.) on the basis of persistent benches held up by resistant marl beds (Matthew's Bridger E is now known to be fossiliferous [West and Hutchison 1981; Evanoff et al. 1994] and should not be included in the definition of the Bridgerian). Wood (1934) recognized the apparent faunal similarity between Bridger A and B and between Bridger C and D and combined these zones into two members, the lower Blacks Fork Member and the higher Twin Buttes Member. West and Hutchison (1981) designated the uppermost part of the Bridger Formation (Matthew's Bridger E) as the Cedar Mountain Member. This member name is precluded because of prior usage for the Cedar Mountain Formation, Cretaceous, of Utah and has been replaced by the term *Turtle Bluffs Member* (Evanoff et al. 1998). McGrew and Sullivan (1970) examined the exposures of Matthew's Bridger A near Opal, Wyoming, and argued for the basic faunal similarity of Bridger A and B. However, Gingerich (1979) recognized different species of adapiform euprimates in Bridger A and Bridger B, and this appears to be the case for much of the fauna (Gunnell 1998a; Zonneveld et al. 2000).

The Bridger Formation has never been called by any other name, and there are only the lithologic subdivisions just mentioned (West 1976b). Other areas where Bridgerian time is represented include elsewhere in the Greater Green River Basin, Wind River Basin, and Bighorn Basin all in Wyoming; the Uinta Basin of Utah and Colorado; the Piceance Creek Basin of Colorado; the northern Raton Basin of Colorado; west Texas, Oregon, New Jersey, Ellesmere Island, and perhaps Axel Heiberg Island, Canada.

UINTA FORMATION AND UINTAN LMA

Comstock (1875) first formally recognized the Uinta Formation of northeastern Utah. Peterson (in Osborn 1895) divided the Uinta Formation into Horizons A, B, and C, a division that was followed by Riggs (1912) and Douglass (1914). As noted by Cashion and Donnell (1974) and Prothero (1996b), Osborn (1929) restricted Uinta A to only the lowermost, barren part of the formation, named Uinta B1 for the sparsely fossiliferous upper part of Peterson's original Horizon A, and named Uinta B2 for Peterson's original Horizon B. As noted by Walsh (1996a), Osborn (1929) also lowered the Uinta B-C boundary to the top of the Amynodon sandstone, which resulted in the grayish Devil's Playground beds being transferred from the upper part of Uinta B to the lower part of Uinta C. Osborn's redefinition of the Uinta B-C boundary is problematic because the Amynodon sandstone is not a widely mappable unit (Cashion 1986). Most recently, Crawford et al. (2002) advocated returning the Uinta B-C lithostratigraphic contact to the striking gray-to-red color change that marked Peterson's original boundary between these units.

Wood (1934) proposed the Wagonhound Member for the lower part of the Uinta Formation (A and B) and Myton Member for the upper part (C). The final alteration in Uinta Formation usage was the separation of the beds above Uinta C as the Duchesne Formation (Peterson 1932), modified to Duchesne River Formation (Kay 1934).

As discussed in Krishtalka et al. (1987), the Uintan LMA originally was based on the fauna and time of deposition of Uinta A–C, but the age of Uinta A is essentially unknown, and this lithostratigraphic-based characterization is replaced by a purely biochronologic definition later in

this chapter. Other areas containing Uintan rocks and faunas include southwestern Saskatchewan; southwestern Montana; northwestern South Dakota; southwestern, central, and northwestern Wyoming; Trans-Pecos and southern Texas; northern New Mexico; northwestern Colorado; southern California; and Mississippi.

DUCHESNE RIVER FORMATION AND DUCHESNEAN LMA

As with the underlying Uinta Formation, the upper part of the Eocene section in the Uinta Basin has had a complex nomenclatorial history. Peterson (1932) named the Duchesne Formation for the sparsely fossiliferous upper part of the original Horizon C of the Uinta Formation. This was soon changed by Kay (1934) to the Duchesne River Formation because the original name was already in use. The Duchesne River Formation overlies and intertongues with the Uinta Formation, although there is a substantial change in lithofacies (Kay 1934; Scott 1945; Anderson and Picard 1972). Three lithostratigraphic and biostratigraphic horizons were recognized by Kay (1934) in the Duchesne River Formation, but they have since been abandoned in favor of the formal lithostratigraphic members of Anderson and Picard (1972). From oldest to youngest, Kay's subdivisions were the Randlett, Halfway, and LaPoint horizons. The Randlett corresponds roughly to the lower two-thirds of the Brennan Basin Member of Anderson and Picard (1972). The Halfway horizon is equivalent to the upper third of the Brennan Basin Member plus the Dry Gulch Creek Member, and the LaPoint horizon is essentially equivalent to the LaPoint Member. The uppermost unit (the Starr Flat Member of Anderson and Picard 1972) has yet to yield fossils.

The entire thickness of the Duchesne River Formation was the original basis for the Duchesnean of Wood et al. (1941), but the Duchesnean LMA has now been restricted to faunas that occur in the Dry Gulch Creek and lower LaPoint members (Gazin 1955; Clark et al. 1967; Tedford 1970; Wilson 1978, 1986; Emry 1981; Lucas 1992; Rasmussen, Hamblin, and Tabrum 1999). In addition to the Uinta Basin, Duchesnean faunas have been found in Saskatchewan, Montana, Oregon, Wyoming, southwestern Texas, New Mexico, and southern California.

BIOCHRONOLOGY OF WASATCHIAN-DUCHESNEAN LMAS

The Wood et al. (1941) committee definitions of NALMA faunal elements have been greatly modified by nomen-

clatural revisions and refinements and by more detailed geologic work. Despite these changes, the basic structure of the Wood et al. framework has held up very well. We present updated biochronologic range information in summary form here. For a more detailed historical review of biochronologic ranges see Krishtalka et al. (1987).

WASATCHIAN

Wasatchian first appearances include Perissodactyla, Artiodactyla, Primates, Hyaenodontidae, Sciuravidae, *Palaeictops, Didelphodus, Macrocranion, Pachyaena, Miacis,Vulpavus,* and *Megalesthonyx* (Schankler 1980; Rose 1981). Of these, the simultaneous appearance of Perissodactyla (*Hyracotherium*), Artiodactyla (*Diacodexis*), omomyid euprimates (*Teilhardina*), adapiform euprimates (*Cantius*), and Hyaenodontidae mark the onset of the Wasatchian and the end of the Clarkforkian.

Important last occurrences in the Wasatchian (a criterion of lesser biostratigraphic utility) include *Meniscotherium*, *Homogalax*, *Xenicohippus*, *Lambdotherium*, *Anacodon*, *Niptomomys*, *Tetonius*, *Pelycodus* (*sensu strictu* [s.s.]), and *Pachyaena* (Schankler 1980; Stucky 1984b; Bown and Kihm 1981).

Wasatchian index taxa (restricted to the Wasatchian) include Ambloctonus, Diacodon, Homogalax, Lambdotherium, Meniscotherium, Pachyaena, Tetonius, Pelycodus (s.s.), Ectoganus, Wasatchia (s.s.), Xenicohippus, Copelemur, Anemorhysis, Loveina, and Notoparamys (Korth 1982). Cantius, once considered a Wasatchian index taxon, is now known from Bridgerian beds in the Piceance Creek Basin (University of Colorado Museum [UCM] loc. 96197), from the Cathedral Bluffs Tongue of the Wasatch Formation, and probably the Huerfano formation as well (UCM loc. 77039).

Taxa typical of the Wasatchian (not all of which are restricted to Wasatchian time) include Hyracotherium (which is probably the wrong name for the North American taxon), Coryphodon, Phenacodus, Ectocion, Hyopsodus, Paramys, Microsyops, Cantius, Absarokius, Prolimnocyon, Prototomus, Arfia, Oxyaena, Didymictis, Viverravus, Diacodexis, Lambdotherium, Homogalax, Esthonyx, and Ectoganus. The presence of abundant Hyopsodus, Cantius, Hyracotherium, and Diacodexis differentiates the Wasatchian from the earlier Clarkforkian. The end of the Wasatchian (= the beginning of the Bridgerian) can now be defined by the penecontemporaneous appearance of Hyrachyus, Palaeosyops, Eotitanops (this genus may occur in latest Wasatchian rocks; Gunnell and Yarborough 2000; Smith and Holroyd 2001), Trogosus, Omomys (the presumed Wasatchian Omomys are now placed in other genera; Stucky 1984a; Bown and Rose 1984; Honey 1990),

Washakius, Anaptomorphus, Smilodectes, Megadelphus, Pantolestes, and Microsus.

Work by Gingerich and coworkers has established numerical biochrons Wao–Wa7 for the Wasatchian LMA. The Sandcouleean (early Wasatchian) includes Wao–Wa2, the Graybullian (middle Wasatchian) spans Wa3–Wa5, and the Lysitean (Wa6) and Lostcabinian (Wa7) together represent the late Wasatchian.

The Sandcouleean is characterized by the occurrence of the following genera (not all limited to the Sandcouleean): *Phenacodus, Coryphodon, Hyracotherium, Hyopsodus, Haplomylus, Apheliscus, Ectocion, Arctodontomys, Phenacolemur, Cantius, Teilhardina,* and *Diacodexis. Plesiadapis* makes its last appearances, and multituberculates are widespread.

The Graybullian is characterized by many of these same genera, but *Arctodontomys* is replaced by *Microsyops, Homogalax protapirinus* appears and is both common and widespread, and rodents become more diverse. The Graybullian is also characterized by the last appearances of *Neoliotomus* and *Haplomylus* (Wa5). *Apheliscus* was thought to be included here, but recent work by Denver Museum parties has documented early Wa6 *Apheliscus* in association with *Heptodon* at Denver Museum of Nature and Science locality 66 in the Wind River Formation.

Lysitean (Wa6) first appearances include *Heptodon*, *Loveina*, and *Hexacodus* (Guthrie 1967; Krishtalka and Stucky 1985). The Lostcabinian (Wa7) is marked by the first appearance of *Lambdotherium*, a genus that is widespread, common, and apparently limited to Wa7. Wa7 as a whole is characterized by the first occurrence of *Shoshonius*, *Antiacodon*, *Orohippus*, *Megalesthonyx*, *Pauromys*, *Sciuravus*, and *Armintodelphys* and derived species of *Esthonyx*, *Diacodexis*, *Absarokius*, *Hyopsodus*, *Cantius/ Notharctus*, and *Hyracotherium*. Last appearances in Wa7 are *Lambdotherium* and *Meniscotherium*.

WASATCHIAN-BRIDGERIAN BOUNDARY

Transitional Wasatchian–Bridgerian faunal assemblages are not widely represented. The best of these are known from the upper part of the Wind River Formation in the Wind River Basin (Stucky 1984a; Stucky and Krishtalka 1983; Krishtalka and Stucky 1983), Huerfano Park in Colorado (P. Robinson 1966), and at South Pass along the northeastern margin of the Greater Green River Basin (Gunnell and Yarborough 2000; Gunnell and Bartels 2001). P. Robinson (1966) originally assigned the fauna from the upper Huerfano Formation to a new subage, the Gardnerbuttean, which he included as the last subage of the Wasatchian. The upper Huerfano and the *Palaeosyops borealis* Assemblage Zone (Bro) faunas (Stucky 1984a) are now considered earliest Bridgerian, an action endorsed by Robinson and other workers. Gunnell (1998a) and Zonneveld et al. (2000) have shown that much of the Gardnerbuttean occurs above Bro in biochron Brıa. Corollaries of this conclusion are that the end of the Lostcabinian (and the *Lambdotherium* Range Zone) marks the end of the Wasatchian, and the Lost Cabin Member in the Wind River Basin straddles the Wasatchian–Bridgerian boundary. The Wasatchian– Bridgerian boundary is now placed near a date of 50.56 \pm 0.13 Ma from the Grey Tuff of the Wilkins Peak Member of the Green River Formation (M. E. Smith et al. 2003).

Another area that preserves faunal elements of the Wasatchian-Bridgerian transition is in the northern Greater Green River Basin north of Tabernacle Butte. In this area, a referred section of the Cathedral Bluffs Tongue was thought to overlie the New Fork Tongue of the Wasatch Formation (West 1973a). Upon reexamination by Roehler (1991), the New Fork Tongue is now considered to be the westward extension of the Cathedral Bluffs Tongue, and what had been considered Cathedral Bluffs Tongue is now considered to be the Laney Shale Member of the Green River Formation. The New Fork Tongue was thought to have produced a mixed late Wasatchian-early Bridgerian fauna from more than 250 feet of strata (Hyracotherium, Meniscotherium, Coryphodon, Palaeosyops, Lambdotherium, Phenacodus, and Oxyaena) (West 1973a). More recent collections from this area by L. Ivy (UCM) indicate that the Wasatchian and Bridgerian faunas are not mixed; these collections indicate that the characteristic Lostcabinian genera of Lambdotherium (UCM loc. 84211, 84228) and Meniscotherium (UCM loc. 84228, 84220) occur in the lower parts of the outcrop area and that the typical Bridgerian taxa of Palaeosyops (UCM loc. 84219) and Hyrachyus (UCM loc. 84213) occur in the upper. None of the stratigraphically higher UCM localities have Wasatchian fossils in them, and none of the lower have Bridgerian. The overlying "Cathedral Bluffs Tongue" (West and Dawson 1973) is miscorrelated (Roehler 1991) and is a fluviatile facies of the Green River Formation and contains a typically Bridgerian faunal sample including Orohippus, Helaletes, Antiacodon, Pauromys, Tillomys, and Mysops. There is a lithologic difference between the "New Fork Tongue" (= Cathedral Bluffs Tongue) and the "Cathedral Bluffs Tongue" (= Laney Shale Member of the Green River Formation) in the northern Green River Basin, and according to Roehler (1991) there is an erosional unconformity between the top of the Cathedral Bluffs Tongue and the overlying Laney Shale member of the Green River Formation in part of this area. Based on this new information (Roehler 1991), the Wasatchian–Bridgerian boundary occurs in the Cathedral Bluffs Tongue of the Wasatch Formation on the western side of the Greater Green River Basin and on the eastern (Honey 1988; Gunnell and Yarborough 2000; Clyde et al. 2001).

The absolute dating of the Wasatchian–Bridgerian boundary is still being evaluated. Recent absolute dates (Clyde et al. 2001; M. E. Smith et al. 2003) are significantly at variance by approximately 2 Ma. As described in the preceding two paragraphs, the physical location of the boundary can be demonstrated in several basins by faunal turnover. The only date that is well placed in regard to the physical position of the boundary is that of the Grey Tuff cited by Smith et al. from the Wilkins Peak Member of the Green River Formation, a lateral correlative of the Cathedral Bluffs Member of the Wasatch Formation. If this date is accurate, then it is the best date available at this time.

The onset of the Bridgerian is defined by the first appearance of *Palaeosyops*, *Trogosus*, *Hyrachyus*, *Homacodon*, *Helohyus*, *Megadelphus*, *Smilodectes*, *Omomys*, *Washakius*, and *Pantolestes*. However, these occurrences are not necessarily simultaneous. *Trogosus* occurs first in such localities as Huerfano VII (Bro). *Hyrachyus* and *Palaeosyops fontinalis* occur slightly higher in the section in the Huerfano Basin (locs. II, III, V; P. Robinson 1966) and apparently in the Green River and Wind River basins as well (Gunnell 1998a; Zonneveld et al. 2000). *Trogosus*, *Hyrachyus*, and *Palaeosyops* are all widespread, and *Palaeosyops* and *Hyrachyus* are particularly common.

Other areas that record the Wasatchian–Bridgerian transition include the Green River Formation–Colton Formation intertonguing area of the eastern Uinta Basin (Utah and Colorado; Doi 1990), the Piceance Creek Basin of Colorado (Kihm 1984; Honey 1990), and the Willwood and Aycross formations (Bown 1979a, 1982; Gunnell et al. 1992) in the Bighorn Basin.

BRIDGERIAN

The earliest Bridgerian (middle and upper Gardnerbuttean, Br1a) is marked by the first appearance of *Palaeosy*ops, Utahia, Trogosus, Uintanius, Hyrachyus, Homacodon, Helohyus, Megadelphus, Patriofelis, Sinopa, Microsus, Thinocyon, Smilodectes, Omomys, Washakius, and Pantolestes. In addition, there are several holdover Wasatchian taxa typical of the earliest Bridgerian, including Esthonyx, Coryphodon, Bunophorus, Diacodexis, Didymictis, Hyracotherium, Shoshonius, Bathyopsis, Absarokius, Thryptacodon, Palaeosinopa, and Knightomys. Other Bridgerian first appearances (Brıb and later) include Pantolestes, Anaptomorphus, Taxymys, Mysops, Mesatirhinus, Harpagolestes, Limnocyon, Mesonyx, Telmatherium, Hemiacodon, Dilophodon, Tillomys, Manteoceras, Parisectolophus, Uintatherium, and leptochoerids.

Bridgerian last occurrences include Vulpavus, Patriofelis, Phenacodus, Hyracotherium, Antiacodon, Diacodexis, Bunophorus, Coryphodon, Bathyopsis, Absarokius, Shoshonius, Hapalodectes, Knightomys, Palaeosinopa, Thryptacodon, Esthonyx, Heptodon, Helaletes, Ectocion, Prolimnocyon, and Didymictis.

Characteristic Bridgerian taxa include Hyopsodus, Miacis, Sciuravus, Paramys, Pauromys, Peratherium, Antiacodon, Microsyops, Notharctus, Orohippus, Helaletes, Apatemys, Scenopagus, Pontifactor, Nyctitherium, Centetodon, Entomolestes, and Uintasorex.

Gunnell (1998a) has proposed a subdivision of the Bridgerian that is similar in concept to that of the Wasatchian. He recognizes Bro, Br1a, Br1b, Br2, and Br3 biochrons. Bro is the *Eotitanops borealis* Range Zone and is the lowest part of the Gardnerbuttean. This biochron is recognized in the Wind River Formation (Upper Lost Cabin Member; Stucky 1984a), in the Aycross Formation (Flynn 1986), in the Cathedral Bluffs Tongue of the Wasatch Formation near Boulder, Wyoming (West 1973a), and in the Huerfano Formation of Colorado (American Museum of Natural History [AMNH] loc. VII). Bro forms the lower part of the Gardnerbuttean Subage of the Bridgerian LMA. *Eotitanops borealis* is restricted to this range zone; *Trogosus*, a Bridgerian immigrant, occurs with it at Huerfano VII.

Bria comprises the middle and later parts of the Gardnerbuttean. It is present in the Wind River Formation (several Carnegie Museum [CM]/UCM Locs), in the Cathedral Bluffs Tongue of the Wasatch Formation and Laney Shale Member of the Green River Formation of the Greater Green River Basin (several localities), in tongues of the Colton and Green River formations at Raven Ridge in the Uinta Basin, in the Green River Formation of the northern Piceance Basin (Honey 1990), and in the Huerfano Formation (AMNH locs. I, II, III, and V). Hyrachyus, Helaletes, Patriofelis, Bathyopsis fissidens, Trogosus, Mesonyx, Notharctus robinsoni, Omomys carteri, Smilodectes, Scenopagus, and Palaeosyops are present and widespread. First appearances are Uintanius, Utahia, and Megadelphus. Eotitanops minimus, Megadelphus lundeliusi, and Didymictis vancleaveae are restricted to Bria. Last appearances in Bria are Hyracotherium, Didymictis, Coryphodon, and Cantius (Green River Formation of the Piceance Creek Basin; Huerfano Formation). We disagree with the assignment by Rose et al.

(1999) of the Uintan *Hesperolemur* to *Cantius* (Gunnell and Rasmussen in prep.).

The Blacksforkian Subage comprises biochrons Brib and Br2. Br1b is the biochron for the fauna from Matthew's Bridger A rocks. It is characterized by a typical Bridgerian fauna with several species restricted to it. Among these are Bathyopsis middleswarti, Anaptomorphus westi, and Smilodectes mcgrewi. It also has several species characteristic of the Br2 or Br3 biochrons such as Washakius insignis, Paramys delicatus, Paramys delicatior, Sinopa rapax, and taxa of Orohippus, Antiacodon, and Microsyops that are very close to Br2 forms. The last appearance of Bathyopsis is recorded in the Brib biochron. Br 1b faunas are rare outside the type area in southwestern Wyoming, but a notable exception is the rich micromammal locality in the Green River Formation at Powder Wash on Raven Ridge in the Uinta Basin (Gunnell and Bartels 1999). Recent fieldwork by Doi (1990) has significantly augmented the Raven Ridge collections, and several Brib localities are now known there.

The Br2 fauna (upper Blacksforkian) is characterized by Notharctus pugnax and N. tenebrosus, Smilodectes gracilis, Orohippus major, Tillodon, and Microsyops elegans. Uintatheres are lacking in this faunal unit. The last appearances of Trogosus and Tillodon are recorded; Trogosus therefore is a very good indicator of Bro to Br2 age rocks. The boundary between the Br2 and Br3 biochrons is not clear-cut. Matthew (1909), Wood (1934), and Wood et al. (1941) assumed that the faunal break occurred at the boundary between Matthew's Bridger B and C, the Sage Creek White Layer (SCWL). Recent collecting by UCM parties has shown that the lower 70 m of Bridger C are sparsely fossiliferous. Br2 faunas are not widespread in North American intermontane basins. Other areas where these faunas are known include Raven Ridge (Uinta Basin) and possibly the Green River Formation of the Washakie Basin.

The Twinbuttean Subage fauna (Br3) contains abundant uintatheres (*Uintatherium*), and its brontotheriid diversity (*Telmatherium*, *Manteoceras*, *Mesatirhinus*)is greater than that of earlier faunas. Two species of large *Notharctus* (Covert et al. 1998), *Homacodon vagans*, *Orohippus sylvaticus*, *Hyopsodus lepidus*, and *Microsyops annectens* are also unique to the late Bridgerian. Br3 age rocks are found in the Washakie Formation (Kinney Rim Member and lower Adobe Town Member; McCarroll et al. 1996a), the Wind River Basin (Wagon Bed Formation at Beaver Divide and Badwater Creek), and the Piceance Creek Basin (*Tethyopsis*, UCM loc. 84115).

It is now evident that the Gardnerbuttean (Bro, Bria; Upper Cathedral Bluffs, Laney Shale Member of the Green River Formation) is the oldest part of the Bridgerian LMA, followed by the Blacksforkian (Br1b, Br2; Bridger A and Bridger B; Bridger C pro parte) and the Twinbuttean (Br3, middle and upper Bridger C and Bridger D) (see Wood 1934; Matthew 1909; P. Robinson 1966; Gazin 1976; Gunnell 1998a). The faunal boundary between the Blacksforkian (Br2) fauna and the Twinbuttean (Br3) fauna apparently does not occur at the Bridger B-C boundary (Sage Creek White Layer, the lithologic boundary between the Blacks Fork Member and the Twin Buttes Member) but some 70 m above it, between the Hickey Mountain Limestone and the Burnt Fork Limestone (Murphey 2001). This probably explains why so many typical Bridger B Notharctus and Smilodectes are recorded from the Twin Buttes member (P. Robinson 1957b; Gingerich 1979) and further illustrates the bad practice of naming faunal and stratigraphic units with the same term. One UCM specimen of Notharctus pugnax (a Br2 species) comes from 69 m above the base of the Sage Creek Limestone near Sage Creek Mountain, and the fauna from the Hickey Mountain Limestone, a thin lacustrine bed some 69 m above the base of the Sage Creek White Layer, appears to be Br2 in age. In general, the lower 70-80 m of Bridger C (lower Tertiary Bridger C [TBC] of Evanoff et al. 1998; Murphey 2001) are sparsely fossiliferous and poorly represented in collections, so most Bridger C specimens present in collections probably have come from the upper two thirds of the unit. Only the UCM collections in the Twin Buttes member made since 1991 have adequate stratigraphic data.

BRIDGERIAN-UINTAN BOUNDARY

There are few sequences that preserve continuous, fossiliferous sequences across the Bridgerian–Uintan boundary. Sediments in the East Fork Basin, Wyoming (McKenna 1980b); the Washakie Basin, Wyoming (Roehler 1973); the Uinta Basin, Utah (Kay 1957); Beaver Divide, Wyoming (Emry 1975); the Baca and Galisteo formations in New Mexico (Lucas et al. 1981; Lucas and Williamson 1993); the Badwater Creek area, Wyoming (Black 1969); the Sand Wash Basin, Colorado (West and Dawson 1975; Stucky et al. 1996); the Trans-Pecos area, Texas (West 1982); the Green River Basin, Wyoming (Evanoff et al. 1994); and the Scripps, Friars, and Santiago formations in southern California (Walsh 1996a) may preserve all or portions of this transitional interval.

One difficulty surrounding the definition of the Bridgerian–Uintan boundary concerns the essentially unknown fauna of Uinta A (as restricted by Osborn 1929 and discussed by Cashion and Donnell 1974). Prothero (1996b) points out that several Uintan taxa assumed by Krishtalka et al. (1987) to have been collected from Uinta A were almost certainly obtained from Uinta B1 of Osborn (1929). Support for this conclusion comes from the fact that Peterson's (1924) "*Dolichorhinus* Quarry" (rediscovered by Bilbey et al. 2002) is listed from Uinta A in Carnegie Museum records (A. Tabrum, pers. comm., 2000) but actually occurs about 122 m stratigraphically above the Uinta A–B contact as mapped by Cashion (1974).

Two areas that may be particularly relevant to the Bridgerian–Uintan boundary issue are the Agua Fria area in Trans-Pecos, Texas, and the newly discovered Bridger E faunal sample from the Green River Basin. In the Agua Fria area, the Devil's Graveyard Formation unconformably overlies the Cretaceous. The basal unit, the basal Tertiary conglomerate, contains two localities, Junction and 0.6 miles east of Junction. These localities are not part of the Whistler Squat Quarry assemblage. The faunal assemblage from these two localities includes a mix of Bridgerian (Herpetotherium, Scenopagus, Omomys, Notharctus, Microsyops annectens, Thisbemys, Mysops, Stylinodon, Hyrachyus, and Helohyus) and Uintan (Triplopus, Ourayia, Macrotarsius, and Leptoreodon) elements as well as some rangethrough taxa (Centetodon, Microparamys, and Uintatherium).

The Bridger E faunal assemblage (Evanoff et al. 1994; UCM loc. 92189) occurs approximately 7 m above the Bridger D–E lithologic boundary and contains faunal elements similar to those found at the Junction localities, including many Bridgerian taxa along with *Triplopus*, Eomyidae, and a very derived *Hemiacodon* that resembles *Macrotarsius*. The base of the Bridger E sequence is dated at 46.16 \pm 0.44 Ma (Murphey et al. 1999).

The Agua Fria and Bridger E assemblages indicate that there is a transitional faunal interval between Bridgerian biochron Br3 and the early Uintan faunal assemblages typified by Uinta B in Utah and the early Uintan samples from southern California, neither of which contain so many holdover Bridgerian taxa. This interval may represent the earliest Uintan and is assignable to biochron Ui1. The typical fauna of Uinta B beds therefore would comprise biochron Ui2 and that of Uinta C and the lower Duchesne River Formation comprise biochron Ui3. The early Uintan appears to fall entirely within chron C20r, which has a duration of 2 Ma (Berggren et al. 1995).

Flynn (1986) proposes a subage of the Uintan, the Shoshonian, as the basal Uintan temporal unit. This subage was originally proposed based on faunal samples from Bone Bed A of the Tepee Trail Formation (McKenna 1980b) and from the greater San Diego area, with faunal samples from the upper part of the lower Adobe Town Member of the Washakie Formation being included with less certainty (Flynn 1986). In two more recent articles, McCarroll et al. (1996a, 1996b) argue for the presence of a Shoshonian interval in the middle unit of the Adobe Town Member in the Washakie Basin. Stucky et al. (1996) also recognize an earliest Uintan or "Shoshonian" (their quotations) interval from above the Robin's Egg Blue Tuff in the Washakie Formation, Sand Wash Basin in Colorado (West and Dawson 1975). McKenna (1990) uses the term *Shoshonian* for the Tepee Trail Bone Bed A Quarry Fauna, most of which remains undescribed.

Flynn (1986) characterizes Shoshonian assemblages as those containing the first appearances of typical Uintan taxa such as *Amynodon*, *Leptoreodon*, *Protoreodon*, *Protylopus*, *Macrotarsius*, *Oligoryctes*, *Achaenodon*, and possibly *Epihippus* and co-occurring Bridgerian taxa such as *Notharctus*, *Microsyops annectens*, *Sciuravus*, *Hemiacodon*, *Washakius*, *Omomys*, *Herpetotherium*, *Apatemys*, and *Uintasorex*. Additional Shoshonian first appearances cited include *Triplopus*, *Uintaceras*, *Ourayia*, *Oromeryx* from the Sand Wash Basin (Stucky et al. 1996; D. T. Rasmussen, pers. comm., 2000), and *Dolichorhinus*, *Eobasileus*, *Metarhinus*, and some of the Sand Wash taxa from the middle Adobe Town Member, Washakie Basin (McCarroll et al. 1996a, 1996b).

Recent taxonomic revision and stratigraphic study have called some of these associations into question. Many of the San Diego primate taxa cited by Flynn as Bridgerian co-occurrences have been assigned to different genera or species from those known in the Bridgerian (Mason 1990; Gunnell 1995; Walsh 1996a; Walsh and Rasmussen in prep.). Some of the co-occurring taxa (Herpetotherium, Nyctitherium, Apatemys, and Sciuravus) are rangethrough taxa with temporal ranges that span much of the Wasatchian through Uintan and therefore are of limited biostratigraphic use. Most of the taxa cited by Flynn (1986) as Uintan first occurrences are not known from all or even most possible Shoshonian localities but are unevenly distributed among the various faunal samples. For these reasons we believe that, although there is clear evidence that a Bridgerian-Uintan transitional interval exists, adoption of a Shoshonian subage may be premature because of the lack of compelling samples from areas other than Agua Fria and especially Bridger E. When such samples do become available and if they corroborate the findings at Agua Fria and Bridger E, then Shoshonian would be the appropriate subage name for this interval. As of now, we prefer to recognize an earliest Uintan biochron (Ui1) best represented by the faunal assemblages at the basal Tertiary conglomerate and

Bridger E (Turtle Bluffs Member) while leaving the question of subage status for the Shoshonian open for further testing and corroboration. It may be that more than one faunal unit is located between Br3 and Ui2. The length of time involved in chron C20r indicates that this may be possible.

The beginning of Uintan biochron, Ui1, can be defined by the first appearances of the taxa listed earlier that characterize the beginning of the Uintan. Its ending is defined by several taxa listed later in this chapter that tentatively characterize the beginning of biochron Ui2. Taxa known only from Uii, and probably the latter part of it, include Patriolestes, Hesperolemur, Stockia, and Merycobunodon (all endemic to southern California). Uii is further characterized by the presence of certain Bridgerian holdover taxa that apparently do not persist into Ui2, including Antiacodon, Hemiacodon, Notharctus, Washakius, and Hyrachyus. Strata and faunas assigned to Ui1 include the lowermost Tepee Trail Formation in the East Fork Basin, Wyoming; Bridger E; the upper Sand Wash Fauna from Colorado; and the lower part of the lower member of the Devil's Graveyard Formation in Texas. The fauna from the upper Friars assemblage in California may be late Ui1. Further collecting from Bridger E, Uinta A and B1 (Utah), and the lower and middle units of the Adobe Town Member of the Washakie Formation (Wyoming) and its correlative in the Sand Wash Basin of Colorado is needed to determine whether Ui1 is represented in these strata.

UINTAN

There is significant disagreement among members of the committee revising this chapter on the definition of the Uintan and its subunits. In part this is caused by the lack of adequate transitional sections and partly by the paucity of good basal Uintan faunal samples. In the Rocky Mountain basins, at least, most of the Bridgerian–Uintan potential or actual boundary sections are in areas of steep exposures where erosion rapidly removes, breaks up, and forces downhill exposed bones. Quarriable sites (Bone Bed A, East Fork Basin; UCM loc. 92189, Bridger E) are limited and not found in sequence above other quarriable sites and often are difficult to access.

Uintan index taxa tentatively include Achaenodon, Amynodon, Diplacodon, Eobasileus, Leptotragulus, Oxyaenodon, Oromeryx, Prodaphænus, Protitanotherium, Protoptychus, Dolichorhinus (= Sphenocoelus), Ourayia, Procynodictis, Metarhinus, Mesomeryx, Bunomeryx, Hylomeryx, and Mytonomeryx; the southern Californian endemic taxa Patriolestes, Dyseolemur, Eohaplomys, Tapoc*hoerus, Merycobunodon*, and a new tapiroid genus (Colbert and Schoch 1998); and the Texas endemic taxon *Prolapsus.*

Uintan first appearances include agriochoerids, Amynodon, lagomorphs, soricids, Sespedectes, Proterixoides, Wallia, Ankylodon, Thylacaelurus, Procaprolagus, Rapamys, Janimus, Pareumys, Pseudocylindrodon, Oligoryctes, Ourayia, Metanoiamys, Protadjidaumo, Simimys, Griphomys, Tapocyon, Uintaceras, Epitriplopus, Colodon, Ibarus, Tapochoerus, Texodon, Malaquiferus, Diplobunops, Simimeryx, Mytonomeryx, Toromeryx, Stockia, Craseops, Tapomys, Eomoropus, Grangeria, Apriculus, Pentacemylus, Macrotarsius, Chipetaia (Rasmussen 1996), and Camelidae (Poebrodon).

Uintan last occurrences include Dinocerata, Hyrachyus, Limnocyon, oxyaenids, Notharctus, Paramys, Sciuravus, taeniodonts, Helohyus, Scenopagus, Macrocranion, Entomolestes, Ourayia, Pantolestes, Washakius, Hemiacodon, Aethomylos, Crypholestes, Thisbemys, Reithroparamys, Mysops, Pauromys, Viverravus, Dilophodon, Antiacodon, Mesonyx, and Microsyops.

Characteristic Uintan taxa are Epihippus, Protoreodon, Amynodon, Eobasileus, Metarhinus, Dolichorhinus, Triplopus, Protylopus, Mytonolagus, and Ischyrotomus.

The Uintan appears to be subdivisible faunally into early (Ui1), middle (Ui2), and late (Ui3) segments. Ui1 was defined earlier, Ui2 is based on the fauna of Uinta B from the Wagonhound Member, and Ui3 is based on the fauna of Uinta C, from the Myton Member of the Uinta Formation, and now also includes faunas from the lower part of the Brennan Basin Member of the Duchesne River Formation. Based on the magnetic polarity scale, in terms of elapsed time, not faunal development, almost half of the Uintan is represented by Ui1 (Berggren et al. 1995).

The beginning of Ui2 can be tentatively defined by the first appearances of Bunomeryx, Mesomeryx, and Protoptychus, and its ending is defined by the appearance of taxa listed later in this section that characterize the beginning of biochron Ui3. Taxa known only from Ui2 include Chipetaia, Eomoropus, Mesomeryx, and possibly Protoptychus, although only the latter two genera are common, and both are known only from the Rocky Mountain region. Crypholestes and Pauromys have their last occurrences in Ui2. Strata assigned to Ui2 include most of Uinta B2 in Utah and the upper part of the middle Adobe Town Member of the Washakie Formation in Wyoming. Strata potentially assignable to Ui2 include Uinta B1 in Utah, the upper part of the Tepee Trail Formation and the Wiggins Formation in Wyoming, the upper part of the lower member of the Devil's Graveyard Formation of Texas, and

the lower member of the Stadium Conglomerate in California.

Some additional comments on Ui1 and Ui2 are warranted here. Ui1 and Ui2 faunas have yet to be demonstrated in a single, superposed section. No distinction between Ui1 and Ui2 faunas has yet been made in the thick Uintan deposits of the Tepee Trail and Wiggins formations (Eaton 1985). However, the Uintan deposits in Texas may show distinct Ui1 (Junction Localities) and overlying Ui1 or Ui2 (Whistler Squat Quarry) faunal assemblages. Unfortunately, micromammal faunas from Uinta B1 and the lower part of Uinta B2 in the Uinta Basin are poorly known, making characterizations of Ui1 and Ui2 biochrons necessarily tentative.

Krishtalka et al. (1987) list camelids (Poebrodon), eomyids, and possibly canids as making first appearances in the late Uintan (Ui3) and also note that limnocyonids decreased in diversity. Other first appearances listed by Krishtalka et al. include Domnina, Thylacaelurus, Colodon, Prodaphænus, Simidectes, Procynodictis, and Epitriplopus. Of these, Colodon (Eaton 1985), Poebrodon (McCarroll et al. 1996a; although Walsh questions this identification), and eomyids (Chiment and Korth 1996; Walsh 1997) are now known from the early Uintan, and canids are known for certain only from the Duchesnean (Bryant 1992). The systematics of Prodaphænus are in question, and a new, undescribed species of Simidectes is now known from the early Uintan Friars Formation. Other first appearances in Ui3 are Sespedectes, Proterixoides, Dyseolemur, Mytonolagus, Rapamys, Janimus, Protadjidaumo, Simimys, Griphomys, Diplacodon, Protitanotherium, Epitriplopus, Ibarus, Tapochoerus, Diplobunops, Mytonomeryx, Malaquiferus, Simimeryx, Pentacemylus, and Toromeryx. Of these, Sespedectes, Proterixoides, Dyseolemur, Rapamys, Simimys, and Tapochoerus may be very useful in characterizing the Ui2-Ui3 boundary.

Taxa making last appearances in Ui3 include Aethomylos, Batodontoides, Macrocranion, Ourayia, Microsyops, Eohaplomys, Sciuravus, Mesonyx, Oxyaenodon, "Proviverra," Limnocyon, Tapocyon, Epihippus (Rasmussen, Conroy, et al. 1999), Hylomeryx, Bunomeryx, and possibly Auxontodon.

Other taxa only known from Ui3 include Dyseolemur, Eotitanotherium, Protitanotherium, Epitriplopus, Ibarus, Tapochoerus, Mytonomeryx, Laredochoerus, Microeutypomys, Laredomys, Toromeryx, Procaprolagus, Tapomys, and Craseops.

Strata and faunas assigned to Ui3 include the Myton Member of the Uinta Formation and the lower part of the Brennan Basin Member of the Duchesne River Formation in Utah; the upper part of the Wagon Bed Formation, Wind River Basin in Wyoming; the Swift Current Creek Local Fauna (L.F.), Cypress Hills Formation in Saskatchewan; the Serendipity L.F. (Devil's Graveyard Formation), Candelaria (Colmena Formation), and Lake Casa Blanca (Laredo Formation) local faunas in Texas; the lower part of member C of the Santiago Formation, the upper member of the Stadium Conglomerate, the Mission Valley Formation, and the lower two members of the Pomerado Conglomerate, San Diego County, California; and the lower part of the middle member of the Sespe Formation, Ventura County, California.

UINTAN-DUCHESNEAN BOUNDARY

The nature of the Uintan–Duchesnean transition in the Uinta Basin is unclear, mostly because, according to Kay (1934), there are approximately 320 m of barren strata between the base of the Brennan Basin Member (which yielded the late Uintan assemblage from Randlett Point) and the base of the LaPoint Member (which has yielded the type Duchesnean assemblage). Krishtalka et al. (1987) define the Uintan-Duchesnean boundary on the first appearances of Duchesneodus, Brachyhyops, Hyaenodon, Simimeryx, Poabromylus, Hyracodon, and Agriochoerus. However, Poabromylus is known from the late Uintan Badwater locality 7 (Black 1978), and a new species of Simimeryx is present in the late Uintan Tapo Canyon Local Fauna (Mason 1988). In his review of the Duchesnean problem, Lucas (1992) lists numerous taxa with Duchesnean first appearances but does not explicitly define the Uintan–Duchesnean boundary. We tentatively use the first appearances of Hyaenodon, Duchesneodus, Duchesnehippus intermedius, Amynodontopsis, and Eoty*lopus* for this purpose. We also accept the proposals of Lucas (1992) and Rasmussen, Hamblin, and Tabrum (1999) to include the "Halfway Fauna" (now apparently consisting only of *Duchesnehippus intermedius*) in the Duchesnean.

The numerical age of the Uintan–Duchesnean boundary is unclear, again mainly because we do not know where this boundary falls in the Duchesne River Formation. The LaPoint Ash (which forms the base of the LaPoint Member) has been dated at 39.74 Ma \pm 0.07 Ma (Prothero and Swisher 1992). The Carnegie Museum *Duchesneodus* Quarry (from which most of the LaPoint Fauna is derived) is located about 37 m above the La-Point Ash (Kay 1934). However, the fauna of the underlying Dry Gulch Creek Member is largely unknown, and the potential Duchesnean index taxon *Duchesneodus* has been recorded from the base of the Brennan Basin Member (Black and Dawson 1966b; Rasmussen, Hamblin, and Tabrum 1999). The faunal assemblage from the La-Point Member has generally been suggested to be of middle to later Duchesnean age given the presence of several Chadronian-aspect taxa (Emry 1981; Wilson 1986; Kelly 1990; Prothero and Emry 1996). Therefore the Uintan–Duchesnean boundary could be significantly older than the 39.74 Ma date obtained on the La-Point Ash.

DUCHESNEAN

Though still far from complete, our knowledge of Duchesnean faunas has increased greatly since the very preliminary characterization of this LMA by Wood et al. (1941). Lucas (1992) reviewed several controversies surrounding the Duchesnean and upheld its validity as a distinct LMA. The Duchesnean is at the heart of a profound middle Eocene faunal replacement in North America (Black and Dawson 1966b) and features an unusual number of first and last appearances but few genera that are restricted to it. Thus the faunal signature of the Duchesnean, instead of being based on the occurrence of typical taxa, is based on the co-occurrence of archaic groups and more advanced genera that came to dominate Chadronian faunas.

The Duchesnean assemblage is all the more difficult to characterize because of the already high and apparently increasing provinciality of the North American fauna at that time (Lillegraven 1979a; Storer 1989, 1996). Typical Duchesnean assemblages and taxa have very different attributes in different faunal provinces (e.g., southern California, west Texas, Gulf Coast Plain, intermontane basins, Great Plains), and it appears that the centers of evolution for most groups were well separated, probably by major physiographic barriers. This combination of provinciality and local evolution makes it exceptionally difficult to correlate assemblages across long distances. However, by the end of the Duchesnean, much of this provinciality disappeared, making Chadronian faunas easier to characterize if not necessarily to correlate.

Lucas (1992) notes that several genera are known only from the Duchesnean, including *Duchesneodus, Amynodontopsis, Rooneyia, Mahgarita, Presbymys, Viejadjidaumo,* and *Haplohippus.* However, he also notes that with the exception of *Duchesneodus* and possibly *Amynodontopsis,* these taxa are either too rare or too limited in geographic distribution to be regarded as Duchesnean index taxa. Lucas also includes *Protictops, Ischnognathus,* and *Hidrosotherium* as taxa unique to the Duchesnean, but *Protictops* is now regarded as a junior synonym of *Centetodon* (Rasmussen, Hamblin, and Tabrum 1999), *Ischnognathus* is of doubtful taxonomic placement (Gustafson 1986; Lucas 1992), and *Hidrosotherium* is now regarded as a junior synonym of "*Leptomeryx*" (*?Hendryomeryx*) defordi (Prothero 1996c).

Other, mostly species-level taxa known only from the Duchesnean include *Simidectes merriami*, *Chumashius balchi*, *Metanoiamys korthi*, *Simimys landeri*, *Simiacritomys whistleri*, *Protoreodon pacificus*, *Protylopus pearsonensis*, and *Simimeryx hudsoni*, all from the Pearson Ranch and Simi Valley Landfill local faunas of the Sespe Formation (Kelly 1990, 1992; Kelly and Whistler 1998), and Trogolemur leonardi, Microparamys nimius, Anonymus baroni, Pseudotomus timmys, Microeutypomys tilliei, Eutypomys acares, Eutypomys obliquidens, Metanoiamys lacus, Protadjidaumo pauli, Adjidaumo craigi, Tachylagus gawneae, and *Heptacodon pellionis*, all from the Lac Pelletier lower and upper faunas of the Cypress Hills Formation (Storer 1995, 1996).

Excluding the aforementioned species, genera with Duchesnean first appearances include Sinclairella, Apternodus, Ischyromys, Ardynomys, Jaywilsonomys, Yoderimys, Aulolithomys, Heliscomys, Hemipsalodon, Hesperocyon, Daphoenus, Mesohippus, Trigonias?, Hyracodon, Subhyracodon?, Menops, Toxotherium, Brachyhyops, Heptacodon, Agriochoerus, Aclistomycter, Heteromeryx, Pseudoprotoceras, Trigenicus, and Leptomeryx.

Excluding the aforementioned species, genera with Duchesnean last appearances include Apatemys, Palaeictops, Didelphodus, Nyctitherium, Talpavus, Sespedectes, Proterixoides, Simidectes, Janimus, Trogolemur, Chumashius, Omomys, Rapamys, Pareumys, Simimys, Griphomys, Mytonomys, Hessolestes, Harpagolestes, Uintacyon, Uintasorex (sensu lato), Miocyon, Amynodon?, Triplopus, Protoreodon, Leptoreodon, Leptotragulus, Protylopus, and Simimeryx.

Wilson (1984) proposed an informal subdivision of the Duchesnean into early and late parts. He characterized the early Duchesnean by the presence of certain Uintan holdover taxa (e.g., Simidectes, Harpagolestes, and Diplobunops) and the absence of certain Chadronian -aspect taxa (e.g., Hemipsalodon, Mesohippus, Toxotherium, Hyracodon primus, Brachyops, and Merycoidodon) known from later Duchesnean faunas. Wilson's general proposal was accepted by Kelly (1990), but Lucas (1992) and Storer (1996) maintained that the Duchesnean record was still inadequate to support a formal subdivision. Nevertheless, we agree with these authors that the relative ages of several Duchesnean assemblages are readily discernible. For example, we agree with Wilson (1986) and Kelly (1990) that the Pearson Ranch

L.F., Badwater Locality 20, and the Skyline Channels are early Duchesnean and that the Porvenir L.F. is late Duchesnean. Prothero and Emry (1996) also propose that the Simi Valley Landfill L.F., the LaPoint Fauna, and the Galisteo Formation assemblage are roughly middle Duchesnean. These suggestions appear reasonable and await corroboration by new fossil discoveries and additional radioisotopic and paleomagnetic work.

The end of the Duchesnean and the beginning of the Chadronian can be characterized by the first appearances of Sciuridae, Nimravidae, Tayassuidae, *Palaeolagus, Daphænictis, Daphænocyon, Penetrigonias, Stibarus, Bathygenys, Merycoidodon, Poebrotherium, Montanatylopus,* and *Hypisodus* (Lucas 1992; note that *Heptacodon* and *Pseudoprotoceras* have now been reported from the Duchesnean by Storer 1996 and Eaton et al. 1999). The numerical age of the Duchesnean–Chadronian boundary is estimated at about 37 Ma by Prothero (1996a) and Prothero and Emry (1996) based on dates obtained from the Buckshot Ignimbrite (underlying the late Duchesnean Porvenir L.F.) and the Bracks Rhyolite (overlying the early Chadronian Little Egypt L.F.) in Texas.

GEOGRAPHIC DISTRIBUTION OF WASATCHIAN-DUCHESNEAN FAUNAL SAMPLES

WIND RIVER BASIN

Northwestern Wind River Basin (Figure 4.2) The oldest fauna in the northwestern Wind River Basin is derived from the upper part of the "lower variegated sequence" (loc. 3, table 4.1) of Love (1947) south of Togwotee Pass in the Fish Creek drainage. Vertebrate assemblages derived from this sequence (McKenna 1980b; Rose 1981) range from Clarkforkian (Red Creek) through Wasatchian (Hardscrabble Creek) as higher levels in the unit are sampled. The presence of *Cantius, Hyopsodus*, and *Diacodexis* firmly places the upper part of the "lower variegated sequence" in the early Wasatchian, but the lower part is clearly Clarkforkian, with *Coryphodon, Plesiadapis dubius*, *P. cookei, Azygonyx ancylion*, and *Arctostylops steini*.

Stratigraphically above the lower variegated sequence is Love's (1947) "upper variegated unit." Its fauna, although not well known, is clearly still Wasatchian in age (McKenna 1980b). Overlying the upper variegated sequence is a volcaniclastic sequence (Aycross Formation) that contains the Coyote Creek flora (MacGinitie et al. 1974), fossil land mollusks, and a few mammalian and other vertebrate remains. The vertebrate fossils are representative of the late Wasatchian or early Bridgerian (McKenna 1980b).

A highly tuffaceous third variegated unit is also present in the northwestern Wind River Basin. This unit and the volcaniclastic sequence beneath it are referred to the Aycross Formation (Love 1939). Locality L-41 (loc. 35, table 4.1) is in these Aycross rocks southwest of the summit of Togwotee Pass, and its small faunal assemblage suggests a latest Wasatchian or early Bridgerian age (McKenna 1980b). Overlying locality L-41 is a greenish volcaniclastic unit, exposed in a small badlands area at the summit of Togwotee Pass (loc. 51, table 4.1), referred to the Aycross Formation. The faunal sample from Togwotee Summit (including *Hyrachyus, Palaeosyops*, cf. *Trogosus, Microsyops, Washakius, Tillomys, Sciuravus, Hyopsodus*, and cf. *Orohippus*) is early Bridgerian (Br2).

Another Wasatchian assemblage is derived from the lower part of the Indian Meadows Formation (Love 1939). This Indian Meadows Fauna (loc. 8, table 4.1) may be Wa2 to Wa3 in age, based on the presence of *Haplomylus speirianus* and an *Absarokius-* or *Absarokius-*like omomyid (Winterfeld 1986).

Approximately 64 km east of Togwotee Pass in the East Fork Basin, a distinctive vertebrate assemblage has been quarried from unit 24 (loc. 68, table 4.1; Bone Bed A) of the type section of the Tepee Trail Formation (Love 1939). It contains several apparently endemic taxa (the "dermopteran" Tarka and Hyopsodus lovei), a new erinaceid also known from the late Uintan of the Badwater area (Krishtalka and Setoguchi 1977), and many characteristic Uintan taxa including eomyid rodents, Epihippus, Dilophodon, Amynodon, cf. Tapocyon, Achaenodon, Uintaceras, and primitive selenodont and bunodont artiodactyls (McKenna 1980b, 1990; MacFadden 1980; Flynn 1991). This assemblage is tentatively assigned to Ui1, although paleomagnetic evidence obtained by Sundell et al. (1984), Flynn (1986), and Prothero (1996c) suggests that Bone Bed A may correlate with some part of Uinta B1 (early chron C2or). The Tepee Trail Formation below Bone Bed A probably is Br3 or Ui1 in age.

At the southeastern end of the Absaroka Mountains, in the drainage of Owl Creek, Eaton (1980, 1982) and Bown (1982) have collected definitive Bridgerian faunas from the Aycross Formation (loc. 39, table 4.1) and other units. The occurrence of *Scenopagus, Microsyops, Uintasorex, Omomys, Anaptomorphus, Washakius, Viverravus, Mesonyx, Hyopsodus paulus, Trogosus, Orohippus, Helohyus, Helaletes,* and *Hyrachyus* confirm a Bridgerian age.

Above the Aycross Formation in the drainage of the North Fork of Owl Creek, Eaton (1980, 1985) has docu-



FIGURE 4.2 Correlation of rock units containing fossil mammals of Wasatchian through Duchesnean (Du) age in northwestern, central, and eastern Wind River Basin, Bighorn Basin, and Powder River Basin. Numerals in ovals refer to localities listed in table 4.1. Fm., Formation.

mented several superposed vertebrate localities (loc. 71, table 4.1) in the Tepee Trail and Wiggins formations. Eaton's "Holy City beds" and "Foggy Day beds" are of early Uintan age (*Amynodon, Uintaceras, Epihippus,* and *Achaenodon*) and possibly assignable to Ui1. The precise ages of Eaton's "upper Tepee Trail" and "lower Wiggins" are uncertain, but the "upper Wiggins" may be of late Uintan age based on taxa such as *Macrotarsius* sp., cf. *M. siegerti,* cf. *Procynodictis, Colodon,* and *Protoreodon* sp., cf. *P. pumilus* (Eaton 1985). Fossils from referred Wiggins exposures at the southern margin of the Wind River Basin also are Uintan in age (Emry 1975).

Central and Eastern Wind River Basin (Figure 4.2) An early Wasatchian fauna has been collected from Shotgun Butte in the Indian Meadows Formation and includes *Hyracotherium, Hyopsodus, Haplomylus, Coryphodon, Diacodexis,* and *Cantius* (Keefer 1965).

The Wind River Formation produces several discrete faunas including a Wa6 assemblage from the Lysite Member (loc. 21, table 4.1), a Wa7 assemblage from the lower part of the Lost Cabin Member (loc. 33, table 4.1), and two assemblages (loc. 33, table 4.1; Bro and Br1a) from the upper part of the Lost Cabin Member (Stucky and Krishtalka 1983; Stucky 1984a; Krishtalka and Stucky 1983; Gunnell and Yarborough 2000). The Lostcabinian is based on the *Lambdotherium* Range Zone; the Gardnerbuttean, originally defined by the Huerfano B fauna (Bria, late Gardnerbuttean; see P. Robinson 1966), is now also characterized by the *Palaeosyops* Assemblage Zone as defined by Stucky (1984a; Bro, early Gardnerbuttean; see Gunnell and Yarborough 2000).

Faunas from the Badwater area (Black and Dawson 1966a) suggest that *Phenacodus*-bearing locality 17 (loc. 47, table 4.1; West and Atkins 1970) is early Bridgerian in age, as is nearby locality 18 (see also Wood et al. 1936). Localities 5, 5A, 6, and 7 (loc. 92, table 4.1) and associated sites are Ui3 equivalents. Still higher are the Wood and Rodent localities and locality 20 (loc. 108, table 4.1). The last of these is particularly important because it probably represents an earliest Duchesnean assemblage (see Maas 1985 for faunal list).

The nomenclatural treatment of rocks of Bridgerian, Uintan, and Duchesnean ages in the central and eastern Wind River Basin remains unclear. *Wagon Bed Formation* may be the appropriate name for units that contain Bridgerian to Duchesnean faunas, but the upper unit, the Hendry Ranch Member, may be a distinct mappable unit, thus deserving formation rank, or it may be a distal (and later) fine-grained expression of the Wiggins Formation (Emry 1975). The Wagon Bed Formation typically crops out at Beaver Divide in the southern Wind River Basin where it contains a Uintan fauna (Emry 1975).

BIGHORN BASIN AND SOUTHWESTERN MONTANA (FIGURE 4.2)

The 770-m Willwood Formation of north-central Wyoming has produced a large series of fossil mammal assemblages (locs. 1, 15, 22, and 30, table 4.1), apparently continuous through Clarkforkian and Wasatchian time. Local disconformities do occur in the sequence. Clarkforkian time is defined on the fauna that appears in both the upper Fort Union Formation and in the lowermost Willwood Formation. Early and middle Wasatchian time (Sandcouleean and Graybullian) is based on assemblages from the Willwood Formation (Van Houten 1945; Gingerich 1980a). Higher beds in the Willwood Formation produce assemblages that correlate with the faunas of the Lysite and Lost Cabin (late Wasatchian) members of the Wind River Formation.

The onset of Wasatchian time is marked by the first appearances of artiodactyls, perissodactyls, euprimates, and hyaenodontid creodonts in the earliest Sandcouleean (Wao). The Graybullian is marked by the first appearance of *Homogalax* (Wa3), and the first appearance of *Heptodon* marks the beginning of the late Wasatchian (= Lysitean, Wa6). The first appearance of *Lambdotherium* indicates the onset of the Lostcabinian (Wa7). It first occurs at about 650 m above the base of the Willwood– Tatman formational contact. Local biozonations based on perissodactyls and euprimates (Gingerich 1980b, 1983, 1989, 2001) and *Haplomylus, Ectocion*, and *Bunophorus* (Schankler 1980) now define Wasatchian biochrons Wao through Wa7.

The Tatman Formation (loc. 53, table 4.1), which conformably overlies and intertongues with the Willwood Formation in the southwestern part of the Bighorn Basin, was presumed to be Bridgerian in age by Van Houten (1944). D. Parris (Bown 1982) has found late Wasatchian mammals from low in the formation. So-called Tatman equivalents are overlain by and intertongue with the Aycross Formation to the south of Carter Mountain (loc. 46, table 4.1) in the southeastern Absarokas (Bown 1982); the Aycross is of early Bridgerian age, as indicated by the work of Jepsen (1939) and Bown (1979a, 1982).

North of Carter Mountain, the Willwood is overlain unconformably by the Wapiti Formation, a lateral equivalent of the Aycross (loc. 46, table 4.1) and Tepee Trail formations (Bown 1982; Eaton 1982). The Wapiti contains a middle Eocene fauna (Bown 1979a) and is overlain unconformably by the Trout Peak Trachyandesite and the Wiggins Formation. A Bridgerian fauna (including *Stylinodon, Notharctus, Washakius, Palaeictops, Hyopsodus, Phenacodus, Orohippus,* cf. *Palaeosyops, Hyrachyus,* and *Helohyus*) is known from rocks referred to the Wiggins Formation at Carter Mountain (Eaton 1980, 1982).

To the west of Cody, Wyoming, along the north and south forks of the Shoshone River, a small vertebrate fauna has been collected from the Willwood and overlying Aycross formations (loc. 28, table 4.1) in Wapiti Valley (Gunnell et al. 1992). This fauna ranges from Lysitean (Wa6) through middle Bridgerian (Br2) and demonstrates that Willwood deposition continued into the Bridgerian along the northwestern margin of the Bighorn Basin.

SOUTHERN CALIFORNIA (FIGURE 4.3)

Southern Californian Eocene mammal-bearing strata crop out in San Diego and Ventura counties and range from the Wasatchian through at least the late Duchesnean, although most deposits are Uintan. Interdigitation of Uintan strata with fossiliferous marine units permits many southern California sites to be correlated with standard marine reference biochronologies (Bukry and Kennedy 1969; Berggren et al. 1978; Flynn 1986; Bukry 1991; Walsh 1996a). A detailed summary of known occurrences of land vertebrate taxa from deposits in southern California can be found in Golz and Lillegraven (1977), Kelly (1990), Kelly et al. (1991), Walsh (1991a, 1991b, 1996a), and Walsh and Gutzler (1999).

A number of areas in San Diego County have yielded early Cenozoic faunal samples, and revisions of stratigraphy (Walsh 1996a; Walsh et al. 1996) have clarified relationships between rock units and allow documentation of a more complete biostratigraphic framework for this area. The oldest known Wasatchian fossil vertebrates in San Diego County are from an unnamed formation situated between the upper Cretaceous Cabrillo Formation and the Mount Soledad Formation (Kennedy and Moore 1971) and disconformably separated from both. The Morena Boulevard Local Fauna (loc. 23, table 4.1; Walsh 1991a, 1996a) contains typical Wasatchian taxa that probably correlate with the Lysitean or Lostcabinian (Wa6–Wa7) of the western interior (Williamson and Lucas 1992).

The only known Bridgerian aged mammals from California come from the Delmar Formation (Swami's Point L.F., loc. 52, table 4.1; Walsh 1996a). Included in this local fauna are *Hyrachyus* and *Trogosus*, which, along with Flynn's (1986) assignment of the Delmar Formation re-



FIGURE 4.3 Correlation of rock units containing fossil mammals of Wasatchian through Duchesnean age in southern California. Numerals in ovals refer to localities listed in table 4.1. Cgl., Conglomerate; Fm., Formation; SS, Sandstone.

versed polarity interval to paleomagnetic chron C21r, point to a Br2 correlation.

Overlying the Delmar Formation in turn are the shallow marine Torrey Sandstone, deep marine Ardath Shale, and the shelfal marine Scripps Formation (Kennedy and Moore 1971). The Ardath Shale and Scripps Formation normal polarity interval was correlated with magnetochron C21n by Flynn (1986). Contained in the conglomeratic sandstones in the basal part of the Scripps Formation is the Black's Beach Local Fauna (loc. 60, table 4.1; Walsh 1991a, 1996a). This sample contains cf. *Uintatherium* and can be assigned to a late Bridgerian or early Uintan age.

Overlying the Scripps Formation is the Friars Formation (loc. 73, table 4.1), which was informally divided by Walsh et al. (1996) into a lower tongue, a middle conglomerate tongue, and an upper tongue, all apparently of Ui1 age. The conglomerate tongue of the Friars Formation was previously mapped as the Stadium Conglomerate (Kennedy and Peterson 1975; Kennedy and Peterson 1975), and the upper tongue was mapped by the same authors as Mission Valley Formation. Clarification of these lithostratigraphic relationships resolves the anomaly observed by Golz and Lillegraven (1977) and Novacek and Lillegraven (1979) concerning the very different mammal assemblages obtained from the southern and northern outcrops of the "Mission Valley Formation" (Walsh 1996a; Walsh et al. 1996). The Friars Formation has yielded the well-known early Uintan fauna from San Diego, whose taxa have been described in publications by Lillegraven (1976, 1979b, 1980), Novacek (1976, 1985), Gunnell (1995), and Walsh (1996b, 1997, 1998, 2000) and references therein. The magnetostratigraphic pattern of several Friars Formation sections is difficult to interpret, but lower normal and upper reversed magnetozones in the type area are correlated with C21n and C20r (Flynn 1986; Walsh et al. 1996).

Disconformably overlying the Friars Formation is the lower member of the Stadium Conglomerate, which contains a distinct assemblage (loc. 75, table 4.1; possibly Ui2) including the oldest known occurrence of *Eohaplomys*, a new species of *Crypholestes*, common specimens of *Pauromys lillegraveni*, and several taxa found in the Friars Formation (Walsh 1996a, 1997). The reversed polarity interval is correlated with C20r by Walsh et al. (1996).

The upper member of the Stadium Conglomerate disconformably overlies the lower member and contains the late Uintan Stonecrest L.F. (loc. 84, table 4.1; early Ui3; Walsh 1996a), similar to the late Uintan faunal assemblage from the gradationally overlying Mission Valley Formation (loc. 89; table 4.1). Both faunal assemblages are very different from the well-documented assemblages from the Friars Formation and lower Stadium Conglomerate in that they contain many taxa characteristic of the late Uintan part of the Sespe Formation such as Sespedectes, Proterixoides, and Simimys. The lower normal and upper reversed magnetozones in the type section of the Mission Valley Formation are correlated with paleomagnetic chrons C20n and C19r by Walsh et al. (1996). A 40 Ar/ 39 Ar date of 42.83 \pm 0.24 Ma was obtained by J. D. Obradovich on a bentonite from the Mission Valley Formation (Walsh 1996a).

Overlying the Mission Valley Formation in the Miramar Reservoir area is the Pomerado Conglomerate, which is divisible into a lower conglomeratic member, the Miramar Sandstone Member (loc. 90, table 4.1), and an upper conglomeratic member (Peterson and Kennedy 1974). The lower two units have yielded late Uintan vertebrate assemblages indistinguishable from those of the Mission Valley Formation. The upper unit (loc. 94, table 4.1) contains a late Duchesnean–early Chadronian assemblage (Walsh and Gutzler 1999), indicating that there is an unconformity between the Miramar Sandstone Member and the upper conglomeratic member of the Pomerado Conglomerate that may represent as much as 5 m.y. In the extreme southwestern part of San Diego County, the Pomerado Conglomerate is absent, and the Mission Valley Formation is overlain by reddish mudstones of the "Sweetwater" Formation. The "Sweetwater" contains sparse mammal fossils of latest Uintan to Duchesnean age (Walsh 1991b, 1996a).

The Santiago Formation in northwestern San Diego County has yielded several faunal assemblages. The local member B (Wilson 1972) assemblage (loc. 74, table 4.1) is early Uintan in age and very similar to that obtained from the Friars Formation, although not as diverse. The local member C assemblage (loc. 95, table 4.1), including the Jeff's Discovery and Rancho del Oro L.F., is late Uintan and very similar to that from the Mission Valley Formation, being dominated by *Sespedectes, Proterixoides, Dyseolemur, Simimys, Eohaplomys, Microparamys*, and several species of *Leptoreodon* and *Protylopus* not present in earlier Uintan assemblages from southern California.

Other Santiago Formation faunas from San Diego County include the Laguna Riviera L.F. (loc. 106, table 4.1; Golz 1976), the Camp San Onofre Locality assemblage (loc. 96, table 4.1; University of California Museum of Paleontology [UCMP] loc. V-72088; Golz and Lillegraven 1977), the San Diego Society of Natural History (SDSNH) loc. 3495 sample, and the Mission del Oro L.F. (Walsh 1996a). All of these faunal samples are of probable late Uintan or earliest Duchesnean age and may correlate best with the Brea Canyon and Strathern local faunas of the Sespe Formation in Ventura County (Kelly 1990; Kelly et al. 1991). The Santiago Formation localities are Ui3 to early Duchesnean in age.

The Sespe Formation (Kew 1924; Dibblee 1966a, 1966b) is a continental clastic unit of great temporal range, extending from the late Uintan at its base to the early Arikareean and, in some areas, the early Hemingfordian at its top (Donohoo and Prothero 1999). The Sespe crops out in numerous places, but most Eocene vertebrates have been found in the well-studied areas north of Simi Valley in Ventura County. As traditionally understood, the Sespe Formation is a large clastic wedge that is thickest to the east and laterally correlative with several marine formations to the west (Van de Kamp et al. 1974). The formation generally has been viewed as representing a gradual, prolonged, and major westward regression of the sea from the southern California landscape.

In the Simi Valley area, the Sespe Formation rests unconformably on the marine Llajas Formation, which may be in part coeval with the Delmar Formation and Ardath Shale in San Diego County (Givens and Kennedy 1979), suggesting that the Llajas Formation is temporally equivalent to the late Bridgerian or early Uintan. The Sespe Formation was divided into three members by Taylor (1983): a conglomeratic lower member, an interbedded sandstone and claystone middle member containing vertebrate fossils, and a thick upper member of heterogeneous lithology.

The oldest known vertebrate fossils (loc. 80, table 4.1) so far recovered from the Sespe Formation come from the top of the lower member (Kelly et al. 1991) and appear to be late Uintan in age based on the presence of Sespedectes singularis and Simimys sp. The well known Tapo Canyon and Brea Canyon local faunas (loc. 81, table 4.1) occur in the basal part of the middle member and are also of late Uintan age (Kelly 1990). The Strathern L.F. (loc. 97, table 4.1) is transitional between the latest Uintan and earliest Duchesnean and was obtained from a stratigraphic interval immediately below the interval that yields the early Duchesnean Pearson Ranch L.F. (loc. 105, table 4.1; Kelly 1990; Kelly et al. 1991). The youngest Eocene assemblage known from the Sespe is the Duchesnean Simi Valley L.F. (loc. 105, table 4.1) from the upper part of the middle member (Kelly et al. 1991).

Northwest of Simi Valley in the Sespe Creek and Pine Mountain areas (Golz and Lillegraven 1977), the Sespe Formation gradationally overlies the Coldwater Formation (Kew 1924; Dibblee 1966a, 1966b). The Coldwater Formation is a mostly marine sandstone unit up to 750 m thick (Prothero and Vance 1996). The Coldwater Formation overlies the Cozy Dell Shale, which in turn overlies the Matilija Sandstone. Based on molluscan faunal samples (Squires 1994) and coccoliths and planktonic foraminifera (Berman 1979) obtained from these formations, the base of the overlying Sespe Formation cannot be older than late Uintan.

The Hartman Ranch L.F. (loc. 97, table 4.1; UCMP loc. V-5814) from upper Sespe Creek is of late Uintan or early Duchesnean age (Lindsay 1968; Kelly 1990; Lander 1994) and was originally reported to occur in the transitional zone between the Sespe and the Coldwater formations. Later, Lander (1994) placed this locality (UCMP V-5814) about 100 feet above the base of the Sespe. Stock (1938) described a brontotheriid from Sespe Creek (loc. Los Angeles County Museum–California Institute of Technology [LACM-CIT] 292) that was later identified as *Duchesneodus* sp., cf. *D. uintensis* by Kelly (1990). LACM-CIT 292 occurs stratigraphically above UCMP loc. V-5814. A specimen of *Amynodontopsis* was discovered by Kelly (1990) from a locality just above LACM-CIT 292. To-
Wasatchian Through Duchesnean Biochronology 125

gether these constitute Kelly's Sespe Creek Local Fauna and suggest a Duchesnean age for this faunal level. If the Hartman Ranch L.F. is of Duchesnean age, then the base of the Sespe Formation in the Sespe Creek and Pine Mountain areas is somewhat younger than the base of the Sespe Formation in Simi Valley.

Paleomagnetic correlations for several sections of the Sespe Formation have been proposed by Prothero and Vance (1996) and Prothero et al. (1996). The latter authors correlated a reversed interval yielding the late Uintan Tapo Canyon and Brea Canyon local faunas (loc. 81, table 4.1) to chron C18r and an overlying normal interval yielding the early Duchesnean Pearson Ranch L.F. (loc. 105, table 4.1) to chron C18n. However, the Tapo Canyon and Brea Canyon faunal assemblages are extremely similar to the late Uintan assemblages from San Diego County (Walsh 1996a), suggesting a close temporal correlation. Walsh et al. (1996) correlated the late Uintan faunal assemblages from San Diego County with chrons C2on-C19r. These correlations indicate that if both the Walsh et al. (1996) and Prothero et al. (1996) magnetochron assignments are correct, then a difference of about 1.5 m.y. exists between the San Diego and Simi Valley late Uintan assemblages according to the Berggren et al. (1995) time scale. Because a correlation of the Tapo Canyon and Brea Canyon faunas with chron C18r makes them younger than the Duchesneodus-bearing basal part of the Duchesne River Formation in Utah (correlated with chron C19n by Prothero 1996b), it seems likely that the correlation of these Ventura County localities with chron C18r may be incorrect.

UINTA BASIN AND PICEANCE CREEK BASIN (FIGURE 4.4)

The Wasatchian faunas in these areas are best represented on the southeastern and northern sides of the Piceance Basin (loc. 7, table 4.1) of Colorado and Raven Ridge (loc. 10, table 4.1) on the eastern margin of the Uinta Basin. In a review of the geology and mammalian paleontology of the Debeque Formation (Wasatch Formation of authors) in the Piceance Basin, Kihm (1984) has recorded 124 mammalian species. They can be assigned to faunas of middle Clarkforkian through late Wasatchian age. Additionally, the presence of Tethyopsis in the Piceance Creek Basin in the intertongues of the "Uinta" and Green River formations provides evidence of Br3 rocks in that basin that cannot be documented in the Uinta Basin, further illustrating the detailed differences in the basinal histories that are a standard feature of intermountain basins. The Plateau Valley Local Fauna, previously assigned to the Tiffanian, is re-



FIGURE 4.4 Correlation of rock units containing fossil mammals of Wasatchian through Duchesnean age in Uinta and Piceance Creek basins, Utah and Colorado. Numerals in ovals refer to localities listed in table 4.1. Fm., Formation.

garded by Kihm as mid-Clarkforkian. However, J. Honey (pers. comm. in Kihm 1984) also reported a Tiffanian fauna from the extreme northwestern part of the Debeque Formation. Apparently, much-if not all-of the Wasatchian is represented in the Piceance Basin, although Wao and Wa1 time may be represented in the less fossiliferous Molina Member. Kihm's work corroborates the Wasatchian faunal sequences established in the Bighorn and Wind River basins, although there are some differences in faunal composition. However, certain Wasatchian biochrons, such as Wa5, are much better represented than others. Indeed, Wa5 may be the best represented biochron in the entire region; extensive faunal samples are present in the San Juan, Raton, Piceance Creek, Uinta, Greater Green River, and Bighorn basins, indicating a regional episode of sedimentation. Beds mapped as tongues of the Uinta Formation intertongue with the Green River Formation in the central Piceance Plateau.

Two fossiliferous early Eocene units are present on the southwest side of the Uinta Basin. The Colton Formation, a clastic fluvial floodplain deposit, is considered to be Wasatchian in age because of its intertonguing relationship with the Wasatchian Flagstaff Limestone (Marcantel and Weiss 1968). Fragments of mammals have been recovered by McKenna from the Colton, but no identifiable material is yet available from the southwestern part of the basin. The Flagstaff Limestone has produced one dentary of *Vulpavus australis* (Rich and Collinson 1973).

A series of localities in the Colton (Wasatch Formation of authors) and Green River formations from Raven Ridge (loc. 10, table 4.1) in the northeastern Uinta Basin, collectively known as the Powder Wash sites (Burke 1935; Kay 1957; Doi 1990), have many Wasatchian assemblages and one rich Bridgerian fauna. The Bridgerian locality (loc. 43, table 4.1) is located 82 m below the Mahogany Oil Shale bed, in the Douglas Creek Member of the Green River Formation (Cashion, written comm. in Dawson 1968) and places the Powder Wash site low in the general Uinta Basin Green River sequence; however, at Raven Ridge the Green River Formation is thinner than elsewhere and it is nearer to the top of the formation as preserved there. Detailed faunal studies for most groups have not been completed; only the marsupials (Krishtalka and Stucky 1984), primates (Gazin 1958; Szalay 1976), rodents (Dawson 1968), an artiodactyl (Burke 1969), and adapisoricid, nyctitheriid, and geolabidid insectivores (Krishtalka 1975, 1976a, 1976b; Lillegraven et al. 1981) have been described. Krishtalka and Stucky (1984) and Gunnell and Bartels (1999) have presented revised faunal lists concluding that this fauna is early Bridgerian and post-Gardnerbuttean in age. Work by Doi (1990) indicates that the lower Green River Formation at Raven Ridge is thick and that the upper (Bridgerian) Powder Wash locality is stratigraphically above the middle of the formation at that locality. The Wa7 and Bro parts of the sequence (loc. 36, table 4.1) are quite thick in comparison with the Wa5 and Wa6 units; this parallels the situation in the eastern part of the Greater Green River Basin (Roehler 1992a). Doi has also found many additional localities in the Raven Ridge area spanning the time between Wa2 and Br2.

The section in the eastern Uinta Basin is not uniform. Near Bonanza, there is a thick sequence of Uinta A that thins dramatically to the north and northeast. At the northwestern end of Raven Ridge on the eastern margin of the Uinta Basin, some 45 km to the north, the underlying Green River Formation is significantly thinner than in the Bonanza area. If the Uinta Formation is present there, it is very thin. Many of the classic Uinta B localities are 5 to 8 km north of Bonanza. North of these localities, the Uinta Formation is much thinner and is overlain by the Duchesne River Formation or covered.

Lacustrine conditions persisted until near the end of the middle Eocene in the Uinta Basin, as recovery of the Duchesnean brontotheriid *Duchesneodus uintensis* from the Green River Formation in Sanpete County, Utah, indicates (Nelson et al. 1980). The younger fluvial formations of the Uinta Basin, the Uinta Formation, and the Duchesne River Formation are the type areas for the two youngest ages (Uintan and Duchesnean) considered in this chapter.

The consensus here is that the faunas from the Wagonhound Member (loc. 72, table 4.1) are primarily Uinta B (= Ui2), and those from the Myton Member (loc. 79, table 4.1) are Uinta C (= Ui3). Much more fieldwork and collecting are necessary, especially in the areas of intertonguing of the Green River and Uinta formations (Cashion 1957; Dane 1954) in the region of the Uinta A deposits. This intertonguing occurs southwest of Raven Ridge in areas where faunal remains are very scarce. The intertonguing indicates that rocks present in that area are missing in the hiatus above the Green River Formation further north at Raven Ridge.

The Brennan Basin Member (loc. 91, table 4.1) of the Duchesne River Formation contains the Randlett Fauna; the Halfway Fauna comes from the lower two-thirds of the Dry Gulch Creek Member (loc. 103, table 4.1) of the Duchesne River Formation. These two are considered Ui3 in age, and the faunal names have been abandoned. The fauna from the LaPoint Member (loc. 104, table 4.1) is Duchesnean.

EASTERN GREATER GREEN RIVER BASIN (GREAT DIVIDE, WASHAKIE, AND SAND WASH BASINS; FIGURE 4.5)

The Wasatch Formation exposed around the flanks of the Washakie Basin and extensively in the Great Divide Basin (Bradley 1964) has yielded numerous local faunas. These demonstrate the apparent presence of most of Clarkforkian and Wasatchian time as the oldest assemblages appear to be roughly equivalent in age to those from the lowest part of the Willwood Formation, and the youngest are transitional into the Bridgerian. The distribution of these faunas is not uniform, however, and local sedimentologic hiatuses may be present. Two major assemblages come from the lower part of the Wasatch Formation. At the southeastern edge of the basin near the divide with the Sand Wash Basin, in Moffat County, Colorado, are the numerous localities that produce the Four Mile Fauna (loc. 5, table 4.1; McKenna 1960). These faunal samples are equivalent to those from the lower Willwood Formation (McKenna 1960). Recent work in the Four Mile Creek area indicates the presence of a slightly younger Wasatchian fauna above the Four Mile Fauna localities cited earlier (Hill et al. 2000).

In the vicinity of Bitter Creek (loc. 9, table 4.1), along the northern edge of the Washakie Basin, C. L. Gazin (1950s and 1960s), D. Savage and associates (1970s), H. H. Covert and students (1980s and 1990s) and K. C. Beard (1990s) made collections from a series of localities through a continuous sedimentary section from the upper part of the Fort Union Formation to the Cathedral Bluffs Tongue of the Wasatch Formation. Faunal sam-



FIGURE 4.5 Correlation of rock units containing fossil mammals of Wasatchian through Duchesnean age in the Greater Green River (G.R.) Basin. Numerals in ovals refer to localities listed in table 4.1. Fm., Formation; Mbr., Member; T, Tongue.

ples from these localities span the entire Clarkforkian and the Wasatchian from Wa3 to Wa7 and either Bro or Bria (P. Holroyd and H. H. Covert, pers. comm., 2000).

Other Washakie Basin and Great Divide Basin Wasatchian localities were cited by Gazin (1962) and have been recollected by recent work of Anemone et al. (2000). Although these are generally small assemblages, they further confirm the age of the Wasatch Formation in the Washakie Basin. Recent work by H. H. Covert in the Bitter Creek area and by P. Robinson (UCM loc. 83120) and J. Honey (1988) on the eastern part of the Washakie Basin confirms the evidence that the Wasatchian–Bridgerian boundary in this area is also in the Cathedral Bluffs member.

The Niland Tongue (= upper Main Body) of the Wasatch Formation along the east side of the Washakie Basin has produced the Dad Local Fauna (loc. 32, table 4.1), which is Wa7 in age. It contains the typical Wa7 perissodactyl *Lambdotherium* and other characteristic late Wasatchian mammals. The Niland Tongue is overlain by the Tipton Tongue and Wilkins Peak members of the lacustrine Green River Formation, and they are overlain by or interdigitate with the uppermost Wasatch Formation subunit, the Cathedral Bluffs Tongue.

The Washakie Formation contains the youngest record of early Tertiary fossil mammals in the Washakie Basin. Biostratigraphic work by Turnbull (1972, 1978), Roehler (1973), and McCarroll et al. (1996a, 1996b) has established the presence of considerable geologic time in the Washakie Formation. Roehler (1973) presented detailed sections for the Washakie Formation and designated two members, the lower Kinney Rim Member and the upper Adobe Town Member, the latter being divided into lower, middle, and upper parts.

The Kinney Rim Member (loc. 54, table 4.1) of the Washakie Formation contains Bridgerian taxa present in both Br2 and Br3; however, one taxon, Hyrachyus eximius, which is found in Br3 and Ui1, occurs near the base of the Kinney Rim Member and indicates that the age of that member is Br3 (McCarroll et al. 1996a). The lowest part of the Adobe Town Member (loc. 59, table 4.1) is Granger's (1909) Washakie A and is equivalent to Br3. Such taxa as Notharctus robustior, Hemiacodon, Stylinodon, Tethyopsis, Uintatherium, and Mesatirhinus secure this age assignment. The middle Adobe Town Member (loc. 69, table 4.1), Washakie B, of Granger (1909) is either Ui1 or Ui2 in age given the occurrence of Protoptychus, Eobasileus, Dolichorhinus, Eomoropus, Triplopus, Amynodon, Achaenodon, and Protylopus. The highest part of the Washakie Formation (upper Adobe Town Member, loc. 77, table 4.1) may represent another zone not recognized by Granger, who assumed that the summit of Haystack Mountain was the uppermost part of the Washakie Basin section (McCarroll et al. 1996a, 1996b).

The Great Divide Basin has produced a few localities of significance ranging in age from early Wasatchian to early Bridgerian Recent fieldwork in the area has been carried out by R. Anemone in the southern part of the basin and by G. F. Gunnell and W. S. Bartels in the northwestern part.

The Sand Wash Basin (loc. 63, table 4.1), the southeastern extension of the Greater Green River Basin, contains Washakie Formation rocks (Stucky et al. 1996) equivalent to, and initially continuous with, the lower and middle parts of the Adobe Town Member of the Washakie Formation. The Robin's Egg Blue Tuff marker is present and aids in correlation with the Washakie Basin. The small upper fauna (West and Dawson 1975; Stucky et al. 1996; D. T. Rasmussen, pers. comm., 2000) is early Uintan (Ui1 or Ui2) (*Triplopus, Eobasileus, Protoreodon, Ourayia*) and includes several Bridgerian holdover taxa such as *Notharctus*.

WESTERN GREATER GREEN RIVER BASIN (INCLUDING HOBACK AND FOSSIL BASINS) (FIGURE 4.5)

The Wasatch Formation is exposed along the western and northern margins of the Western Green River Basin (Bradley 1964). In the type area, near Evanston (Fossil Basin) in southwestern Wyoming, there is a small Wa6 mammalian assemblage (loc. 26, table 4.1) that includes *Heptodon*. Clarkforkian and early Wasatchian mammals have been reported from near LaBarge (loc. 27, table 4.1), on the western side of the Green River Basin (Dorr and Gingerich 1980). Younger Wa7 equivalents have been found at several localities along the western and northern margins of the basin (Gazin 1952, 1962; West 1970, 1973a). The age is confirmed by the presence of *Lambdotherium* in the LaBarge and Cathedral Bluffs (formerly New Fork) faunas (loc. 41, table 4.1) and by the positions of the fossiliferous fluvial rocks relative to the tongues of the Green River Formation.

The Bridger Formation crops out in the southern part of the western Greater Green River Basin. This formation has been famous since its discovery in the 1860s for the abundance and quality of its vertebrate fauna and became the basis for the Bridgerian LMA. Matthew (1909) divided the Bridger Formation into five ascending lithologic units, A to E, and separated them on the basis of lithologic marker beds ("white layers"), many of which are lacustrine. At the time of Matthew's monograph, Bridger A was considered sparsely fossiliferous, Bridger B, C, and D were considered rich, and Bridger E was thought to be barren. Bridger A (loc. 42, table 4.1) is found north of highway Interstate 80 near the town of Opal, Wyoming; Bridger B (loc. 45, table 4.1) crops out extensively between the towns of Lyman and Green River; and Bridger C-D (loc. 55, table 4.1) and E (loc. 66, table 4.1) are found in a more restricted southern area at Sage Creek, Cedar and Hickey Mountains. Outliers of the upper Bridger formation occur north of Farson (Tabernacle Butte). Work by McGrew and Sullivan (1970) and more recently by Gunnell and Bartels (1994) and Gunnell (1998a) has demonstrated that the Bridger A beds (loc. 42, table 4.1) intertongue with the upper units of the Green River Formation and that they have a diverse fauna. Mapping of the Bridger B, C, and D has developed a significant number of stratigraphic markers, allowing more detailed stratigraphic positioning of fossil collections (Evanoff et al. 1998). The Bridger E faunal assemblage is now considered earliest Uintan. Following suggestions in Matthew (1909), UCM parties have accumulated significant microvertebrate samples from lacustrine units in Bridger C and D.

Clyde et al. (2001) place the onset of Bridgerian time at greater than 52 Ma; however, more recent work by M. E. Smith et al. (2003) suggests a date of 50.39 Ma based on the Grey Tuff of the Wilkins Peak member of the Green River Formation. More recent dates on three tuffs from the Bridger Formation (Murphey et al. 1999) indicate that middle Bridgerian was at about 48 Ma and that the Bridgerian ended near 46 Ma. The Bridger Formation proper may represent only about 60 percent of Bridgerian time (approximately 3.2 m.y.) from Bridger A through Bridger D (Murphey 2001). On the basis of the various referred areas in the South Pass and Bridger Basin, we regard the Bridgerian as possibly lasting as much as 5 million years, from greater than 51 Ma to about 46 Ma.

Isolated areas of Bridgerian rocks crop out in the northern Green River Basin, in downdropped blocks related to the western end of the Continental Fault system (McKenna et al. 1962; West and Atkins 1970; West 1973a; West and Dawson 1973). The oldest Bridgerian assemblage in this region comes from arkosic rocks of the Cathedral Bluffs Tongue of the Wasatch Formation (loc. 41, table 4.1) and seems best placed in Br1a. It is overlain by more typical Bridger Formation rocks that produce a Brıb fauna (loc. 44, table 4.1). Conformably overlying this early Bridgerian sequence are the tuffaceous rocks of Tabernacle Butte (loc. 56, table 4.1) with a late Bridgerian assemblage (McGrew 1959). This particular assemblage is of interest because it contains a late Bridgerian Phenacodus and the only multituberculate known from the Bridgerian.

Fossil Basin (loc. 26, table 4.1) is a separate depositional basin a few miles west of the western edge of the Green River Basin proper from near Evanston north to near Kemmerer, Wyoming. Mammalian assemblages of Wasatchian age have been found at several localities (Gazin 1962; Oriel et al. 1962), and the upper assemblages (Wa6 and Wa7) are physically coincident with fish-bearing beds of the Green River Formation. Recently, exposures of the Wasatch and Green River Formations at Fossil Butte National Monument have produced Wa6 and Wa7 vertebrates (Ambrose et al. 1997; Froehlich and Breithaupt 1998).

Nelson (1973, 1974, 1977) collected a suite of Bridgerian mammals from the Fowkes Formation (loc. 57, table 4.1), northwest of Evanston, Wyoming. The Fowkes Formation was initially recognized by Veatch (1907) as the middle part of the Wasatch Group. Oriel and Tracey (1970) have shown that this formation is younger than the Wasatch Formation. Nelson's faunal sample from the Fowkes Formation includes *Notharctus, Hemiacodon, Omomys, Uintasorex, Hyopsodus lepidus, Orohippus*, and several late Bridgerian ischyromyid rodents.

North of the western Green River Basin is a small physiographic depression, the Hoback Basin. J. A. Dorr and students from the University of Michigan demonstrated virtually continuous sedimentation from Paleocene into medial Wasatchian time (Dorr 1952, 1958, 1969; Dorr and Steidtmann 1971; Dorr et al. 1977). Although the paleontological record from the Wasatch and Pass Peak formations (loc. 6, table 4.1) is not particularly good, samples (Dorr 1978) are adequate to demonstrate the presence of Clarkforkian and early and middle Wasatchian sites (Dorr and Gingerich 1980).

WEST TEXAS (FIGURE 4.6)

Rocks producing fossils of late Wasatchian, Uintan, and Duchesnean ages are present in three areas of West Texas: Big Bend National Park, the Agua Fria area of Brewster County, and the Vieja-Ojinaga area of Presidio County.

The oldest Eocene faunas have been collected from the Hannold Hill Formation (loc. 29, table 4.1) in Big Bend National Park (Schiebout 1974; Rapp et al. 1983; Rose 1981). These faunas include *Phenacodus, Phenacolemur*, and two species of *Hyracotherium*, a possible *Lambdotherium*, and several disarticulated skeletons of *Coryphodon* from the Fossil Bone Exhibit locality. These Hannold Hill assemblages are clearly Wasatchian and probably late Wasatchian (Wa7), especially if the record of *Lambdotherium* is valid (but there are several small assemblages from differing levels that have been combined into one "local fauna" for the Hannold Formation, so it is possible that other biochrons of the Wasatchian are also represented).

Unconformably overlying the Hannold Hill Formation is the Canoe Formation, which contains two distinct faunal assemblages, Canoe assemblage A and Canoe assemblage B. Canoe assemblage A (loc. 67, table 4.1) is from just below the lower basalt. Canoe assemblage A and an equivalent sample from inside Big Bend National Park (from the Devil's Graveyard Formation) have a mixed



FIGURE 4.6 Correlation of rock units containing fossil mammals of Wasatchian through Duchesnean age in western Texas. Numerals in ovals refer to localities listed in table 4.1. Fm., Formation.

Bridgerian–Uintan fauna including *Hyrachyus*, *Helohyus*, *Hyopsodus*, *Prolapsus*, *Peratherium*, *Scenopagus*, *Microsyops*, *Uintasorex*, *Omomys*, *Triplopus*, *Amynodon*, *Leptoreodon*, *Microparamys*, *Leptotomus*, and *Pauromys*. Both of these faunal samples can best be interpreted as early Uintan (Ui1), possibly equivalent with the Junction localities (J. A. Wilson 1967 1977; Runkel 1988). Canoe assemblage B (loc. 82, table 4.1) is located beneath the upper basalt in the Canoe Formation. The Canoe assemblage B, along with an equivalent sample from the Chisos Formation, includes *Metamynodon*, *Protoreodon*, *Leptoreodon major*, *Leptoreodon pusillus*, *Leptoreodon edwardsi*, *Uintacyon scotti*, *Epihippus gracilis*, and *Triplopus*. These faunas are equivalent to the Serendipity L.F. from Agua Fria and are late Uintan (Ui3).

North of Big Bend National Park is the Agua Fria area, where a series of superposed localities are found in the Devil's Graveyard Formation. The earliest occurring faunal assemblage comes from the Junction and o.6 miles east of Junction localities (loc. 65, table 4.1; basal Tertiary conglomerate; Wilson 1986). These samples include *Herpetotherium, Scenopagus, Centetodon, Nyctitherium, Omomys, Ourayia, Notharctus, Microsyops, Thisbemys, Microparamys, Mysops, Prolapsus, Hyopsodus, Uintatherium, Stylinodon, Hyrachyus, Triplopus, Helohyus, Parahyus,* and *Leptoreodon pusillus.* This assemblage is very similar to that of Bridger E (Evanoff et al. 1994), and we interpret it to represent the earliest Uintan (Uii).

The Whistler Squat Quarry (loc. 78, table 4.1) occurs above the Junction Locality and has a fauna containing Amynodon, "Sthenodectes," Protoreodon, Malaquiferus, and Leptoreodon and is interpreted as Ui1 or Ui2. Above Whistler Squat is the Serendipity L.F. (loc. 85, table 4.1), which appears equivalent to Canoe B and the Chisos Formation sample (Ui3). Higher in the Devil's Graveyard Formation, above the Ash Spring Basalt, are the Skyline Channels localities (loc. 99, table 4.1). These localities have produced a typical Duchesnean assemblage including Simidectes, Leptotomus, Mahgarita, Hyaenodon, Harpagolestes, Amynodontopsis, Toxotherium, Protoreodon pumilus, Agriochoerus, Hendryomeryx, and an unidentified brontotheriid. The Cotter Channel faunal assemblage (loc. 101, table 4.1), found above the Skyline Channels, probably is early Duchesnean and includes Mytonomys, Duchesneodus?, Amynodontopsis, Protoreodon pumilus, Protoreodon petersoni, Agriochoerus, Hypertragulus, Aclistomycter, and Eotylopus. Above these localities are several localities of the Chadronian Coffee Cup L.F.

Approximately 100 km northwest of the park in the Vieja-Ojinaga area is another fossiliferous sequence

(Wilson 1978; Walton 1992). The lower part of the Vieja Group, which unconformably overlies Cretaceous rocks, includes the fossiliferous Colmena Formation. The Colmena produces the Candelaria L.F. (loc. 87, table 4.1; Manitsha, Pseudotomus, Epihippus, Sthenodectes, Protoreodon, Leptoreodon, and Toromeryx), which correlates well with the Randlett Fauna (loc. 91, table 4.1) of Utah (Ui3) and with other Texas local faunas including Canoe assemblage B, Chisos Formation, and Serendipity L.F. The Porvenir L.F. (loc. 100, table 4.1) comes from the Chambers Formation, above the Buckshot Ignimbrite (37.8 Ma; Swisher and Prothero 1990). It correlates biostratigraphically with the Montgomery bone bed and is considered late Duchesnean. Above the Porvenir L.F. are found the Chadronian Little Egypt, Airstrip, and Ash Spring localities. Across the Rio Grande in Mexico, the Rancho Gaitan sample appears to correlate with the Chadronian Little Egypt locality.

SAN JOSE, HUERFANO, RIO GRANDE RIFT (FIGURE 4.7)

Several separate occurrences of fossil mammals are present in southern Colorado and New Mexico. The most extensive assemblage occurs in the San Jose Formation (loc. 18, table 4.1) of the northern San Juan Basin of northwestern New Mexico. Granger (1914) and Simpson (1948) recognized two main fossiliferous units of the San Jose Formation: the lower Almagre and upper Largo beds or facies. Baltz (1967) divided the San Jose into four members: the Regina Member, including the Almagre beds;



FIGURE 4.7 Correlation of rock units containing fossil mammals of Wasatchian through Duchesnean age in New Mexico and eastern Colorado. Numerals in ovals refer to localities listed in table 4.1. Fm., Formation.

the Tapicitos Member, including the Largo beds; the Llaves Member; and the Cuba Mesa Member. The two main faunal assemblages, one from the Almagre and the other from the Largo, are Wasatchian. Van Houten (1945) and Simpson (1948) regarded them as spanning the Graybullian to early Lysitean, a conclusion corroborated by Lucas et al. (1981), Stucky and Krishtalka (1983), Smith and Lucas (1991), and Lucas and Williamson (1993). These two faunas are not as different as previously thought, and Lucas et al. (1981) suggested abandonment of the Largo–Almagre faunal distinction. For the most part, the San Jose faunas may be Wa6 in age.

The Galisteo Formation of north-central New Mexico (Stearns 1943) is represented by as much as 1300 m of fluvial mudstone, sandstone, and conglomerate (Lucas and Williamson 1993). A small Wasatchian sample (the Cerrillos Local Fauna, loc. 24, table 4.1) has been found in the lower part of the Galisteo Formation and includes Ectoganus, Coryphodon, Microsyops, Hyopsodus powellianus, Homogalax, Hyracotherium, and paramyid rodents. The age is indeterminate, but Wa5 or Wa6 is probable. The upper part of the Galisteo Formation has yielded the Tonque L.F. (loc. 111, table 4.1) and includes Duchesneodus, Hemipsalodon grandis, Amynodon, Protoreodon, Poabromylus, brontotheriids, hyracodontids, and protoceratids (Lucas and Williamson 1993), indicating a Duchesnean age. Other scattered fossils from the Galisteo (Galusha 1966; Galusha and Blick 1971) are Eocene in aspect but not definitive of any particular subage.

The Baca Formation may be as much as 1100 m thick and is well exposed in western New Mexico. It has produced small suites of fossil mammals from localities west of the Rio Grande that indicate an age span of Uintan to Chadronian (Schiebout and Schrodt 1981; Lucas et al. 1981; Lucas and Williamson 1993). The Baca Formation faunal assemblage (locs. 112-113, table 4.1) includes Hyaenodon, Diplacodon, Brachyops, Protoreodon, an agriochoerid, a protoceratid, and a camelid. The fauna seems to be a mix of Uintan and Duchesnean taxa, but no stratigraphic organization of Baca Formation localities exists, so it is difficult to sort out the precise distribution of these various taxa. Lucas (1990) and Lucas and Williamson (1993) noted the presence of a small brontotheriid metacarpal from the base of the Baca Formation in Cibola County that may indicate that Baca deposition began in the late Bridgerian. The Baca Formation preserves three mammalian trackways in Socorro County (Lucas 1983; Lucas and Williamson 1993) that are interpreted as representing those of artiodactyls.

Lucas and Williamson (1993) recognized a new formation, the Hart Mine Formation, for rocks in the Carthage–La Joya Basin, east of the Neogene Rio Grande rift in Socorro and Valencia counties in central New Mexico. These rocks originally were assigned to the Baca Formation but are lithologically distinct from the Baca Formation west of the rift. A small assemblage of vertebrates from the Hart Mine Formation (loc. 49, table 4.1) includes *Glyptosaurus, Telmatherium,* and *Notharctus*. These indicate a Bridgerian age, probably Br3 (Lucas and Williamson assign the *Notharctus* specimen to *N. tenebrosus* based on tooth size but point out that it could represent a later species of *Notharctus* as well; the presence of *Telmatherium* suggests a later rather than earlier Bridgerian interval).

Other Eocene sediments represented in New Mexico include the Cub Mountain Formation (loc. 112, table 4.1), the Rubio Peak Formation, the Palm Park Formation, and the Love Ranch Formation. There are small vertebrate samples from these formations that indicate ages ranging from the Wasatchian through the Chadronian (Lucas and Williamson 1993).

Well to the north, in the northern Raton Basin of southern Colorado, five superposed assemblages have been collected from the Huerfano Formation (P. Robinson 1966; Stucky 1984b). They correspond to biochrons Wa5 (loc. 20, table 4.1; Huerfano Locality XIII or UCM loc. 77041; P. Robinson 1963), Wa6 (loc. 20, table 4.1; Huerfano locs. VIII, IX, and XII; lower part of Huerfano A), Wa7 (locs. IV, VI, and XI; upper part of Huerfano A), and Bro-Bria (locs. 20 and 40, table 4.1; loc. VII, uppermost part Huerfano A; University of Michigan locs. I, II, III, and V; Huerfano B). As in the Wind River Basin, the Wa7 biochron is defined by the presence of Lambdotherium. The Gardnerbuttean, first defined by P. Robinson (1966) on the basis of the fauna from Huerfano B (loc. 40, table 4.1), is now also recognized in the Wind River, Green River, and Uinta basins. The Huerfano Formation is at least 1525 m thick in the vicinity of the Spanish Peaks (central Raton Basin), where it unconformably overlies the Paleocene Poison Canyon Formation; scant faunal remains from that area may indicate that pre-Wa5 sediments occur there as well (P. Robinson 1960). The Farisita Formation (loc. 34, table 4.1; Johnson and Wood 1956) contains sediments that in part intertongue with the Huerfano Formation and in part overlie it (Briggs and Goddard 1956; Berner and Briggs 1958). The only known faunas from the Farisita Formation come from beds of the intertonguing sequence, and these contain both Wa7 and Br1a taxa (P. Robinson 1966). The term Cuchara Formation (loc. 14, table 4.1) has been applied to beds that supposedly underlie the Huerfano Formation (Johnson and Wood 1956; Johnson et al. 1958) but that in part are in fact contemporaneous with the lower part of the Huerfano Formation (P. Robinson 1966) and from localities that cannot be distinguished from the Huerfano Formation lithologically (P. Robinson 1960, 1963, 1966).

MISCELLANEOUS LOCALITIES

A number of miscellaneous North American sites produce fossil mammals that are Wasatchian through Duchesnean in age. Most are geologically and geographically isolated from the aforementioned areas and usually are single fossiliferous levels correlative with other areas only biochronologically. Continued discovery of these sites indicates that much is yet to be found in North America.

Mexico: Baja California A small collection from the Lomas las Tetas de Cabra (loc. 13, table 4.1) Formation, 30 km south of the village of Punta Prieta, Baja California del Norte, correlates with the Early Eocene Bateque formation (marine). The fauna includes Hyracotherium, an endemic marsupial Esteslestes ensis, Esthonyx, an endemic pantodont, Meniscotherium, Hyopsodus, and a creodont (Morris 1966; Flynn and Novacek 1984; Novacek et al. 1991). The age of the fauna, originally suggested as Clarkforkian (Morris 1966; Rose 1981), is now thought to be early Wasatchian (Novacek et al. 1991), based primarily on the occurrence of Wyolestes. Other elements of the fauna include typical Wasatchian genera such as Meniscotherium (Wao-Wa7), Ectocion (Tiffanian-Wa7), Prolimnocyon (Wa3-Br1a), Diacodexis (Wao-Wa7), Oxyaena (Wa1-Wa7), Phenacodus (Tiffanian to Bridgerian), Hyopsodus (Clarkforkian-Ui3), Dissacus (Torrejonian-Wa4), and Esthonyx (Wao-Bria). There is also a new pantolambdid pantodont, a group usually Paleocene in distribution. The presence of the brontotheriid Eotitanops (usually considered early Bridgerian) in the fauna raises some questions because even its late Wasatchian occurrence in Wyoming (Smith and Holroyd 2001) indicates a younger age for the fauna than the other taxa present do. This specimen was not collected at the same time as most of the material cited by Novacek et al., and its provenience is not as certain. Preliminary paleomagnetic study suggests that this sequence can be correlated with either chron C23r or C24n.

Mexico: Guanajuato Paleogene vertebrates from Guanajuato, Mexico, at the Marfil locality (loc. 61, table 4.1) have been described by Fries et al. (1955), Black and Stephens (1973), Ferrusquia-Villafranca (1984, 1989). The mammals so far recovered from Marfil include a sciuravid rodent, *Floresomys guanajuatoensis*, two rodents of uncertain taxonomic placement (*Guanajuatomys hibbardi* and *Marfilomys aewoodi*), fragments of a tapiroid forelimb, a small carnivoran possibly representing *Viverravus*, a hyopsodontid condylarth of uncertain affiliation, and a small palaeanodont. These taxa do not permit a precise age assignment, but a probable Bridgerian– Uintan interval is most likely. A K–Ar date from an andesitic lava flow near the Marfil site produced a date of 49.3 Ma, but the precise stratigraphic relationship between this basalt and the Marfil sediments is not yet known.

Alaska A recent discovery represents the only known Paleogene mammalian record from Alaska. In the Matanuska Valley east of Palmer, individual footprints and trackways of mammals and birds have been discovered. Two of the mammalian ichnomorphs represent a perissodactyl and a possible amblypod (K. May, pers. comm., 2001). The trackways were found in the Chickaloon Formation, which spans the Paleocene–Eocene boundary (Triplehorn et al. 1984).

Golden Valley The fluvial Golden Valley Formation (loc. 11, table 4.1) conformably overlies the Sentinel Butte Shale Member of the Fort Union Formation in southwestern North Dakota. A collection made by Jepsen (1963) and supplemented by West (1973b) is early Wasatchian in age. The Golden Valley Formation extends well below the mammal-producing level and, if fossiliferous, could yield a series of faunas spanning the Tiffanian through Wasatchian in southwestern North Dakota.

Powder River Basin Delson (1971) reported on collections from the Powder River Basin (loc. 2, table 4.1) of northeastern Wyoming. The rocks there are regarded by the U.S. Geological Survey as belonging to the Wasatch Formation, although they are separated from the typical Wasatch Formation of the Greater Green River Basin by the Wind River Basin with its Wasatchian Indian Meadows and Wasatchian/Bridgerian Wind River Formations. The assemblage discussed by Delson is early Wasatchian in age, mostly Wa2, with one locality, Monument Blowout (UCM loc. 88052) of Wa3 age based on the presence of *Homogalax protapirinus*.

Recent work by University of Colorado parties has found that several early Wasatchian faunas are represented in the Powder River Basin (Robinson and Ivy 1994; Robinson and Williams 1998). These faunas are correlative with the Sandcouleean (Wao–Wa2) and early Graybullian (Wa3) of the Willwood Formation. Reexamination of a deciduous perissodactyl premolar (USNM 187546) from Pumpkin Buttes ascribed to *Lambdotherium*

(Whitmore in Soister 1968; Sharp et al. 1964; Robinson and Ivy 1994) indicates that it is not that taxon and that no Wasatchian sediments younger that Wa3 definitely occur in the Powder River Basin. The Homogalax protapirinus from North Pumpkin Butte cited by Sharp et al. (1964) is the highest fossil occurrence yet documented from the Wasatchian rocks of the Powder River Basin and is a species usually found in Wa3-Wa5 rocks. Coryphodon and Hyracotherium, also present in the Powder River Basin "Wasatch" Formation (Wegemann 1917; Sharp et al. 1964; Soister 1968), generally indicate only a Wasatchian age. The Powder River Basin sediments are in sharp contrast to the coeval Willwood Formation of the Bighorn Basin because of the large number of lignites present in the former and by the lack of beds definitely younger than Wa3. The Powder River sequence may well represent a much more paludal environment.

Laramie and Shirley Basins A small mammalian fauna from rocks in the Cooper Creek area (loc. 16, table 4.1) referred to the Wind River Formation 40 km northwest of Laramie, Wyoming, was studied by Prichinello (1971). The fauna includes *Cantius, Tetonius, Haplomylus, Hyopsodus, Phenacodus, Coryphodon,* and *Hyracotherium* and is early Wasatchian in age.

In the Shirley Basin, north of the Laramie Basin, Harshman (1972) mapped both the Wind River and Wagon Bed formations. Fossils found in the Wind River Formation are characteristic of the Wasatchian (Harshman 1972) but cannot be assigned more precisely. The Wagon Bed conformably overlies the Wind River in the Shirley Basin; a specimen of *Notharctus tenebrosus* (Harshman 1972) suggests an early Bridgerian age for the Wagon Bed Formation there.

New Jersey An isolated lower molar of the tillodont *An-chippodus* (*?Trogosus*) was collected from the marine Shark River Marls of northeastern New Jersey. The tooth is at the same stage of evolutionary development as those of western Bridgerian genera (Gazin 1953).

Canada: British Columbia Two teeth referable to the Bridgerian tillodont *Trogosus* have been collected at a coal mine near the town of Princeton (Russell 1935; Gazin 1953).

An assemblage from the Kishenehn Formation (loc. 116, table 4.1) in the Flathead Valley of southeastern British Columbia includes the type material of *Thylacaelurus* and also citations of *Peratherium*, *Pseudocylindrodon*, *Protadjidaumo*, *Paradjidaumo*, *Desmatolagus*, and *Leptotragulus* (Russell 1954). The Kishenehn Fauna was

originally thought to be Duchesnean (Russell 1954), but Lucas (1992) considered that the assemblage was more likely to be Chadronian. It is difficult to be certain considering the number of taxa now known.

A brontotheriid lower molar from the Australian Creek beds along the Fraser River at Quesnel was interpreted by L. S. Russell (figured in McAnally 1996) as Chadronian. It has been used to correlate a critical palynofloral sequence with the Eocene–Oligocene boundary (Ridgway et al. 1995). This area should be restudied because the modest size of the specimen in question raises the distinct possibility that it might be Uintan or Duchesnean.

Canada: Saskatchewan In the Cypress Hills Formation, Swift Current Plateau (loc. 88, table 4.1) of southwestern Saskatchewan, a diverse mammalian fauna has been collected by the Canadian Museum of Nature (Russell and Wickenden 1933), the Royal Ontario Museum (Russell 1965), and the Royal Saskatchewan Museum (Storer 1978, 1984; Krishtalka 1979). The presence of *Procaprolagus, Miocyon, Auxontodon, Colodon, Epihippus, Protoreodon,* and *Leptoreodon* confirms a late Uintan (Ui3) age.

Two superposed Duchesnean local faunas (loc. 117, table 4.1; Lac Pelletier Lower Fauna, Lac Pelletier Upper Fauna) occur in the Cypress Hills Formation, also on the Swift Current Plateau (Storer 1996). Both would be interpreted by most authors as late Duchesnean because of a group of first appearances of typically Chadronian genera including Sinclairella, Hesperocyon, Heptacodon, Pseudoprotoceras, and Trigenicus. Lucas (1992) has suggested that this assemblage actually is Chadronian. On the other hand, Palaeictops, Didelphodus, Apatemys, Talpavus, Sespedectes, Nyctitherium, Uintasorex, three omomyid primates, Miocyon, Janimus, and Microeutypomys are also present in these samples and are not known from any Chadronian faunas. Storer (1996) hesitated to assign these assemblages to either early or late Duchesnean, noting only that they appear older than the latest Duchesnean Porvenir Local Fauna of Texas (Wilson 1986).

No Duchesnean assemblages are documented from the Cypress Hills Plateau, although the Duchesnean index taxon, *Duchesneodus primitivus* (Lambe 1908; Lucas and Schoch 1989), comes from an undetermined locality there.

Canadian Arctic Vertebrates from several localities at 79°–80° north latitude on Ellesmere Island (Dawson et al. 1976; West and Dawson 1978; McKenna 1980a) and Axel Heiberg Island (Dawson et al. 1993), Nunavut Territory, Canada, suggest a Wasatchian and possible early Bridger-

ian age. These fossils occur in the Eureka Sound Group (loc. 37, table 4.1), the formations within which are differently named and divided by Miall (1986) and Ricketts (1986). As currently known, the assemblages do not correlate readily with any particular southern fauna, and the high diversity of plagiomenids is their most striking peculiarity.

Slightly higher in the Eureka Sound Group of Axel Heiberg Island, the beds preserving the Geodetic Hills (loc. 98, table 4.1) mummified forest appear to be Uintan or Duchesnean, based on fragments of brontotheriid teeth found there (Eberle and Storer 1999).

Oregon The Clarno Formation has two mammalproducing levels. The lower level, the Nut Bed (loc. 58, table 4.1), has produced a small assemblage (*Patriofelis*, *Orohippus, Telmatherium*, and *Hyrachyus*) indicative of the Bridgerian. A stratigraphically higher locality, Hancock Quarry (loc. 110, table 4.1), has produced *Epihippus* and *Diplobunops*, generally regarded as Uintan, but other taxa (*Hemipsalodon, Haplohippus, Protapirus*, cf. *Procadurcodon*, and *Caenopus*) are more usually considered Duchesnean or Chadronian.

South Dakota The Slim Buttes Formation (loc. 109, table 4.1) of northwestern South Dakota contains *Duchesnehippus intermedius*, *Duchesneodus*, *Colodon*, *Amynodontopsis*, an indeterminate agriochoerid, and an indeterminate leptotraguline (Bjork 1967). A Duchesnean age is assignable to this small assemblage (Lucas 1992), which is similar to the LaPoint Fauna of Utah.

Virginia Rose (1999) has recently reported on a small fauna from the Fisher/Sullivan site, Nanjemoy Formation (loc. 17, table 4.1), which may well be middle Wasatchian (Wa3–Wa5) in age. Included in this fauna are isolated teeth of a probable pantolestid, a miacid carnivoran, an esthonychid tillodont, a hypsodontid condylarth, an isectolophid perissodactyl, an undetermined rodent, and a single dentary containing three teeth of a possible nyctitheriid insectivoran.

Mississippi The Tuscahoma Formation of Lauderdale County (loc. 4, table 4.1) has yielded a fauna of 25 species of land mammals and other vertebrates (Red Hot L.F. of Beard et al. 1995 and Beard and Dawson 2001). This assemblage probably is Wa1 in age, based on the co-occurrence of *Ectocion parvus* and *Haplomylus speirianus* (Thewissen 1990; Robinson and Williams 1998). On the basis of associated marine fossils, Beard et al. (1995) correlated the Red Hot L.F. with nannoplankton zone NP9, which straddles the Paleocene–Eocene boundary (Berggren et al. 1995). The Bashi Formation (loc. 12, table 4.1) overlies the Tuscahoma Formation and has produced an omomyid primate of probably Wasatchian age (Beard and Tabrum 1990).

A single brontotheriid skull, the holotype of *Notiotitanops mississippiensis*, was found in Clark County, Mississippi, in strata previously referred to the Lisbon Formation (Gazin and Sullivan 1942). The locality is now referred to the Archusa Marl Member of the middle Eocene Cook Mountain Formation (Westgate 1986). The skull is morphologically closest to several Uintan brontotheriids of the Utah–Wyoming region (Mader 1989), and the locality is best considered late Uintan in age (Westgate, pers. comm., 2002).

Alabama Westgate (2001) cites a single specimen of *Coryphodon* from the Hatchetigbee Bluff L.F. (loc. 31, table 4.1) in the Hatchetigbee Formation, Wilcox Group, in Washington County. *Coryphodon* occurs from the Clarkforkian to earliest Bridgerian (Br1a); the location of this specimen argues for a Wasatchian age.

Another Alabama locality with a single mammalian specimen is the Little Stave Creek L.F. (loc. 62, table 4.1) in the Gosport Sand, Claiborne Group, in Clarke County (Westgate 2001). This locality has a produced the miacid carnivore *Vulpavus*, indicating a Wasatchian or Bridgerian age.

Arkansas Westgate (2001) notes the presence of *Diplobunops* and *Pantolestes* in the Jackson Group (loc. 64, table 4.1) of St. Francis County. These two genera are not usually found together. *Pantolestes* normally is restricted to the Bridgerian and early Uintan (although probable sister taxa survive into the Chadronian in North America) and *Diplobunops* to the late Uintan (Ui3).

Texas Coastal Plain A diverse late Uintan vertebrate assemblage (loc. 86, table 4.1; Casa Blanca L.F.) has been collected from strata of the Laredo Formation in Webb County, Texas (Westgate 1988, 1990, 1994c, 1999; Wilson and Westgate 1991; Walton 1993a, 1993b). Marine invertebrates in the Laredo Formation permit a correlation with the Cook Mountain Formation, which contains nannoplankton assigned to zone NP16 (late medial Eocene; Berggren et al. 1995). A bentonite in the Cook Mountain Formation has been dated at 42.0 \pm 0.8 Ma (Berggren et al. 1992).

Westgate (1988, 1994a–1994c, 2001) summarizes the Lake Casa Blanca L.F. (loc. 86, table 4.1) from near Laredo in Webb County. This diverse vertebrate assemblage contains many Uintan mammals and is correlated with Ui3 and the Serendipity L.F. of the Big Bend area. The age assignment is derived from the artiodactyls present at Lake Casa Blanca and the presence of the rodent *Mytonomys*.

Montana There are several small faunal samples from isolated areas in Montana representing the Bridgerian through Duchesnean. The earliest of these is from the type area (loc. 38, table 4.1) of the Sage Creek Formation, Beaverhead County, Montana, and includes *Helaletes, Hyrachyus, Eotitanops,* and *Palaeosyops,* indicating a Bridgerian age, perhaps even early Bridgerian (Bro–Bria; Wallace 1980; Tabrum et al. 1996). Two successive late Uintan local faunas, the Douglass Draw L.F. and the Hough Draw L.F. (loc. 93, table 4.1), are located in the "Dell beds" stratigraphically above the Sage Creek Formation (Tabrum et al. 1996).

Two local faunas are known from the Climbing Arrow Formation near Three Forks, in the Beaverhead Basin. Shoddy Springs (G. E. Robinson 1963; Black 1967; G. E. Robinson et al. 1957; Krishtalka 1979; Krishtalka and Black 1975; Lillegraven and Tabrum 1983) is a Duchesnean locality (loc. 107, table 4.1) tentatively correlated with Locality 20 (loc. 108, table 4.1) in the Wagon Bed Formation, Wind River Basin. An additional latest Duchesnean or earliest Chadronian sample from the Diamond O L.F. (loc. 118, table 4.1) was reported by Tabrum et al. (1996).

CORRELATION AND CALIBRATION

GEOCHRONOLOGY

During the last two decades of magnetostratigraphic and radioisotopic research, significant progress has been made toward placing the NALMA record into a chronostratigraphic framework that can be readily correlated to the global time scale. Table 4.2 gives a summary of the most recent reliable geochronologic constraints on the Wasatchian through Duchesnean NALMA record. Unfortunately, several intervals remain poorly sampled and controversial. The following is a brief discussion of the key information that constrains the NALMA record in time, with particular attention to intervals that are still characterized by uncertainty.

No global stratotype section and point (GSSP) has yet been determined for the Paleocene–Eocene boundary, so the position of the Clarkforkian–Wasatchian NALMA boundary with respect to the Paleocene–Eocene boundary remains ambiguous (Aubry 2000). However, it is clear

CALIBRATION POIN	T AGE	BIOCHRON	NALMA SUBAGE	NALMA	LOCATION	REFERENCE	COMMENTS
Paleocene–Eocene isotop excursion	e 54.96	Wao	Sandcouleean	Wasatchian	Bighorn Basin	Wing et al. 2000	Age corroborated by Norris and Rohl 1999
Chron C24r–C24n.3n	53.35	Wa4–Wa5	Graybullian	Wasatchian	Bighorn Basin	Clyde et al. 1994 Tauxe et al. 1994	
Chron C24n.3n–C24n.2r	52.90	Wa6	Lysitean	Wasatchian	Bighorn Basin	Clyde et al. 1994 Tauxe et al. 1994	
Chron C24n.2r-C24n.2n	52.80	Wa6	Lysitean	Wasatchian	Bighorn Basin	Clyde et al. 1994 Tauxe et al. 1994	
Chron C24n.2n–C24n.1r	52.76	Wa6	Lysitean	Wasatchian	Bighorn Basin	Clyde et al. 1994 Tauxe et al. 1994	
⁴⁰ Ar/ ³⁹ Ar-sanidine	$52.8 \pm 0.3 (WM)$	Wa7	Lostcabinian	Wasatchian	Bighorn Basin	Wing et al. 1991	Upper Willwood Formation
⁴⁰ Ar/ ³⁹ Ar–sanidine	52.6 (TG)	Wa7	Lostcabinian	Wasatchian	Bighorn Basin	Wing et al. 1991	Upper Willwood Formation
Chron C24n.1r–C24n.1n	52.66	Wa7	Lostcabinian	Wasatchian	Bighorn Basin	Tauxe et al. 1994	
Chron C24n.1n–C23r	52.36	Wa7	Lostcabinian	Wasatchian	Green River Basin	Clyde et al. 1997, 2001	
Chron 23r–C23n.2n	51.74	Bria	Gardnerbuttean	Bridgerian	Green River Basin	Clyde et al. 1997, 2001	
Chron C23n.2n–C23n.1r	51.05	Bria	Gardnerbuttean	Bridgerian	Green River Basin	Clyde et al. 1997, 2001	
Chron C23n.1r–C23n.1n	50.95	Bria	Gardnerbuttean	Bridgerian	Green River Basin	Clyde et al. 1997, 2001	
Chron 23n.1n–C22r	50.78	Bria	Gardnerbuttean	Bridgerian	Green River Basin	Clyde et al. 1997, 2001	
Chron C22r–C22n	49.71	Brıb	Bridger A	Bridgerian	Green River Basin	Clyde et al. 1997, 2001	
Chron C22n–C21r	49.04	Br2	Bridger B	Bridgerian	East Fork Basin	Flynn 1986	
4ºAr/39Ar-sanidine/ biotite/plagioclase/ hornblende	47.96 ± 0.13 (WM)	Br2	Bridger B	Bridgerian	Green River Basin	Murphey et al. 1999	Bridger Formation
Chron C21r–C21n	47.91	Br2	Bridger B	Bridgerian	Washakie Basin East Point Basin	Flynn 1986	
⁴⁰ År/ ³⁹ År–sanidine/ biotite/plagioclase/ hornblende	46.92 ± 0.17 (WM)	Br3	Bridger C	Bridgerian	Green River Basin	Murphey et al. 1999	Bridger Formation

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TABLE 4.2 Geochronology of North American Land Mammal Ages (NALMAs)

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CALIBRATION POINT	T AGE	BIOCHRON	NALMA SUBAGE	NALMA	LOCATION	REFERENCE	COMMENTS
⁴⁰ Ar/ ³⁹ Ar-sanidine	46.29 ± 0.05	Uii?	"Shoshonian"	Uintan	Trans-Pecos Texas	Henry et al. 1986	Below Alamo Creek Basalt Junction L.F.
Chron C21n–C20r	46.26	Uit?	"Shoshonian"	Uintan	Washakie Basin Uinta Basin Southern California	Flynn 1986 Prothero 1996b Walsh 1996b	Correlation A of McCarroll et al. 1996a, Washakie Formation
⁴⁰ Ar/ ³⁹ Ar–sanidine/ biotite/plagioclase/ hornblende	46.16 ± 0.44 (WM)	Uir?	Bridger E	Uintan	Green River Basin	Murphey et al. 1999	Bridger Formation
Chron C20r-C20n	43.79	Ui3	Uinta A/B	Uintan	Uinta Basin	Prothero and Swisher 1992	
40 Ar/39 Ar–sanidine	42.83 ± 0.24 Ui2		Uinta C	Uintan	Southern California	Obradovich in Walsh 1996b	Mission Valley Formation
Chron C20n–C19r	42.54	Ui3	Uinta C	Uintan	Uinta Basin	Prothero and Swisher 1992	
Chron Cı9r–Cı9n	41.52	Ui3	Uinta C	Uintan	Uinta Basin	Prothero 1996b	Brennan Basin Member, Duchesne River Formation
Chron Cı9n–Cı8r	41.26	Ui3	Uinta C	Uintan	Uinta Basin	Prothero 1996b	Brennan Basin Member, Duchesne River Formation
Chron C18r-C18n.2n	40.13	Ui3/Du	Uinta C/Duchesnean	Uintan/Duchesnean	Texas Southern California	Prothero 1996c Prothero et al. 1996	
Chron C18n.2n–C18n.1r	39.63	Ui3/Du	Uinta C/Duchesnean	Uintan/Duchesnean	Texas Southern California	Prothero 1996c Prothero et al. 1996	
⁴⁰ Ar/ ³⁹ Ar-biotite	39.74 ± 0.07	Du		Duchesnean	Uinta Basin	Prothero and Swisher 1992	LaPoint Tuff
Chron C18n.1r–C18n.1n	39.55	Du		Duchesnean	Texas	Prothero 1996c	
Chron Cı8n.ın–Cı7r	38.43	Du		Duchesnean	Texas New Mexico	Prothero 1996c Prothero and Lucas 199	96
Chron C17r–C17n.3n	38.11	Du		Duchesnean	Texas New Mexico	Prothero 1996c Prothero and Lucas 199	96
Chron C17n.3n–C17n.2r	37.92	Du		Duchesnean	Texas New Mexico	Prothero 1996c Prothero and Lucas 199	96

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TABLE 4.2 (continued)

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CALIBRATION POINT	AGE	BIOCHRON	NALMA SUBAGE	NALMA	LOCATION
Chron C17n.2r–C17n.2n	37.85	Du		Duchesnean	Texas New Mexico
⁴⁰ Ar/ ³⁹ Ar-sanidine	37.8 ± 0.15	Du		Duchesnean	Texas

TABLE 4.2 (continued)

Ages of magnetic reversals are from the most recent Geomagnetic Polarity Time Scale (Cande and Kent 1995). L.F., Local Fauna; TG, total gas; WM, weighted mean.

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confirmed by Henry et al.

1994

Bracks Rhyolite,

Prothero and Lucas 1996

New Mexico

Texas Texas

Chadronian Chadronian

Texas

Duchesnean

Du

37.60

Chron C17n.2n-C17n.1r

Chron C17n.1r-C17n.1n ⁴⁰Ar/³⁹Ar-sanidine

ß G

 36.7 ± 0.07 37.47

Prothero 1996c

Prothero and Swisher 1992

Prothero 1996c

woodburne_04 2/1//04 1:34 PM Page 13/

Buckshot Ignimbrite

Prothero and Swisher 1992

Prothero 1996c Prothero and Lucas 1996

COMMENTS

REFERENCE

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that the Clarkforkian–Wasatchian boundary correlates with a global carbon isotope excursion (CIE) that occurs within chron C24r and has been dated at approximately 55.5 Ma (Koch et al. 1992; Wing et al. 2000; Rohl et al. 2000). Although the 55.5 Ma age for the CIE conflicts with one of the calibration points for the most recent GPTS (Cande and Kent 1995; see discussion in Berggren and Aubry 1998) and therefore is not included in table 4.2, the age of the CIE changes only slightly when it is estimated independently of the GPTS (Wing et al. 2000, model 2). This CIE represents a profound global biogeochemical event that lasted only 200,000 years (or less) and therefore represents a potentially powerful point for intracontinental and intercontinental correlations of mammalian biostratigraphies.

Studies from the Bighorn Basin (Butler et al. 1981; Clyde et al. 1994; Tauxe et al. 1994), Baja California (Flynn et al. 1989), and West Texas (Rapp et al. 1983) confirm that the Wasatchian LMA extends from late chron C24r to at least early chron C23r. Although there is some uncertainty as to the placement of the C24r–C24n.3n boundary with respect to the Wa4–Wa5 faunal zone boundary (Clyde et al. 1994; Tauxe et al. 1994), research in progress should resolve this soon. Reanalysis of the magnetostratigraphy from the Eureka Sound Group in Ellesmere Island provided no support for previous suggestions of large-scale faunal and floral latitudinal diachroneity during Wasatchian time (Tauxe and Clark 1987; see also Hickey et al. 1983; Kent et al. 1984).

The age of the Wasatchian–Bridgerian NALMA boundary is less clear. It was traditionally placed at ~50 Ma in chron C22r (Krishtalka et al. 1987:91–95; Prothero 1995; Clyde et al. 1997, Correlation 2), but new studies in the Green River Basin suggest that the boundary may be significantly older, in chron C23r at ~52 Ma (Clyde et al. 1999, 2001; Murphey et al. 1999). More recent work by M. E. Smith et al. (2003) indicates that the boundary is near the Grey Tuff, dated at 50.39 \pm 0.13 Ma.

The geochronology of the Bridgerian–Uintan NALMA boundary is also poorly constrained at present because of contradictory evidence from well-sampled sections in the Washakie Basin, Bighorn Basin, Uinta Basin, Bridger Basin, southern California, and Texas that span this interval (see discussions in Flynn 1986; Prothero 1996b; McCarroll et al. 1996a; Stucky et al. 1996; Walsh 1996b, 2001). Despite various magnetobiostratigraphic inconsistencies with these sections, it is generally agreed that rocks characterized by Bridgerian mammalian assemblages extend into chron C21n; rocks characterized by Uintan mammalian assemblages correlate to chron C20r and C20n and above and may occur in C21n (Flynn 1986; Walsh et al. 1996; Prothero 1996b). Resolving the detailed chronostratigraphy of the intervening interval that includes the Bridgerian–Uintan NALMA boundary (and the proposed Shoshonian subage) will entail further fieldwork.

Magnetostratigraphic and radioisotopic data from the Uinta Formation in Utah, mixed volcanic and sedimentary strata from Trans-Pecos Texas, and the Coldwater Sandstone/Sespe Formation in California all suggest that the Uintan NALMA extends into chron C18r (Prothero 1996b, 1996c; Prothero and Vance 1996; Prothero et al. 1996). An earliest Duchesnean fauna from California (Pearson Ranch Local Fauna) is known from a normal interval correlated to chron C18n, indicating that the Uintan-Duchesnean boundary lies somewhere in chron C18 (Prothero et al. 1996). This correlation is further supported by radioisotopic dates and magnetostratigraphy from Trans-Pecos Texas (Prothero 1996c). The Texas sections also provide the best evidence for constraining the timing of the Duchesnean-Chadronian boundary. A late Duchesnean local fauna (Porvenir Local Fauna) lies just above the Buckshot Ignimbrite, dated at 37.8 \pm 0.15 Ma (Ar³⁹/Ar⁴⁰; Prothero and Swisher 1992). An early Chadronian fauna (Little Egypt Local Fauna) from the Vieja area of Trans-Pecos Texas immediately underlies the Bracks Rhyolite, dated at 36.7 \pm 0.07 Ma (Ar³⁹/Ar⁴⁰; Prothero and Swisher 1992; Henry et al. 1994). The intervening interval is characterized by predominantly normal polarity and was correlated to chron C17n by Prothero (1996c). This suggests that the Duchesnean-Chadronian NALMA boundary lies in chron C17n at about 37 Ma.

POSTSCRIPT

After having reflected on what has been presented here, the two principal authors of this chapter (G.G. and P.R.) feel it is appropriate to look back on what has been accomplished since the last edition of this volume and what lies ahead. It is clear that a great deal has been learned since 1987 about the NALMAs that make up the subject of this chapter. Yet there is also a lingering feeling that much more must be learned before a true understanding of the intricacies of this important time period will be realized. The problems that remain, though intellectual in nature, can be addressed only by additional field exploration using the most advanced technology available to fieldworkers.

It is clear that we have a much better understanding of the biochronologic history of the Wasatchian and Bridgerian than we did in 1987. However, we still don't know just how applicable the biochronologies developed in the Bighorn and Green River basins will be outside these type areas. The biochronologic frameworks of the Uintan and Duchesnean are still in their infancy and await much better records not only from the type areas of these land mammal ages but also from other areas that will affect our understanding of each of these time periods. It is still not clear that similar biochronologic approaches will be equally applicable to each of these land mammal ages, and we almost certainly will have to adapt as our knowledge becomes greater. We are getting a much better understanding of intercontinental relationships but are also raising many questions that need to be addressed. Additional fieldwork in areas that can add to our knowledge of these events must be undertaken. Much of our considerations of this are east-west focused. Perhaps we should also consider more north-south possibilities.

We believe that the issues surrounding the recognition and placement of the Paleocene-Eocene boundary will be resolved in the near future, perhaps even before this volume appears in print. Other issues will take more time and effort. As befits transitional periods, the Wasatchian-Bridgerian, Bridgerian–Uintan, and Uintan–Duchesnean will remain contentious for the foreseeable future. We believe that the Wasatchian-Bridgerian transition has come into focus recently, yet we still do not understand the mechanisms of this change particularly well. There is tantalizing evidence of the possible existence of an additional recognizable subage at the Bridgerian-Uintan boundary, yet the evidence is far from compelling. The Uintan-Duchesnean transition remains shrouded in mystery, as does the very nature of these two land mammal ages.

Much has been accomplished since 1987, yet not all questions have been answered and not all problems solved. With new information come new questions. Renewed efforts are needed to address the issues raised by what has been presented in this chapter. We look forward to seeing what the next 15 years will bring.

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5

The Chadronian, Orellan, and Whitneyan North American Land Mammal Ages

Donald R. Prothero and Robert J. Emry

N THE 16 YEARS SINCE EMRY, BJORK, and Russell (1987)reviewed the Chadronian, Orellan, and Whitneyan land mammal ages for the original version of this volume, an enormous amount of information has been published concerning this interval of time. Many of the crucial sections have been studied by means of magnetic stratigraphy, and many new 40 Ar/39 Ar dates have been analyzed, which have radically changed our concept of the correlation of these beds (Swisher and Prothero 1990; Prothero and Swisher 1992; Prothero 1996b; Prothero and Whittlesey 1998). Systematic reviews of most of the biostratigraphically informative taxa have been completed (see chapters in Prothero and Emry 1996b), allowing a formal range zone biostratigraphy to be erected for most of this interval (Prothero and Emry 1996a; Prothero and Whittlesey 1998). Calibrated by means of magnetostratigraphy, these biostratigraphic zones now offer very high-resolution dating of most of this time interval. In Emry et al. (1987), it was not possible to resolve many events to the nearest 2-3 million years, but the current high-resolution chronostratigraphic framework now allows many events in better-studied sections to be dated to the nearest 100,000 years or less.

In addition to the improvements in chronostratigraphy, the new dates have radically changed our correlation of the Chadronian, Orellan, and Whitneyan land mammal ages to the global time scale. When these terms were originally coined by the Wood committee (1941), they were thought to correlate with the early, middle, and late Oligocene, respectively. But the new 40 Ar/39 Ar dates, combined with the magnetostratigraphy (Swisher and Prothero 1990; Prothero and Swisher 1992), and changes in the dating of the global time scale (Berggren et al. 1992, 1995) showed that the Chadronian correlates with the late Eocene, the Orellan and Whitneyan with the early Oligocene, and the Arikareean (long considered early Miocene) with the late Oligocene and earliest Miocene (as first shown by Evernden et al. 1964 and Tedford et al. 1987). Thus the original concept of the Chadronian, Orellan, and Whitneyan land mammal ages as the "Oligocene" chapter in the original book has lost its meaning. This chapter now covers the late Eocene to early Oligocene, and the rest of the Eocene and Oligocene is covered in other chapters. Nevertheless, the Chadronian, Orellan, and Whitneyan land mammal ages are important because they represent the best-studied terrestrial record of the Eocene-Oligocene transition in the world and are therefore an important data set for studying the climatic changes that occurred when the global climate shifted from greenhouse to icehouse states (Prothero 1994; Prothero and Emry 1996b; Prothero and Heaton 1996; Prothero 1999).

LITHOSTRATIGRAPHY OF CHADRONIAN, ORELLAN, AND WHITNEYAN STRATA

In this chapter, we will not repeat the historical introduction to the White River Group (figure 5.1), more fully discussed in Emry et al. (1987), or much of the stratigraphic background discussed in the latter part of that chapter. Instead, we will summarize the recent developments in



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FIGURE 5.1 Index map showing location of rock units mentioned in text (after Emry et al. 1987). L.F., Local Fauna.

biostratigraphy, magnetostratigraphy, and ⁴⁰Ar/³⁹Ar dating that were published since 1987 (Swisher and Prothero 1990; Prothero and Swisher 1992; various chapters in Prothero and Emry 1996b, including Prothero and Emry 1996a; Prothero and Whittlesey 1998).

Some important changes in the lithostratigraphic framework have taken place, however (figure 5.2). Terry (1998) proposed a new lithostratigraphic framework for the lower part of the White River Group in South Dakota and Nebraska. The lowest part of the former Chadron Formation in South Dakota (containing the Interior and Weta paleosols) was named the Chamberlain Pass Formation. Of the three members of the Chadron Formation recognized in South Dakota by Clark (1937), only the Peanut Peak Member is recognized in Nebraska. Terry (1998) rejects the old correlation of the Ahearn and Crazy Johnson Members with Chadron A and B in Nebraska. Chadron B and C and Orella A in Nebraska (sensu Schultz and Stout 1955, 1961) are now placed in the new Big Cottonwood Creek Member of the Chadron Formation by Terry (1998) and Terry and LaGarry (1998).

LaGarry (1998) also proposed revisions of the Brule Formation in Nebraska. As just mentioned, "Orella A" in Nebraska has been reassigned to the Big Cottonwood Creek Member of the Chadron Formation. With this change, the Orellan North American land mammal age (NALMA) now coincides even better with the Orella Member as redefined. LaGarry (1998) redefined the boundary between the Orella and Whitney members to a position slightly lower in the section.

Finally, Swinehart et al. (1985) and Tedford et al. (1996) recognized a unit above the Whitney Member of the Brule Formation that they informally called the "brown siltstone" member. Many of the rocks that were once assigned to the upper Whitney Member or lower Gering Formation by Schultz and Stout (1955, 1961) were reassigned to this unit.

GEOGRAPHY OF THE CHADRONIAN, ORELLAN, AND WHITNEYAN NALMAS

All three of these NALMAs were originally based of parts of the White River Group and its contained faunas in northwestern Nebraska and southwestern South Dakota (Wood et al. 1941). With the exception of the earliest Chadronian, the subdivisions of these units that we now recognize are still based on parts of the White River Group and its faunas, although several of the subdivisions are based on White River sequences that are well outside the original type areas of the whole NALMAs. This primarily reflects the fact that faunas of Chadronian age are much better known in these other areas. Therefore it seems worthwhile to generalize briefly about the geographic distribution of the White River Group and the non–White River faunal correlates.

The White River Group is exposed widely in southwestern South Dakota and northwestern Nebraska and north of the Pine Ridge escarpment in adjacent Niobrara County, Wyoming (figure 5.1). From there it can be traced, nearly continuously, westward to the vicinity of Douglas, Wyoming, and from there southward east of the Laramie Range nearly to the Colorado border and westward north of the Laramie Range to the vicinity of Glenrock. The White River Group crops out extensively in the valley of the North Platte River and its tributaries in western Nebraska and eastern Wyoming. In northeastern Colorado, extensive outcrops are found along the southfacing escarpment where the High Plains break off into the Colorado Piedmont. In northwestern South Dakota, southeastern Montana, and southwestern North Dakota, isolated remnants of White River are preserved, mainly in the upper parts of buttes and higher elevations. Figure 5.1 indicates the approximate areal extent, at the surface, of the White River Group.

Intermontane basins of central Wyoming have extensive White River deposits that are not continuous with the main body of the White River Group farther east. In the Bates Hole Area, at Flagstaff Rim at the southeastern end of the Wind River Basin, and at Beaver Divide along the southern margin of the Wind River Basin, the White River deposits have the general lithologic characteristics that justify the White River terminology but are generally so uniform that they are not subdivided lithologically and are locally treated as a formation rather than group. At their westernmost limit, deposits that can be recognized lithologically as White River lap onto the eastern end of the Wind River Range and extend from there southeast into the northwestern edge of the Great Divide Basin in Wyoming and northeast along Beaver Divide. These areas of White River Formation undoubtedly are remnants of a blanketing deposit that once extended north across the Wind River Basin and continued northeast across the Powder River Basin (where remnants remain at the top of Pumpkin Buttes) and east into the classic areas of White River in eastern Wyoming, western Nebraska, and southwestern South Dakota. The White River deposits retain their general lithologic character over such a broad area (across what would have been separate depositional basins with respect to fluvial components) because the bulk of the formation consists of eolian volcaniclastics, transported and deposited across this broad area irrespective of the fluvial systems.



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FIGURE 5.2 Correlation chart of deposits of Chadronian, Orellan, and Whitneyan age in North America. Time scale after Berggren et al. (1995), Prothero and Emry (1996a), and Prothero and Whittlesey (1998). Lithostratigraphic and magnetostratigraphic correlations after Emry et al. (1987), Swisher and Prothero (1990), Prothero and Swisher (1992), Prothero (1996a, 1996b), Tabrum et al. (1996), Tedford et al. (1996), Prothero and Whittlesey (1998), Terry (1998), and various other chapters in Prothero and Emry (1996b). KSW, Keasey Springs West; Lept. Nods., *Leptauchenia* Nodules; LN, Lower Nodules; LWA, Lower Whitney Ash; PWL, Persistent (= Purplish) White Layer; UN, Upper Nodules; UO, Upper Oreodon Beds; UPW, Upper Purplish White Layer; UWA, Upper Whitney Ash.

Chadronian faunas occur in several areas in rocks that are beyond the geographic limits of the White River Group. Among the more important of these are the Chambers Tuff (with the Porvenir and Little Egypt local faunas) and the Capote Mountain Tuff (with the Airstrip Local Fauna) of the Vieja Group in Trans-Pecos Texas. Other important Chadronian faunas occur in the Cypress Hills Formation in southwestern Saskatchewan and in the Climbing Arrow, Dunbar Creek, and Renova formations (the latter with the important Pipestone Springs Local Fauna), all in southwestern Montana (Tabrum et al. 1996). Mammalian assemblages from these units can be correlated, with varying degrees of precision, with the White River faunal sequence. The Vieja Group of Trans-Pecos Texas is especially important for the recognition and definition of earlier Chadronian subdivisions.

Through the Chadronian–Whitneyan interval, the known geographic range of faunas becomes progressively limited. Orellan faunas occur in southwestern Montana in the Dunbar Creek Formation of the Three Forks, Clarkston, and South Townsend basins, in the Dunbar Creek Member of the Renova Formation in the Jefferson Basin, and in the Cook Ranch Local Fauna east of Lima. Otherwise, Orellan faunas are largely limited to the Brule Formation in its typical areas: isolated localities in southwestern North Dakota, northwestern South Dakota, the Scenic Member in the Big Badlands of South Dakota, the Orella Member in western Nebraska and eastern Wyoming, and the equivalent Cedar Creek Member in northeastern Colorado.

Whitneyan faunas are even more limited geographically, essentially to the Brule Formation: the Whitney Member in western Nebraska and eastern Wyoming, the Vista Member in northeastern Colorado, and the Poleslide Member in South Dakota. Possible outliers are the Cedar Ridge Local Fauna in the Badwater Creek area in the northeastern part of the Wind River Basin of Wyoming (Black 1968; Setoguchi 1978) and the I-95 Local Fauna (Patton 1969) in northern Florida.

To our knowledge, no assemblages of Chadronian or Whitneyan land mammals occur in deposits that can be related unambiguously to any marine sequence. Orellan mammals have been reported from the lower Oligocene Byram Formation, Mississippi (Manning et al., 1986; Manning, 1997). Correlation with other chronologies is accomplished principally through radiometric dates and magnetic polarity stratigraphy. It does appear that brontotheres, whose latest occurrences caused confusion in defining and recognizing the Chadronian–Orellan boundary, can be rehabilitated as a useful biochronologic taxon; the extinction of brontotheres appears now to have been a global event at the end of the Eocene and thus provides supporting evidence for correlating the Chadronian–Orellan boundary with the Eocene–Oligocene boundary.

CHADRONIAN

The original definition of the Chadronian by Wood et al. (1941) has caused considerable confusion about recognizing the Chadronian-Orellan boundary. Wood et al. (1941:11) wrote that "the Chadronian is based on the Chadron formation, type locality near Chadron, Nebraska, type area, northwestern Nebraska and southwestern South Dakota, includes the old term 'Titanotherium beds,' used in its most extended sense. It may also be defined, faunally, as the time during which Mesohippus and titanotheres coexisted." As several authors have pointed out (Emry et al. 1987; Prothero and Whittlesey 1998), this definition combines lithostratigraphy (the geochron of the Chadron Formation) and biochronology (the overlapping ranges of Mesohippus and brontotheres, or titanotheres). As long as *Mesohippus* was not known in strata older than the Chadron Formation and brontotheres were not known above the Chadron Formation, the dual definition was not internally inconsistent and remained workable.

Confusion regarding the Chadronian–Orellan boundary results ultimately from the uncritical definition of the Chadron Formation-Orella Member boundary by Schultz and Stout (1938). In the Toadstool Park area of northwestern Nebraska (the type localities for the Orella and Whitney members of the Brule Formation), the uppermost of several "purplish white layers" (volcanic ash beds) was defined by Schultz and Stout (1938, 1955) as marking the top of the Chadron Formation. What is apparently the same purplish white ash occurs widely in the Seaman Hills area to the west in Niobrara County, Wyoming, and can be traced eastward into Sioux County, Nebraska, where it occurs in a sequence similar to that at the Orella type locality. In the Seaman Hills area, the lithology is the same above and below this ash bed, so there is no logical reason to place a formational, lithologic boundary at this ash bed. Moreover, as mentioned by Emry et al. (1987) and Prothero and Whittlesey (1998), brontothere (titanothere) bones have been found up to 25 feet above the ash bed in the Seaman Hills area. On September 6, 1953, Morris Skinner (unpublished section book, vol. 5, pp. 9-11, in Department of Vertebrate Paleontology Archives, American Museum of Natural History) discovered titanothere bones in a channel-fill de-
posit that cut down from about 6.5 m (20 feet) above the "Persistent White Layer" (PWL), Skinner's term for the "purplish white layer" of Schultz and Stout. In his unpublished 1960 summary of Seaman Hills stratigraphy, Skinner indicated "Chadronian age at least to here" at the level 6.5 m (20 feet) above the PWL. There are other occurrences of brontotheres (titanotheres) that would be above the top of the Chadron Formation as it was recognized by Schultz and Stout (1938, 1955). Emry et al. (1987) and Prothero and Whittlesey (1998) mention another occurrence in the White River southeast of Douglas, Wyoming, about 25 feet above a white ash bed that Skinner called the "100' correlator white zone" and Evanoff et al. (1992) call the "5 tuff," which is presumed to be the same ash bed as the upper PWL of Schultz and Stout. Even Schultz and Stout (1955, figure 10) indicate a titanothere metapodial in a channel sandstone incised from about 7 feet above the upper PWL at Scottsbluff National Monument in the Platte Valley of western Nebraska, and in a footnote (1955:27) they comment that "all parts of the Chadron and the lowest parts of the Brule (basal Orella or Orella A) should be expected to yield titanothere remains."

It is important to note that Skinner did not consider these brontothere occurrences to be in the Brule Formation. On the contrary, in his section books and the unpublished summary mentioned earlier and in his daily diaries that he maintained, Skinner referred to the beds above the PWL (in northwestern Nebraska and Niobrara County, Wyoming) as the "Trunk Butte Member of the Chadron Formation." In the Seaman Hills area in Niobrara County, Wyoming, Skinner recognized about 30 m (100 feet) of this unit above the PWL and lesser thicknesses to the eastward into Nebraska as far as the vicinity of Chadron (Trunk Butte is southwest of Chadron). Skinner's name for this unit was never published, but Terry and LaGarry (1998) applied the name Big Cottonwood Creek Member of the Chadron Formation to this body of rock.

Thus the apparent inconsistency in the definition of the Chadronian by Wood et al. (1941) really resulted from the uncritical definition of the top of the Chadron Formation by Schultz and Stout (1938, 1955). In the Toadstool Park area, the base of the Toadstool Park channel sequence is disconformable, and at some places the channel sequence has cut nearly to the level of the PWL, but as Terry and LaGarry (1998) clearly show, and Skinner had recognized long before, lateral to the channel sequence the Chadron Formation extends well above the PWL. The Chadronian–Orellan boundary as it was determined by Prothero and Whittlesey (1998) in the Douglas, Wyoming, sequence and in the Seaman Hills sequence includes these latest known brontothere occurrences.

Emry et al. (1987) reviewed the problems with the original Wood committee definition of the Chadronian and made some suggestions for an improved definition of this time interval. They recommended that the Chadronian be defined in faunal or biostratigraphic terms and argued that lithostratigraphic units had no role in the definition of a biochronologic unit. One of the major problems at that time was that there was much debate and confusion over how to distinguish the Chadronian from the preceding Duchesnean age and whether the Duchesnean could be distinguished at all. Some authors (Emry 1981; Wilson 1984, 1986) even recommended that the early Duchesnean be considered a subage of the Uintan and the late Duchesnean a subage of the Chadronian. But subsequent authors (Kelly 1990; Lucas 1992) pointed out the distinctiveness of the Duchesnean, and since then its biostratigraphy and chronostratigraphy have become much better understood (several chapters in Prothero and Emry 1996b).

Prothero and Emry (1996a) reviewed the latest biostratigraphic, magnetostratigraphic, and geochronologic data of the Chadronian and proposed a revised definition. The Chadron Formation in South Dakota and Nebraska proved to be too poorly fossiliferous and its biostratigraphy too poorly resolved to serve as the basis for the chronostratigraphy of the Chadronian. Instead, Prothero and Emry (1996a) recommended that the faunas of much better sections in Trans-Pecos Texas and at Flagstaff Rim and Douglas, Wyoming, serve as the chronostratigraphic standards for the Chadronian.

Prothero and Emry (1996a) designated the first appearance of Bathygenys, Merycoidodon dunagani, Brachyrhynchocyon (formerly Daphoenocyon) dodgei, and Archaeotherium as the best indicators of the beginning of the Chadronian, with Bathygenys as the defining taxon and the rest as characterizing taxa. In Trans-Pecos Texas, these distinctive earliest Chadronian taxa all occur in the Little Egypt Local Fauna, which lies immediately above the late Duchesnean Porvenir Local Fauna. Both faunas are bracketed by $^{40}\text{Ar}/^{39}\text{Ar}$ dates of 37.8 \pm 0.15 Ma and 36.7 \pm 0.07 Ma, placing the Duchesnean-Chadronian boundary at approximately 37.0 Ma (and thus coincident with the middle-late Eocene boundary on the time scale of Berggren et al. 1995). If a stratotype were to be designated for this boundary, then the Trans-Pecos region of Texas is the only suitable place.

Because of the problem with the highly variable and infrequent occurrence of the latest surviving brontotheres with respect to the top of the Chadron Formation, the original Wood committee (1941) definition of the end of the Chadronian is insufficient by itself, and although it can be part of the definition, it is impractical as a means of recognizing the end of Chadronian time. Prothero and Whittlesey (1998) instead recommended that the Chadronian–Orellan boundary be placed at the first appearance of the distinctive taxon *Hypertragulus calcaratus*, along with the first appearance of a number of additional reference taxa. This boundary is discussed further later in this chapter.

SUBDIVISIONS OF THE CHADRONIAN

As reviewed by Emry et al. (1987), early concepts of the Chadronian essentially used lithostratigraphic units as de facto subdivisions of the time interval. Clark (1937, 1954) proposed a threefold division of the Chadron Formation in the Big Badlands of South Dakota into Ahearn, Crazy Johnson, and Peanut Peak members and suggested that these could also serve as time divisions of the Chadronian. Schultz and Stout (1955, 1961) designated informal members A, B, and C of the Chadron Formation in the Toadstool Park area of Nebraska. These rocks were also subdivided by the oreodont faunal zones of Schultz and Falkenbach (1968). The stratigraphic schemes of Schultz and Stout (1955, 1961) have not stood the test of time, with revised definitions (Terry 1998) placing Orella A in the Chadron Formation and changing the correlation with South Dakota radically from earlier concepts. Unfortunately, both the Clark (1954) and Schultz and Stout (1955, 1961) schemes used lithostratigraphic units for essentially biochronologic and biostratigraphic concepts, so they were fundamentally unsound. In addition, the actual stratigraphic range of the key fossils in these units was poorly documented, so they were unsuitable for a detailed range zone biostratigraphy. A much better, more complete section with excellent biostratigraphic data representing most of the Chadronian occurs at Flagstaff Rim, Wyoming (Emry 1973, 1992; Emry et al. 1987), and this serves as the basis for the much of the present zonation of the Chadronian.

Prothero and Emry (1996a) suggested a subdivision of the Chadronian into four biostratigraphically defined intervals, based on the best available lithostratigraphic sections known and calibrated by magnetostratigraphy and ⁴⁰Ar/³⁹Ar dating. These four intervals were known informally as earliest, late early, middle, and late Chadronian. Each of these four intervals is about 1 million years in duration, except for the earliest Chadronian, which is only about500,000 years in duration. Although possible biostratigraphic index taxa were suggested, no formal biostratigraphic zones were erected in that publication. In this chapter, we will finish this procedure by formally designating these zones.

Earliest Chadronian (36.5-37.0 Ma) Prothero and Emry (1996a) suggested that the biochronologic interval represented by the Little Egypt Local Fauna of Texas and Rancho Gaitan Local Fauna in Chihuahua, Mexico, be considered earliest Chadronian. This interval might be represented by the very base of the section at Flagstaff Rim, Wyoming, but the faunal evidence is very limited. Based on the local magnetostratigraphy (Prothero 1996a), this interval falls entirely in magnetic chron C16r, so it apparently spans the time interval from 36.5 to 37.0 Ma. As discussed earlier, the first appearances of Bathygenys and several other index taxa characterize this interval, so if a formal biostratigraphic zonation were needed, it could be known as the Bathygenys Interval Zone, and its stratotype is here designated as the Reeves Bonebed section (Wilson 1978, figure 9; Prothero 1996a) in Trans-Pecos Texas.

Late Early Chadronian (35.7–36.5 Ma) This interval is much more completely represented and geographically widespread than the earliest Chadronian. The main reference section is at Flagstaff Rim, Wyoming (from just above the base of the section to 50 feet below Ash B), and the principal correlatives are the McCarty's Mountain Local Fauna of Montana, the faunas of the Ahearn Member in South Dakota, and the Yoder Local Fauna of Wyoming. Based on the magnetostratigraphy, this interval correlates with magnetic chron C15n2 (35.7-36.2 Ma). Ash B has been 4° Ar/ 3° Ar dated at 35.9 \pm 0.2 Ma (Prothero and Swisher 1992) or 35.41 ± 0.14 Ma (Obradovich et al. 1995), with the more recent Obradovich date taking into account some laboratory problems with Swisher's date and better fitting all the other age constraints. This places an upper age constraint on the late early Chadronian.

Prothero and Emry (1996a) gave a list of taxa that first appear in and are limited to this interval, including *Palaeolagus primus*, *Merycoidodon presidioensis*, *Pseudoprotoceras semicinctus*, *Litoyoderimys lustrorum*, *Yoderimys stewarti*, and *Leptomeryx yoderi*. In addition, a number of taxa (including *Daphoenictis tedfordi*, *Hyaenodon montanus*, *Ischyromys veterior*, *Centetodon chadronensis*, *Parvitragulus priscus*, *Patriomanis americanus*, *Trigenicus profectus*, and *Sinclairella dakotensis*) first occur at this time but range into the middle Chadronian. Prothero and Emry (1996a) suggested that this interval be named the *Leptomeryx yoderi* Interval Zone, with its type section in the main Flagstaff Rim section along Little Lone Tree Gulch (Emry 1973). Middle Chadronian (34.7-35.7 Ma) The middle Chadronian is much better known than the two earlier Chadronian time intervals. It is typified by the large fossil collections recovered from the interval from 50 feet below Ash B to 50 feet above Ash G at Flagstaff Rim, Wyoming (Emry 1973, 1992). There are several principal correlatives, including the Pipestone Springs and Little Pipestone Creek local faunas of Montana (Tabrum et al. 1996), the Raben Ranch Local Fauna of Nebraska (Ostrander 1985), and the fauna of the Crazy Johnson Member of South Dakota. These beds all appear to correlate with magnetic chrons C15n-C15r (34.7-35.7 Ma). This interval has been dated not only by the 40 Ar/39 Ar date on Ash B cited earlier but also by dates of 35.7 ± 0.1 Ma (biotite) and 35.8 ± 0.04 Ma (anorthoclase) on Ash F and 35.6 \pm 0.06 Ma (biotite) and 35.7 \pm 0.03 Ma (anorthoclase) on Ash G (Swisher and Prothero 1992).

Prothero and Emry (1996a) noted a number of taxa that are limited to this interval, including Leptomeryx mammifer, Zemiodontomys burkei, Miniochoerus forsythae, Prosciurus vetustus, Hyaenodon microdon, Hyaenodon megalodon, Chadrolagus emryi, and Frictops emryi. A number of taxa first appear in the middle Chadronian and range into younger strata, including Palaeolagus temnodon, Dinictis felina, Meliakrounomys, Eutypomys magnus, Mesohippus westoni, Leptomeryx speciosus, Pseudoprotoceras longinaris, large Ischyromys, Hoplophoneus mentalis, Miohippus grandis, and Megalagus brachyodon. Emry et al. (1987) and Prothero and Emry (1996a) recommended that Leptomeryx mammifer be designated the index fossil of this zone (which could be called the Leptomeryx mammifer Interval Zone), with a type section in the Flagstaff Rim section from 50 feet below Ash B to 50 feet above Ash G. We so designate it in this chapter.

Late Chadronian (34.7–33.7 Ma) The Flagstaff Rim section is sparsely fossiliferous from about 50 feet above Ash G, so Prothero and Emry (1996a) suggested the section below the PWL (= Ash J at Flagstaff Rim, the 4 tuff at Douglas, Wyoming, according to Larson and Evanoff 1998) in the Seaman Hills section, north of Lusk, Wyoming, better typifies this interval. Additional referred sections include the Douglas section below the 4 tuff (Evanoff et al. 1992), the late Chadronian in western Nebraska (Ostrander 1985; Terry 1998), the Peanut Peak Member in South Dakota, and possibly the Ash Spring Local Fauna in Texas. All of these strata appear to correlate with late chron C13r–C15n (33.7–34.7 Ma). Ash J at Flagstaff Rim has been 40Ar/39Ar dated at 34.7 ± 0.04 Ma (Prothero and Swisher 1992) or 34.36 ± 0.11 Ma

(Obradovich et al. 1995). As discussed earlier, the Obradovich date probably is more reliable.

Only a few taxa, such as Pseudoprotoceras taylori, are limited to the late Chadronian at Flagstaff Rim (Emry 1992). In other late Chadronian sections, the interval is marked by the first occurrences of Merycoidodon culbertsoni, Poebrotherium franki, Miniochoerus chadronensis, Ischyromys typus, Mesohippus exoletus, Mesohippus bairdi, and Scottimus viduus. A number of taxa last appear in this interval and terminate near the Chadronian-Orellan boundary, including Brontotheriidae, Xenocranium, Pseudocylindrodon, Toxotherium, Palaeolagus temnodon, Hoplophoneus mentalis, Miohippus grandis, Mesohippus westoni, Eotylopus reedi, Poebrotherium eximium, and Archaeotherium coarctatum. Prothero and Emry (1996a) recommended that Miniochoerus chadronensis is the best candidate for index fossil in this interval because it is abundant, distinctive, and limited to the late Chadronian. Thus the late Chadronian could be designated as the Miniochoerus chadronensis Interval Zone and typified by the Seaman Hills section in Niobrara County, Wyoming. We formally designate the type section of the Miniochoerus chadronensis Interval Zone as the interval from 25 m below to 7 m above the PWL in the Boner Ranch section (SW sec. 9, T35N R61W, South Oat Creek 7.5' Quadrangle, Niobrara County, Wyoming; see Prothero and Whittlesey 1998, figure 5).

ORELLAN

The Wood committee (1941:11) based the Orellan on "the Orella member of the Brule Formation, type locality, Orella, northwestern Nebraska, southwestern South Dakota and eastern Wyoming; includes the old term, 'Oreodon beds,' used in the most extended sense." Once again, the Wood committee based a biochronologic concept on a lithostratigraphic unit, which is no longer acceptable in modern stratigraphic practice (Emry et al. 1987). In addition, Terry (1998) transferred Schultz and Stout's (1955, 1961) "Orella A" to the Chadron Formation, so that the Chadron-Orella lithostratigraphic boundary now closely corresponds to the Chadronian-Orellan biochronologic and biostratigraphic boundary. Emry et al. (1987:139) pointed out that the "old term 'Oreodon beds' used in the broadest sense" applies to many rocks not considered Orellan. As discussed by Prothero and Whittlesey (1998), the Wood committee's (1941) original criteria for recognizing the Chadronian-Orellan boundary (the last occurrence of brontotheres

and the top of the Chadron Formation) is also unsuitable, but with Terry's revision, this definition is no longer in conflict because at least four documented occurrences of brontotheres are now known above the Chadron– Brule contact of Schultz and Stout (1955, 1961) but within the Chadron Formation as redefined by Terry (1998).

For these reasons, Prothero and Whittlesey (1998) recommended redefining the Chadronian-Orellan boundary as the first appearance of Hypertragulus calcaratus, with the first appearances of Leptomeryx evansi, Palaeolagus intermedius, and small Miniochoerus chadronensis (= "M. douglasensis" of Stevens 1977) serving as characterizing biostratigraphic datums. The last appearance of Poebrotherium eximium and Miohippus grandis (with brontotheres being used only in a secondary role) can also be used to mark this boundary. The Chadronian-Orellan boundary falls in the upper part of magnetic chron C13r, 7 m (20 feet) above the 5 tuff at Douglas, Wyoming, and the same distance above the PWL in the Seaman Hills, near Lusk, Wyoming. Swisher and Prothero (1990) and Prothero and Swisher (1992) reported a 40 Ar/ 39 Ar date of 33.91 \pm 0.058 Ma on the 5 tuff, and, based on the Berggren et al. (1995) time scale, the Chadronian-Orellan boundary falls very close to 33.7 Ma, or the Eocene-Oligocene boundary.

SUBDIVISIONS OF THE ORELLAN

Emry et al. (1987) reviewed the earlier attempts to subdivide the Orellan, based on the lithostratigraphy of the Orella Member or on the "oreodont faunal zones" of Schultz and Falkenbach (1968), and showed that they were inadequate as then constituted. Korth (1989) proposed a biostratigraphy of the Orellan, again based on the Orella Member in Nebraska, but as Prothero and Whittlesey (1998) pointed out, there were several problems with this zonation. First of all, it was based on the University of Nebraska collections, most of which do not offer stratigraphic resolution of taxa in the alphabetically labeled units in the Orella Member, so the "biostratigraphic zones" of Korth (1989) are essentially equivalent to lithostratigraphic units. In addition, Prothero and Whittlesey (1998) found problems with several of the zonal indicator taxa proposed by Korth (1989). Finally, Korth's (1989) biostratigraphic zones lacked several key criteria (such as type sections) required by the North American Code of Stratigraphic Nomenclature (North American Commission on Stratigraphic Nomenclature 1983).

For these reasons, Prothero and Whittlesey (1998) proposed a division of the Orellan into four successive biostratigraphic zones, complete with defining and characterizing taxa based on the fine-scale biostratigraphic data available from the Frick Collection at numerous localities and including all information required by the code, including type sections. Thus the Orellan is now based on formal biostratigraphic zones as required by the code and can now be considered a stage and age in the sense of the code rather than an informal biochronologic unit.

Earliest Orellan *Hypertragulus calcaratus* **Interval Zone** (**33.7–33.4 Ma**) As discussed by Prothero and Whittlesey (1998), the earliest Orellan is now marked by the first appearance of *Hypertragulus calcaratus* and characterized by the first appearances of *Leptomeryx evansi* and *Palaeolagus intermedius*. Its upper limit is marked by the first appearance of the indicator of the next zone, *Miniochoerus affinis*. The type section for this interval zone was designated as the strata from 7 to 17 m (20–50 feet)above the 5 tuff in the Douglas area (full details given in Prothero and Whittlesey 1998:55). This zone is also known from the Seaman Hills section near Lusk, Wyoming. It is correlated with the latest part of magnetic chron C13r and the earliest part of chron C13n (33.7–33.4 Ma).

Late Early Orellan Miniochoerus affinis Interval Zone (33.4–33.1 Ma) Prothero and Whittlesey (1998:55) recognized an interval defined by the first appearance of the oreodont Miniochoerus affinis and characterized by the first appearances of Eumys elegans, Pelycomys brulanus, Adjidaumo minutus, Cedromus wardi, and Hoplophoneus occidentalis. This end of this interval is also marked by the last appearance of Ischyromys parvidens and the first appearance of Miniochoerus gracilis. They designated the type section of the Miniochoerus affinis Interval Zone as the strata between 17 and 27 m (63-80 feet) above the PWL in the Boner Ranch section in the Seaman Hills, near Lusk, Wyoming. Principal referred sections include the interval between 17 and 25 m (50-75 feet) above the 5 tuff in Douglas, Wyoming (Evanoff et al. 1992), portions of Orella B in Toadstool Park, Nebraska, and the Lower Nodular Zone in the Big Badlands of South Dakota. These strata correlate with the later part of magnetic chron C13n (33.4–33.1 Ma).

Early Late Orellan *Miniochoerus gracilis* **Interval Zone** (33.1–32.5 Ma) Prothero and Whittlesey (1998:56) recognized a zone defined by the first appearance of the dwarfed oreodont *Miniochoerus gracilis* and characterized by the first appearance of *Mesohippus barbouri, Agnotocastor readingi, Paradjidaumo validus, Eutypomys thomsoni,* and *Eumys parvidens.* Its end is marked by the last

appearance of *Ischyromys parvidens* and the first appearance of the next zonal indicator, *Merycoidodon bullatus*. They designated the type section as the strata 27–50 m (80–150 feet) above the PWL at Boner Ranch in the Seaman Hills, near Lusk, Wyoming. Principal reference sections included Orella C in Toadstool Park, Nebraska, and the strata just above the Lower *Oreodon* Beds but below the Upper *Oreodon* Beds in the Big Badlands of South Dakota. This zone correlates with the latest part of chron C13n and the early part of chron C12r (33.1–32.5 Ma).

Latest Orellan Merycoidodon bullatus Interval Zone (32.5–32.0 Ma) The latest Orellan is marked by a large number of distinctive taxa. Prothero and Whittlesey (1998:56) recognized a biostratigraphic zone based on the first appearance of the large-bulla oreodont Merycoidodon bullatus and characterized by the first appearance of Miniochoerus starkensis, Palaeolagus burkei, Prosciurus magnus, Ecclesimus tenuiceps, Tenudomys basilaris, Pelycomys placidus, Heliscomys vetus, Heliscomys mcgrewi, Wilsoneumys planidens, and Campestrallomys annectens. A large number of characteristically Orellan taxa last appear in this interval, including Hyaenodon crucians, Ischyromys typus, Paratylopus labiatus, Archaeotherium mortoni, Thinohyus lentus, Stibarus quadricuspis, Leptochoerus emilyae, Subhyracodon occidentalis, "Hesperocyon" coloradensis, Prosciurus, Pelycomys, Protosciurus, Oligospermophilus, Eutypomys, Adjidaumo, Paradjidaumo, Heliscomys, Wilsoneumys, Eoeumys, Tenudomys, Pipestoneomys, Megalagus, Palaeolagus intermedius, Centetodon marginalis, Leptictis haydeni, Herpetotherium fugax, Copedelphys stevensoni, Nanodelphys hunti, and all surviving species of Mesohippus (M. bairdi, M. exoletus, M. westoni, and M. barbouri). This concentration of last appearances (especially of micromammals) may be partially an artifact of poor collecting and lack of screenwashing from strata of the early Whitneyan and may be modified by range extensions once adequate sampling is done. However, for most of the larger mammals, this is not the case, and these taxa almost certainly last occur in this zone.

Prothero and Whittlesey (1998) designated the type section of this zone as the Upper Nodular Zone on the east side of Sheep Mountain Table in the Big Badlands (full details given in Prothero and Whittlesey 1998:56). Principal reference sections include the upper part of Orella C and Orella D in the Toadstool Park area, Nebraska, and the upper part of the Cedar Creek Member in Colorado. These beds correlate with the early part of magnetic chron C12r (32.0–32.5 Ma).

WHITNEYAN

Wood et al. (1941:11) based the Whitneyan "on the Whitney Member of the Brule Formation, type locality, Whitney, northwestern Nebraska, type area, northwestern Nebraska, southwestern South Dakota and eastern Wyoming, including the old term, '*Protoceras–Leptauchenia* beds,' used in the most extended sense." As Emry et al. (1987) pointed out, there were numerous problems with this definition, not the least of which is the fact that it bases a biochronologic interval of time on a lithostratigraphic unit. They recommended that the Whitneyan be defined on biostratigraphic criteria and suggested some possibilities for an appropriate set of criteria.

The multiple sections and high-resolution biostratigraphic data for the Orellan allowed Prothero and Whittlesey (1998) to finely subdivide it into four zones, each less than a million years in duration. Unfortunately, such data are not yet available for the Whitneyan. Most of the best biostratigraphic data come from the Poleslide Member of the Brule Formation in the Big Badlands of South Dakota, which was typically subdivided into the Upper Oreodon, Protoceras, and Leptauchenia beds of Osborn (1907), Osborn and Matthew (1909), Wanless (1923), Skinner (unpublished field notes), and many other workers. A smaller biostratigraphic database comes from the Whitney Member of the Brule Formation in northwestern Nebraska, which was subdivided into units A, B, and C by Schultz and Stout (1955, 1961). Because fossils usually were zoned only to one of the three subdivisions of the Whitneyan in these regions, the Whitneyan cannot be more finely subdivided than the original data resolution allows. In addition, Whitneyan fossils are much scarcer and more sparsely distributed than they are in the Orellan, further hampering fine-scale biostratigraphic zonation. Finally, the Whitneyan is known well only from two regions (Nebraska and South Dakota), with lesser collections from Colorado, North Dakota, and Wyoming, so many of the key index taxa only occur in one place.

SUBDIVISIONS OF THE WHITNEYAN

Prothero and Whittlesey (1998) proposed a formal division of the Whitneyan into two biostratigraphic zones, based on the excellent biostratigraphic data now available from the Frick Collection. These zones include the following.

Early Whitneyan *Leptauchenia major* **Interval Zone** (32.0–31.4 Ma) A number of taxa are typical of the early Whitneyan, including abundant *Leptauchenia decora* (the

traditional indicator of this zone but known to occur rarely in older rocks) and the first occurrences of Leptauchenia major, Hyracodon leidyanus, Paratylopus primaevus, Paralabis cedrensis, Diceratherium tridactylum, Protapirus obliquidens, Ectopocynus antiquus, Oxetocyon cuspidatus, Cynodesmus thooides, Agnotocastor praetereadens, and Oropyctis pediasius. Last occurrences in this zone include Miniochoerus starkensis, Stibarus obtusilobus, Hyaenodon horridus, Cedromus wilsoni, Metadjidaumo hendryi, Agnotocastor praetereadens, and Oropyctis pediasius. Prothero and Whittlesey (1998) designated a type section for this zone as the Upper Oreodon Beds (0-30 m, or 0-90 feet, above the Scenic-Poleslide contact) on the south side of Sheep Mountain Table in the Big Badlands of South Dakota (see Prothero and Whittlesey 1998:56 for details). Its principal reference section is Whitney A in the Toadstool Park area, Nebraska, and the lower part of the Vista Member in Colorado. This zone correlates with the middle of magnetic chron C12r (32.0-31.4 Ma). It is calibrated by the Lower Whitney Ash, which was 40 Ar/39 Ar dated at 31.8 ± 0.023 Ma (Swisher and Prothero 1990; Prothero and Swisher 1992).

Late Whitneyan Merycoidodon major Interval Zone (31.4-30.0 Ma) The traditional "Protoceras beds" and "Leptauchenia beds" of the Big Badlands yield an essentially homogeneous fauna, as does Whitney B-C in Nebraska. For that reason, Prothero and Whittlesey (1998) were not able to maintain this distinction based on lithostratigraphy rather than faunal change. Instead, they recognized a single late Whitneyan zone, defined by the first appearance of the distinctive large oreodont Merycoidodon major and characterized by the first appearances of Protoceras celer (the traditional zonal indicator but known only from the channel sandstones in the Big Badlands); the camel *Pseudolabis dakotensis*; the horses Miohippus intermedius, Miohippus annectens, Miohippus equinanus, and Miohippus gidleyi; and Hoplophoneus dakotensis, Eusmilus cerebralis, Nimravus brachyops, Hyaenodon brevirostrus, Eumys brachyodus, and Scottimus lophatus. Last occurrences include Palaeolagus burkei. Prothero and Whittlesey (1998) designated this interval as the Merycoidodon major Interval Zone, with its type section as the strata between 30 and 103 m (90-310 feet) above the Scenic-Poleslide contact on the south side of Sheep Mountain Table in the Big Badlands (see Prothero and Whittlesey 1998:57 for full details). This interval correlates with late chron C12r to early chron C11r (31.4–30.0 Ma). It is calibrated by the Upper Whitney Ash, which was 4° Ar/ 3^{9} Ar dated at 30.58 ± 0.61 Ma, and by the overlying Nonpareil Ash in the Arikareean, which was dated at 30.05 ± 0.19 Ma (Swisher and Prothero 1990; Prothero and Swisher 1992).

WHITNEYAN-ARIKAREEAN BOUNDARY

Tedford et al. (1996) reviewed the abundant new data on strata spanning the Whitneyan-Arikareean boundary, including the previously undescribed "brown siltstone member" of the White River Group above the Whitney Member in Nebraska. After reviewing all the available biostratigraphic data, they placed the end of the Whitneyan and beginning of the Arikareean at the first appearance of Nanotragulus loomsi, Palaeolagus hypsodus, Palaeocastor nebrascensis, Leidymys blacki, and Mesoreodon minor. These taxa first occur low in the Sharps Formation in South Dakota (near the Rockyford Ash) and near the second Nonpareil Ash Zone of the "brown siltstone" in Nebraska. This boundary occurs near the base of chron C11n (30.0 Ma). The end of the Whitneyan is also marked by the last occurrences of a number of taxa typical of the White River Chronofauna, including Leptomeryx, Merycoidodon, Paratylopus, Paralabis, Perchoerus, Heptacodon, Leptochoerus, Colodon, Protapirus, Hesperocyon, Osbornodon, Dinictis, Paradjidaumo, Eumys, and Scottimus.

CONCLUSION

Although the fossils of the White River Group have been known for more than 150 years, only recently has it been possible to use these collections for classic range zone biostratigraphy. The enormous, stratigraphically zoned collections made by the Frick Laboratory and the stratigraphic research of Frick workers such as Morris Skinner finally made that achievement possible. The additional breakthroughs of magnetic stratigraphy and ⁴⁰Ar/³⁹Ar dating allowed numerical dating, detailed correlation of individual sections, and calibration of these biostratigraphic zones to the global time scale. Consequently, some the great potential of the White River Group, with its excellent sections, abundant ashes, and enormous fossil collections, can now be realized.

We now have four biostratigraphically distinctive intervals in the Chadronian, four formally proposed range zones in the Orellan, and two formal zones in the Whitneyan. For the Orellan and Whitneyan, at least, this means that these land mammal ages are actually based on biostratigraphic zones and stages, and so they are true stage/age units in the sense of the North American Code of Stratigraphic Nomenclature (North American Commission on Stratigraphic Nomenclature 1983). The Chadronian subdivisions have not yet been formally proposed, but Prothero and Emry (1996a) and this chapter have indicated the best candidates for the zonal index fossils and for type sections. Each of the four Chadronian, four Orellan, and two Whitneyan intervals are quite short, most less than a million years in duration, which offers the first highresolution, well-calibrated chronostratigraphy for the White River Group. Such high-resolution data have already proven useful for a number of evolutionary and paleoclimatic studies (Prothero and Heaton 1996; Prothero 1999), where precise dating of faunal events is necessary.

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6

Mammalian Biochronology of the Arikareean Through Hemphillian Interval (Late Oligocene Through Early Pliocene Epochs)

N THIS CHAPTER, as in its predecessor (Tedford et al. 1987), we review the most important evidence bearing on the chronologic succession of the North American mammal faunas as revealed by stratigraphic superposition and biological correlation. The assembled record is calibrated by reference to the radioisotope ages of volcanic rocks interbedded with fossil mammal-bearing deposits (see "Appendix") or by reference of magnetostratigraphies containing fossil mammals to the Geomagnetic Polarity Time Scale (GPTS). The wealth of new geochronologic data gives this treatment further rigor and guides the biochronology across zoogeographic discontinuities. This is easily seen in comparing the correlation charts in the 1987 work (figure 6.2) with that herein (figure 6.2). We have included nearly all the data shown in the previous correlation chart to present a comprehensive summary of knowledge of the temporal relationships of all assemblages discussed in Tedford et al. 1987 and in this revision. We follow the calibration of the GPTS given by Berggren et al. (1995) throughout this chapter.

The focus of the present work is to emphasize information gathered since 1987, particularly that important in assessing the relationship of faunal data to independent chronologic systems. Localities or districts where no new information has been obtained are not reconsidered here, nor is their significance called into question.

The geographic scope of this compilation has been extended to the southern Great Basin of New Mexico, Texas, and Mexico; the northern Great Plains of Saskatchewan, Canada; the Atlantic coast of the northeastern United States; and southern Mexico and Central America (figure 6.1). This extended geographic coverage will again Richard H. Tedford, L. Barry Albright III, Anthony D. Barnosky, Ismael Ferrusquia-Villafranca, Robert M. Hunt Jr., John E. Storer, Carl C. Swisher III, Michael R. Voorhies, S. David Webb, and David P. Whistler

serve as a test of the application of the North American land mammal ages (NALMAs) to the limits of the evidence available from the middle and southern latitudes of the continent.

Over the past years there have been a number of reviews and restatements of the principles discussed in the 1987 work (Lindsay and Tedford 1990; Woodburne and Swisher 1995; Woodburne 1996). Walsh (1998, 2000) presents a more detailed analysis of biochronology in the context of paleobiological event terms in general. Woodburne (chapter 1, this volume) reviews a number of Walsh's recommendations, but some are worth brief additional remarks as they impinge on the principles used in this chapter. Fundamental to our data analysis is the use of the local sample of paleontological materials derived from a single site or compiled from separate sites at a single stratigraphic level in a limited geographic area. These samples are called a local fauna (note that this term was given greater stratigraphic and, necessarily, geographic scope in Tedford 1970 than is recommended in Tedford et al. 1987 or here). As Walsh (2000:769) emphasizes, these are not biostratigraphic units (i.e., they are not bodies of rock that contain fossils) but the cooccurrences of specific taxa at a geologic instant in time. Local faunas may occur in stratigraphic relationship to each other, thus acquiring a relative temporal position, and such data are used to establish the biological content of temporal units derived from them. Thus local faunas are operational units (sensu Walsh 1998) in that they are empirical entities whose components are observed to coexist in nature. "Faunas" are theoretical units of greater temporal and geographic scope. Their components are

170 Richard H. Tedford, et al.



FIGURE 6.1 Map of part of North and Central America showing (lettered black quadrangles) geographic regions from which data for the correlation charts (figure 6.2) were derived. Lines linking these regions indicate the sequence of regions discussed in the text.

united on taxonomic (usually species-level) content rather than empirical occurrence. They resemble neontological "faunas" as they characterize zoogeographic regions but obviously differ from the former in that a substantial temporal span is necessarily implied. They have been confused with assemblage zones, but they are purely biological associations, not bodies of rock. Faunas can be composed of many local faunas that share the same taxonomy. Commonly in continental strata, fossil remains are scattered geographically and stratigraphically within a given lithostratigraphic unit. In cases in which these data have not been gathered biostratigraphically but there is an overall taxonomic uniformity of the composite assemblage, it may be called the "fauna of the X-Formation, Member etc.," or simply the "X-Fauna." In this case the composite assemblage or fauna is assumed to represent a coeval association present throughout the time span implied by the rock unit from which it was obtained.

With the help of the timely supraspecific classification of mammals of McKenna and Bell (1997), we have continued to upgrade the taxonomy of the assemblages discussed in this volume. However, we do not review all the taxa mentioned in the 1987 work, so this version will not suffice as a completely up-to-date taxonomy. We continue the practice of denoting original taxonomy, which we still question by placing quotation marks around the original usage.

In making this compilation we have often referred to the monumental compilation of various authors under the editorship of Janis, Scott, and Jacobs (1998) on matters of taxonomy, phylogeny, and geologic and geographic ranges, but we are not altogether constrained by this source. Likewise we have turned to Korth's (1994) review of the record of rodents in the Tertiary of North America. Thanks to the generosity of M. S. Stevens, we have had the benefit of her comprehensive review of the oreodonts, most of which remains unpublished (see Stevens and Stevens 1996 for the methods used in that work). Our oreodont references are drawn from her work. Ongoing revision of the Canidae (Wang 1994; Wang et al. 1999) have resulted in many nomenclatural changes cited here.

THE FAUNAL SUCCESSION

CALIFORNIA COAST RANGES

San Francisco Bay Area (A) A significant addition to our knowledge of the chronology of this region was provided by Baskin's (1981) discussion of the Black Hawk Ranch Local Fauna in the course of his contribution to the study of the temporally related fauna of the Love Bone Bed in Florida. This work (missed in the compilation of Tedford et al. 1987) provides a revision of the Carnivora of the California site, especially the recognition of the biochronologically important Barbourofelis lovei ("machairodont" of Macdonald 1948). Wang et al. (1999) confirmed the presence of Aelurodon taxoides ("Aelurodon aphobus," Macdonald 1948) and attributed Macdonald's (1948) "Osteoborus diabloensis" to Borophagus littoralis. Baskin (1981) pointed out the close similarity of Nimravides thinobates to Nimravides galiani from the Love Bone Bed. Kelly's (1998) description of the horses strongly suggests that the Black Hawk Pliohippus leardi does belong to that genus, although he continued to refer this taxon to Dinohippus. Savage (1955) based most of the biological typification of his Montediablan Stage on the Black Hawk Ranch Local Fauna. In an effort to test the correlation of the local faunas used to characterize this stage and those held typical of the underlying Cerrotejonian Stage, Prothero (in Prothero and Tedford 2000) ran a long magnetostratigraphic section from the upper part of the shallow marine San Pablo Group at the level of the

ostensibly Cerrotejonian Sycamore Creek Local Fauna through the Black Hawk Ranch Quarry and upward for 350 m of the enclosing continental Sycamore Canyon Formation (Green Valley Formation in Tedford et al. 1987). The entire sequence was reversely magnetized and correlated with part of chron C4A (8–9 Ma).

Southern San Joaquin Valley (B) The composite suite of taxa present at the Tecuya Formation sites are best regarded as representing an early Arikareean fauna, limited by the presence of *Nanotragulus* and *Desmatochoerus-megalodon* (= *Promerycochoerus erythroceps* Stock 1932 *fide* M. S. Stevens, pers. comm., 2002) and the limit of the range of the White River relict *Protosciurus*. This limits the temporal range of these sites shown in Tedford et al. (1987:156 and figure 6.2).

In 1987 Tedford et al. (p. 156) mentioned in passing the terrestrial mammal faunas from the predominantly marine Temblor Formation outcrops on the western and eastern margins of the southern San Joaquin Valley. These assemblages can be directly related to marine megafaunal and microfaunal biostratigraphies, which in turn have been calibrated radiometrically. The most important assemblage is the North Coalinga Local Fauna ("The fauna of the Merychippus zone," Bode 1935a, 1935b), which lies near the top of the correlated Temblor strata in deposits that represent either the upper part of the Relizian benthonic foraminiferal stage or the boundary between the Relizian and superadjacent Luisian stages (Durham et al. 1954). In 1970 Turner calibrated the boundary between these stages as 13.7-14.5 Ma but admitted that large analytic uncertainties and tenuous correlations to the benthonic time scale limit the accuracy of this determination. These results were referred to by Tedford et al. (1987) in determining the age of the North Coalinga Local Fauna. The presence of Proboscidea in that fauna was said to correlate the assemblage with the Barstow Fauna despite previous workers' (Downs 1956, 1961; Bode 1935a) placement of this fauna in the proximity of the Mascall and Virgin Valley faunas of the Columbia Plateau and definitely older than the "Barstow Fauna" (having the same connotation to those authors as in this volume, i.e., the youngest faunal unit in the Barstow Formation). A review of the North Coalinga Local Fauna confirms their opinion: Stirton (1935) referred the Monosaulax sp. of Bode (1935a) to M. pansus in the sense of his sample from Stewart Springs, Nevada, which has in turn been allocated to M. skinneri Evander (1999) by Korth (1999c). The North Coalinga borophagines include Paracynarctus kelloggi, Protomarctus cf. optatus, and Aelurodon asthenostylus; the amphicyonid is Amphicyon sinapius; the horses

172 Richard H. Tedford, et al.

include Hypohippus cf. osborni, Archaeohippus mourningi, Desmatippus avus, Merychippus brevidontus, and "Merychippus" californicus; a rhino near Aphelops is present; the camels include Aepycamelus and Miolabis; and the cranioceratine dromomerycid seems to be Bouromeryx. The composition of this fauna has a Columbia Plateau-like character and also includes taxa found in the early Barstovian of the Great Plains. There are some range extensions (higher for Prototomarctus, lower for Aelurodon) for an early Barstovian assemblage. This conclusion is now confirmed by the latest calibration of the Relizian-Luisian boundary at 15.7 Ma by Barron and Isaacs (2001). This occurrence lends additional support for the early Barstovian appearance of Proboscidea, especially mammutids (Zygolophodon, "Miomastodon sp.," of Bode 1935a, figure 5a, c, and d), and possibly gomphotheriids as well (Bode 1935a, figure 5b) and extends the geographic range to the Pacific coastal sites in California. Curiously, the North Coalinga Local Fauna shares few taxa with early Barstovian assemblages of the nearby Transverse Ranges and Mojave Desert reviewed in this chapter.

Along the southeastern outcrop of the Temblor Formation, faunas of like composition include the late Hemingfordian Barker's Ranch Local Fauna and early Barstovian Sharktooth Hill Local Fauna (also with *Zygolophodon*) mentioned in Tedford et al. (1987:156 and footnotes 3 and 4), the latter attributed to the late Barstovian.

Savage (1955) typified his Cerrotejonian Stage with the South Tejon Hills Fauna (composite of Los Angeles County Museum [LACM] California Institute of Technology [CIT] sites 303, 304, and 307) from the Tejon Hills outcrops in the southeastern margin of the San Joaquin Valley. At the time the containing strata were referred to the marine Santa Margarita Formation, but later Bartow and McDougall (1984) revised the lithostratigraphy of the Tejon Hills in light of the regional relationships of the rock units in the southeastern San Joaquin Valley. They now attribute these mammal-bearing strata to the nonmarine Bena Formation, which underlies a thin representative of the Santa Margarita with local angular unconformity. The South Tejon Hills Fauna includes Hipparion tehonense, "Pliohippus" tejonensis, Megahippus sp., Borophagus littoralis (Wang et al. 1999), Ustatochoerus sp., Cranioceras sp., and Paracosoryx cf. furlongi.

In the northern part of the hills, the thin Santa Margarita equivalent contains the Comanche Point Local Fauna with *Cormohipparion* cf. *occidentale* and "*Pliohippus*" *tehonensis*. These shallow water marine beds grade laterally and upward into the nonmarine Chanac Formation. This younger interval contains the North Tejon Hills Fauna (LACM [CIT] localities 104, 302, and 305): Hipparion forcei, Pliohippus leardi, Barbourofelis cf. lovei, Borophagus littoralis, Epicyon, Nimravides cf. thinobates, Ustatochoerus cf. californicus, Cranioceras sp., and Plioceros sp. This fauna closely resembles that from the Black Hawk Ranch Quarry and was Savage's (1955) principal reference assemblage for his Montediablan Stage. Thus the Tejon Hills contained not only the typifying fauna for the Cerrotejonian but also the superposed Montediablan reference. In an effort to calibrate this sequence, Wilson and Prothero (1997) constructed a nearly 200-m magnetostratigraphic section in the northern Tejon Hills extending from below the level of the Comanche Point Local Fauna through the exposed Chanac Formation. This sequence begins in a mixed-polarity interval containing the Comanche Point Local Fauna overlain by a long reversed section containing the North Tejon Hills Fauna. Unfortunately a magnetostratigraphy could not be constructed in the South Tejon Hills, but like Savage, Wilson and Prothero (1997) assumed that the northern hills section included correlative strata ("Santa Margarita") at the base. These results were interpreted to indicate that the Cerrotejonian and Montediablan stages pertained to successive magnetic chrons assumed to be chron C5An to C5r (11-12 Ma). Later work (Prothero and Tedford 2000), informed by studies in the Cuyama Valley, shifted the correlation of the reversed interval to chron C4Ar.

Transverse Ranges (C) Continued study of the faunal sequence in the Transverse Ranges south of the San Joaquin Valley has improved our knowledge of the taxa that occur there and the chronologic relationships of the fossil assemblages.

Recent work on the lithostratigraphy, magnetostratigraphy, and radioisotopic age determination of faunal occurrences in the upper part of the Sespe Formation (Mason and Swisher 1989; Prothero et al. 1996) has confirmed the relationships of these scattered assemblages. Prothero et al. (1996) constructed a composite Sespe section on the north side of Simi Valley, eastern Ventura County, including the Alamos Canyon Local Fauna in the upper part of a 370-m segment of the upper member of the Sespe Formation above the intraformational hiatus separating the medial Eocene from late Oligocene rocks. The Alamos Canyon Local Fauna (R. W. Wilson 1949; Lander 1983) lies within a reversed interval that Prothero et al. (1996) correlate with chron C9r (27.9-28.3 Ma). It contains ?Archaeolagus, Leidymys nematodon, and Hypertragulus cf. hesperus, all taxa that occur in the John Day Formation in the interval between the Deep Creek and

Tin Roof tuffs (27.9–25.9 Ma). This suggests either a somewhat younger correlation with the GPTS than indicated by Prothero et al. (1996) or an upward extension of the local range zones for these taxa.

The Kew Quarry Local Fauna has been a consistent enigma as to its age, largely because of inadequate identification of constituent taxa and knowledge of their biochrons. Revision of some of the Kew Quarry canid, nimravid, and camelid taxa (in Prothero and Emry 1996) yields a revised mammal faunal list: ?Palaeolagus, Sespemys thurstoni, ?Paciculus sp., Temnocyon altigenis, Mesocyon brachyops (Wang 1994), Archaeocyon pavidus (Wang et al. 1999), Nimravus brachyops (Bryant 1996), Eusmilus cerebralis (Bryant 1996), Miohippus, Subhyracodon occidentalis, Elomeryx armatus, Miotylopus gibbi (Prothero 1996), and Hypertragulus calcaratus. Judging from the ranges of these taxa in the older part of the John Day Formation and younger part of the Brule Formation, this assemblage is of early Arikareean age, ca. 28-29 Ma, and shows the characteristic persistence of elements of the White River Chronofauna coupled with new elements (Mesocyon, Miotylopus, possibly Paciculus if truly present, and Temnocyon; Hunt 1998). A 500-m section to determine the polarity of the structurally isolated Kew Quarry Local Fauna was found to be reversed except for the lowest site. The reversed strata in which it occurs probably lies in chron C10r.

In the folded Sespe outcrops at South Mountain, north of the Simi Valley, elements of the South Mountain Fauna occur through 640 m of section (Mason and Swisher 1989). The tiny leptauchenine Sespia occurs throughout the entire sequence, with isolated occurrences of other taxa: Eporeodon thurstoni Stock (1934; ?Eporeodon thurstoni of Stevens, pers. comm, 2002) in the lower part of the section and Promerycochoerus hesperus Stock (1930; Desmatochoerus megalodon of Stevens, pers. comm., 2002), Diceratherium, and Gregorymys (or Grangerimus) near the top. The composition of this fauna resembles those of the volcaniclastic aeolian deposits of the lower Arikaree Group of the Great Plains. In California they occur in an interval dominated by variegated sandstones and red mudstones, carrying the same implications of well-oxidized sediments above groundwater. A datable ash bed (Willard Canyon Tuff) occurs near the top of the fossiliferous interval and gives a K–Ar date of 28.20 ± 0.2 Ma. It lies in a normal polarity interval (Prothero et al. 1996) that appears to be chron C10n. The stratal range of the South Mountain Fauna probably encompasses most of chrons C10 and C9r, approximately 29.4-27.9 Ma. The fauna thus is partly an ecofacies of the Kew Quarry Local Fauna and partly succeeds it.

A significant faunal occurrence, the Vedder Local Fauna, in a nonmarine tongue in the otherwise marine Branch Canyon Formation of the eastern Caliente Range was briefly mentioned by Tedford et al (1987:158). This late Hemingfordian assemblage provides a larger view than other West Coast sites of the diversity of mammals during that span. The local fauna was described by Hutchinson and Lindsay (1974), Lindsay (1974), and Munthe (1979a) and is particularly notable in containing the only North American occurrence of the Eurasian petauristine squirrel Blackia. The microfauna has broad resemblances to late Hemingfordian assemblages of the Great Plains and late Hemingfordian to early Barstovian faunas elsewhere in North America in the occurrence of Hypolagus, Miospermophilus, Pseudotheridomys, Leptodontomys (= "Eomys," Korth and Bailey 1992), Mookomys, Proheteromys sulcatus, and Proheteromys magnus. The ochotonid Cuyamalagus is present, as are such mammals as Protomarctus cf. optatus, Archaeohippus cf. penultimus, Parapliohippus carrizoensis, Ticholeptus zygomaticus, Protolabis, and a dromomerycid. Many of these taxa are also present at CIT loc. 315 (Dougherty 1940) and the Hidden Treasure Springs Site in the Caliente Formation to the east and southeast into the Cuyama Badlands. Like CIT loc. 315, the Vedder site lies below the projection of the lowest Triple Basalt K–Ar dated at 16.5 \pm 1.3 Ma (Turner 1970).

In recent years Kelly (Kelly and Lander 1988) has reevaluated the biostratigraphy of the Caliente Formation in the Cuyama badlands first monographed by James (1963). Kelly reviewed the horses (1995, 1998) and camels (1992), and Lander (Kelly and Lander 1988) reevaluated the oreodonts. The biochronology was later reaffirmed (Kelly and Lander 1992). A redating of the upper biotite tuff, or "Dated Tuff," in the section by Swisher (1992) using 40 Ar/ 39 Ar has shown it to be markedly younger (13.4 ± 0.14 Ma) than previously believed (15.6 Ma). This important sequence is revised here: The lowest assemblage, the Hidden Treasure Spring Fauna, lies in the lower part of the Caliente Formation as exposed locally. It contains a limited number of large mammal taxa, including "Parahippus, "Parapliohippus, Acritohippus cf. tertius, a chalicothere, Ticholeptus zygomaticus, Aepycamelus, and "Merycodus." These taxa indicate correlation with the Vedder site to the northwest in the Caliente Range, as suggested earlier. A newly available magnetostratigraphy that includes the Hidden Treasure Springs level places this faunal association in the earlier part of chron C5Cn or in C5Cr, roughly equivalent to the position of the Red Division Quarry Local Fauna of the Barstow Formation. These sites share Parapliohippus carrizoensis but no other taxa.

174 Richard H. Tedford, et al.

Higher in the section, the West Dry Canyon and overlying Lower Dome Spring faunas (*sensu* Kelly and Lander 1988) are biologically correlated with the Green Hills Fauna of the Barstow Formation and contain *Parapliohippus, Acritohippus, Cynorca occidentale, Brachycrus, Miolabis fricki, Aepycamelus,* and *Rakomeryx raki* among the taxa in common. In addition, these faunas contain the cranioceratine dromomerycid *Bouromeryx* cf. *milleri*.

A larger assemblage is represented by the Upper Dome Spring Fauna, whose elements occur above the Lower Dome Spring Fauna and extend nearly to the base of the "Dated Tuff." This fauna includes the lowest local occurrences of Copemys cf. dentalis, Perognathus furlongi, Proheteromys maximus, and Petauristodon uphami. Perognathus and Proheteromys overlap only in the early Barstovian. The presence of the immigrant Lanthanotherium may be its earliest North American occurrence. Species of this genus have their first local occurrence in the younger part of the span of the Barstow Fauna. The large mammal fauna, which includes Tomarctus hippophaga, Acritohippus quinni, Merychippus brevidontus, Archaeohippus mourningi, Cynorca occidentale, Miolabis fricki, Paramiolabis taylori, Hesperocamelus cf. alexandrae, and Bouromeryx milleri, shows a close resemblance to the Lower Dome Spring Fauna except that it lacks the limited early Barstovian Brachycrus and Rakomeryx and adds Paramiolabis and Hesperocamelus. Tomarctus hippophaga seems limited to the early Barstovian (Wang et al. 1999). This and the rodent evidence suggest a late early Barstovian assemblage rather like that of the Second Division Fauna of the Barstow Formation.

The faunal evidence suggests that despite the close proximity of the "Dated Tuff" to the highest stratigraphic occurrence of the Upper Dome Spring Fauna, there must be a hiatus greater than 1 m.y. separating the fauna and ash.

Only scattered fossils occur above the Dome Spring faunas. The Doe Spring Canyon Fauna of Quatal Canyon in the western part of the Cuyama badlands lies above the "Dated Tuff." It contains *Gomphotherium*, *Acritohippus quinni* (highest local occurrence), *Merycodus* cf. *cerroensis*, *Ramoceros*, and *Petauristodon uphami*.

Although the sites containing the Doe Spring Canyon Fauna lack direct superposition with the interval in the Caliente Formation containing the Mathews Ranch and Nettle Spring faunas to the east in Apache Canyon, there seems little doubt of its relative stratigraphic position (Kelly and Lander 1988). These younger faunas contrast in their horse taxa but are largely conspecific with regard to their rodent assemblages. The Mathews Ranch faunal span lies mostly in a mixed-polarity interval correlative with chron C5An and the older part of C5r, whereas the immediately overlying Nettle Spring Fauna lies in the younger part of chron C5r (Prothero and Tedford 2000). Savage (1955) regarded these faunas as part of the reference sequence for the Cerrotejonian and Montediablan stages, but in fact the supposed Montediablan Nettle Spring Fauna lacks the horse and other taxa characteristic of that stage. Nevertheless, the faunal correlation of Mathews Ranch and South Tejon Hills faunas seems valid, and the magnetics thus suggest a chron C5An–C5r age for the Cerrotejonian, or about 11.5–12.5 Ma. Thus in the Cuyama badlands, the superposed faunal sequence in the Caliente Formation suggests that older Clarendonian faunas extend to 12.4 Ma. The meager evidence hints at a faunal turnover in this coastal site that approximates the striking change in the Mojave Desert at the end of the Barstovian.

Peninsular Ranges (D) Important new information is now available regarding Arikareean faunas from the western flanks of the Peninsular Ranges in southern Los Angeles, Orange, and San Diego counties of southwestern California.

The large collection from the Otay Formation, south of San Diego (Démere 1988), the East Lake Local Fauna, closely resembles early Arikareean faunas of western Nebraska and adjacent Wyoming. Notable genera in common are Leidymys, Mesocyon, Hyaenodon, Subhyracodon, Mesoreodon, Sespia, Miotylopus, ?Dyseotylopus, and Nanotragulus. The fossiliferous beds lie in a reversed interval correlated with chron C1or (incorrectly correlated in the "emended" figure 3 of Prothero 1991), as do coeval faunas of similar character in the Great Plains. Except for the occurrence of Meniscomys and Mesocyon coryphaeus, which are limited to rocks of comparable age in the John Day Formation of Oregon, the Otay Fauna closely resembles those of the earliest Arikareean of northern Great Plains, indicating very broad zoogeographic regions within North America in the late Oligocene, as already suggested by the Sespe Formation assemblages of the Transverse Ranges.

Newly discovered local faunas in the undifferentiated Sespe–Vaqueros formation strata of the Santa Ana Mountains (northern Peninsular Ranges) of Orange County include the Upper Oso Dam and Bee Canyon Landfill faunas (Raschke 1984), the Bolero Lookout Local Fauna (Lucas et al. 1997), and sites encountered during development of the Eastern Transportation Corridor (Prothero and Donohoo 2001). Many of these sites were discovered during recent road and housing development. They indicate the presence of early Hemingfordian assemblages resembling those of the Vaqueros and basal Caliente formations in the Transverse Ranges ("A" sites in Repenning and Vedder 1961) and more widely into the midcontinent.

One of the most diverse of such assemblages is that from the Santiago Canyon Landfill, which contains such widely distributed early Hemingfordian taxa as Trogomys, Proheteromys, Schizodontomys, Cupidinimus, Pseudotheridomys, Leidymys, Yatkolamys, Metatomarctus, Menoceras barbouri, Parahippus pawniensis, Anchitherium clarencei, Merychyus arenarum, Pseudoblastomeryx advena, Machaeromeryx, Michenia agatense, and Tanymykter brevidontus (Lander 1994). The correlative Bolero Lookout Local fauna adds Dinohyus hollandi and contains Parahippus pawniensis and Michenia agatense (Lucas et al. 1997). Magnetostratigraphic work by Prothero and Donohoo (2001) indicates that the Sespe red beds containing such faunas lie below marine sandstones with Vaquerosian mollusks and reversed polarity in an interval of mixed polarity that can be correlated with chron C5Dr (18.3–17.6 Ma), slightly younger than the calibration of the lower part of the Runningwater Formation of Nebraska, which begins in chron C5Er (at 18.8 Ma) and extends to 18.0 Ma in chron C5Dr (MacFadden and Hunt 1998).

A thick sedimentary wedge on the northeastern flank of the Peninsular Ranges outlined by the San Andreas (north) and San Jacinto (south) faults includes the late Hemphillian Mount Eden Formation and Local Fauna near the base and succeeding Blancan assemblages in the conformably overlying San Timoteo Formation (Frick 1921; Albright 1999a). Frick (1921) described the Mount Eden Local Fauna, later adding an updated faunal list in his study of the Proboscideans (Frick 1933). In 1937 he added the presence of the dromomerycid Pediomeryx (mistaken for a cervid and named Procoelius; Frick 1937). A few other taxa were added by later authors: Repomys (May and Repenning 1982) and Megacamelus (Harrison 1985). Biochronologically important taxa include megalonychid sloths, the cricetine Repomys maxumi, the ursid Agriotherium gregoryi, the horse Dinohippus osborni, the rhino Teleoceras, the camel Megacamelus, and the dromomerycid *Pediomeryx*. The magnetostratigraphy of Albright (1999a) supports a correlation with chron C3r and an interpolated age of 5.6 Ma for the Mount Eden Local Fauna, comparable to the latest Hemphillian sites in the Panhandle of Texas and adjacent Oklahoma.

NORTHERN GREAT BASIN

Mojave Desert, California (E) Major advances have been made in the knowledge of the chronology of the faunal sequence in the Barstow Formation of the Mud Hills, central Mojave Desert (MacFadden et al. 1990; Woodburne et al. 1990), and the Ricardo faunal sequence of the Dove Spring Formation of the Ricardo Group on the northwestern edge of the desert (Whistler and Burbank 1992). In addition, other early Hemingfordian faunas have been discovered in the eastern part of the province (Reynolds et al. 1995) that help to define, and partially calibrate, such assemblages in the southwestern United States.

Woodburne et al. (1990) have provided a more detailed faunal sequence in the type area of the Barstow Formation (also principal reference sequence for the Barstovian land mammal age) than presented in Tedford et al. (1987). The oldest local fauna was obtained at a single site, Red Division Quarry, which contains only Parapliohippus carrizoensis, Paramiolabis tenuis, and Merychyus relictus fletcheri (included in Merychyus elegans by Lander in Kelly and Lander 1988), clearly equating it with the Upper Cady Mountains Local Fauna farther east in the Mojave (see also Woodburne 1998:208) and the Phillips Ranch Local Fauna of the Tehachapi Mountains on the western desert margin. The limited occurrence of P. tenuis in the Sheep Creek Formation of western Nebraska indicates correlation with the principal reference fauna of the Hemingfordian land mammal age. At Barstow the local fauna from the Red Division Quarry lies in chron C5Cr (MacFadden et al. 1990) at about 16.7 Ma (Woodburne 1998).

The fauna of the Rak Division of the Barstow sequence lies stratigraphically between the late Hemingfordian Red Division Quarry and the diverse Green Hills Fauna of early Barstovian age. Chronologically the Rak Division encompasses chron C5Cn3-C5Cn1 (MacFadden et al. 1990; Woodburne, pers. comm., 1999). The Rak Division contains Protomarctus optatus (Wang et al. 1999), Amphicyon cf. sinapius, Acritohippus cf. tertius, Aphelops, Paramiolabis tenuis, P. cf. singularis, Protolabis, Michenia, Aepycamelus, and Meryceros. The top of this interval also contains the lowest observed occurrence of Copemys in the Barstow Formation (Lindsay 1995; at the base of chron C5Cn1, 16.2 Ma; Woodburne pers. comm., 1999). It was used by Tedford et al. (1987) as a defining taxon, along with Plithocyon, for the beginning of Barstovian time (see discussion in Lindsay 1995). The Rak Division assemblage contains a mixture of taxa found only in the late Hemingfordian Sheep Creek Fauna or early Barstovian Lower Snake Creek Fauna of the classic sequence of western Nebraska, that is, Protomarctus optatus, Acritohippus cf. tertius, and Paramiolabis tenuis of the Sheep Creek coupled with Amphicyon cf. sinapius and Paramiolabis cf. singularis of the Lower Snake Creek, although we cannot demonstrate that the ranges of all these taxa are strictly coeval in the Rak Division.

176 Richard H. Tedford, et al.

The Green Hills Fauna is based on material from many local concentrations of remains and scattered finds. It maintains taxic uniformity through chron C5Br (15.3-16.0 Ma), and its containing strata are conformable with the Rak Division deposits below and with those containing the younger Barstow assemblages above. The Green Hills Fauna included the oldest known occurrence of Hemicyon (Plithocyon) in North America (at Steepside Quarry at the base of the stratal span containing the fauna) at approximately 16.0 Ma. The remaining fauna contains genera and species limited to the early Barstovian: Tomarctus hippophaga, Amphicyon ingens, Acritohippus stylodontus, Brachycrus buwaldi, Rakomeryx, and Merriamoceros. Microtomarctus conferta (Wang et al. 1999) first appears in the Green Hills and some correlative assemblages. This interval contains the last occur-

rence of Euoplocyon. Woodburne et al. (1990) distinguish a Second Division Fauna that extends from Valley View Quarry upward to just below New Year Quarry. This interval is marked by an increase in diversity among the borophagine canids (Wang et al. 1999), especially taxa such as Protepicyon raki and Aelurodon asthenostylus that presage the late Barstovian and Clarendonian ascension of species in these clades. Species of Cynarctus and Paratomarctus also appear at these levels, and Cynarctoides has its last appearance there. The interval has a brief co-occurrence of the two common Barstow horse species, Acritohippus stylodontus and "Merychippus" intermontanus at the level of the Skyline Quarries. Archaeohippus (A. mourningi) is limited to just below the Skyline Tuff in the Second Division. The Second Division spans chron C5Bn (15.3-14.8 Ma).

The first local appearance of Proboscidea (here nearly synchronous for both mammutids and gomphotheriids) occurs near the base of the First Division (at about the level of New Year Quarry and just below the Dated Tuff, 14.8 Ma; Woodburne et al. 1990) at the initiation of the interval typified by the limited Barstow Fauna. Important taxa characterizing this interval (Barstow Fauna s.s.) include *Ischyrocyon* (Hunt 1998), *Hemicyon* (*Plithocyon*) barstowensis, "Merychippus" intermontanus "Merychippus" sumani, rare rhinos, Meryceros joraki, Paramoceros, and Procamelus. The anchitherine horse Megahippus (M. *mckennai*) has its first occurrence. *Parapliosaccomys* has its first, and the oreodont Mediochoerus (M. mohavensis) has its only Great Basin appearance and the latest for the genus. Radioisotopic dating of ash beds and magnetostratigraphy calibrate the span of the First Division as 14.8-13.4 Ma in chrons C5AD-C5ACn. In the eastern Mojave Desert the Cronese Local Fauna, a correlative of the Barstow Fauna, is associated with an ash date of 12.6 Ma,

suggesting a somewhat longer span for the biochron of the Barstow Fauna. If accurate, this date and that for the basal part of the Ricardo faunal sequence nearly overlap, pointing to a phase of rapid turnover in western North America in the medial Miocene.

In 1998 Woodburne reviewed the lithostratigraphy and biostratigraphy of the Hector Formation in the Cady Mountains and clarified the correlation of the faunal successions in the northern and southern parts of the outcrop belt. Critical in this correlation was the recognition that the Logan Mine Local Fauna in the southern part of the range was contained in sands and gravels whose source was the Peach Springs Tuff, whereas the Lower Cady Mountains Local Fauna in the northern part of the outcrop was obtained from rocks underlying the tuff itself. Thus the Logan Mine is slightly younger than the Lower Cady Mountain assemblage, both about 18-19 Ma, in agreement with their early Hemingfordian faunal content. The Hector Formation contains faunas of late Arikareean to early Hemingfordian age and supports the calibration of that boundary near 19 Ma. Their strong biological relationships with correlative faunas of the midcontinent suggest that ecological similarity across the western half of the continent seen in the Late Oligocene continued into early Miocene time.

In recent years a number of mammal faunas have been collected in eastern San Bernardino County, California, by R. E. Reynolds and parties from the San Bernardino County Museum. One of the more informative of these (Reynolds et al. 1995) was obtained in Hackberry Wash from lacustrine deposits laid down on the margin of the Woods Mountain volcanic center and intercalated with the regionally traceable Peach Spring Tuff (18.5 Ma) and the Wild Horse Mesa Tuff (17.75-17.73 Ma). Fossil mammals were obtained at several sites in these deposits and are called the Hackberry Fauna, which seems to represent a coeval assemblage including (list revised from that of Reynolds et al. 1995 using casts generously donated by Reynolds): ochotonid, cf. Trogomys, Metatomarctus cf. canavus, Menoceras barbouri, Protolabis sp., cf. Hesperocamelus, and Aletomeryx occidentalis. This fauna is of early Hemingfordian age, correlative with the Boron Local Fauna of the western Mojave Desert and also the Peninsular Range sites in Orange County, California, discussed earlier. Chronologic information accompanying all these sites places them between 17 and 19 Ma, similar to the calibration of early Hemingfordian faunas in the northern Great Plains (MacFadden and Hunt 1998).

Continued work by one of us (D.P.W.) on the biostratigraphy of the Dove Spring Formation (Ricardo Group) has resulted in a biostratigraphy for the mammals

(Whistler in Whistler and Burbank 1992) and a chemical characterization of ash beds (Perkins et al. 1998) to provide radioisotopic ages by correlation of the ash beds with their sources. This work has shown that there is a significant hiatus in the lower part of the section where chron C₅r is almost entirely removed at roughly the transition between the Iron Canyon and Ricardo faunas of our previous discussion (Tedford et al. 1987:159). Using the "base defines boundary" principle in chronostratigraphy, the Cupidinimus avawatzensis/Paracosoryx furlongi Assemblage Zone is still defined by the biostratigraphy even though the upper part of the zone is lost in the unconformity. Further difficulties with the composite magnetostratigraphy below this hiatus have led to some uncertainty in the calibration of the Iron Canyon interval, but a credible ash identification in this interval (Cougar Point Tuff V, 12.07 ± 0.04 Ma, of Perkins et al. 1998, about 100 m above the base) suggests that the age of the base of the formation is close to 12.5 Ma. A concordance of all evidence indicates that the top of the Dove Spring Formation extends to 8.0 Ma and beyond into unfossiliferous rocks.

The new work has been fortunate in finding a local fauna in the basal gravels of the Dove Spring Formation that clearly links the base of the unit faunally to the Iron Canyon Fauna above. This local fauna contains *Copemys russelli, Cupidinimus tertius,* sciurids, *Pliohippus* cf. *tantalus,* and *Paracosoryx.*

Whistler (in Whistler and Burbank 1992) subdivide the Dove Spring biostratigraphy into four assemblage zones, characterized by the coexistence in each zone by two taxa: the Ustatochoerus profectus/Copemys russelli Assemblage Zone and the Cupidinimus avawatzensis/Paracosoryx furlongi Assemblage Zone (together roughly equivalent to the Iron Canyon Fauna of Tedford et al. 1987), the Epi cyon aphobus (= haydeni)/Hipparion forcei Assemblage Zone roughly equivalent to the Ricardo Fauna s.s., and the Paronychomys/Osteoborus diabloensis (= Borophagus littoralis) Assemblage Zone (roughly equivalent to the Dove Spring Fauna).

One of the important conclusions that emerges from this biostratigraphy is the length and overlap of the local range zones of the horse taxa used by Savage to define his Cerrotejonian and Montediablan stages in coastal California (Prothero and Tedford 2000). All the taxa have longer ranges in the Dove Spring Formation, with broad overlap between *Hipparion tehonense* and *Pliohippus tehonensis* (Cerrotejonian) and the supposedly replacing *Hipparion forcei* and *Pliohippus leardi* (Montediablan). The only replication of a like biostratigraphic character lies in the *E. haydeni/H. forcei* Assemblage Zone, in late chron C5n and C4Ar, where the local range zones of the Cerrotejonian pair terminate before the Montediablan pair. Such evidence would confirm the young position for the Montediablan but leaves the exclusive overlap of the Cerrotejonian taxa in an interval attributed to chron C5n by Prothero and Tedford (2000). This conclusion is compatible with the biostratigraphic relationships of other component taxa of these stages.

The succession of taxa in the Dove Spring Formation is similar to that seen in the upper Valentine and Ash Hollow formations of north-central Nebraska. Of particular interest is the correlation of the oldest Dove Spring levels (Iron Canyon Fauna). As advocated by Tedford et al. (1987), this assemblage shares Cormohipparion occidentale, Megahippus cf. matthewi, Ischyrocyon, Ustatochoerus medius, and large merycodonts (Paracosoryx rather than the Great Plains Cosoryx) with the Burge Fauna. Judging from the Dove Spring evidence, this association of taxa would have an age of about 12-12.5 Ma. In great contrast to western North America, however, there is no faunal turnover in the Great Plains at the close of the Barstovian but rather chronofaunal continuity between the faunas of the Burge and older parts of the Valentine, a situation strikingly unlike the relationships between the faunas of the Barstow and Dove Spring formations. The effect of this turnover in the West is the introduction of faunas more like those of the Great Plains to western assemblages of Clarendonian and Hemphillian ages. This evidence also highlights the strong zoogeographic contrast between the Barstow Fauna and its temporal equivalents in the lower part of the Valentine Formation of north-central Nebraska.

Western Nevada (F) New ⁴⁰Ar/³⁹Ar dates now available for the Barstovian Tonopah Local Fauna and Stewart Springs Fauna of western Nevada (Swisher 1992) were obtained from ash beds more intimately associated with these assemblages and help clarify their temporal positions. Biotite and plagioclase separated from ash falls in the Siebert Tuff immediately below the main fossil quarry of Tonopah yielded dates of 15.16 \pm 0.063 Ma (mean of three determinations), and a biotite tuff overlying the Stewart Springs Tedford Pocket locality yielded 14.96 ± 0.24 Ma on biotite and 14.89 \pm 0.53 Ma on plagioclase. These dates confirm the near contemporaneity of these faunas and give a 14.9 Ma date for the occurrence of mammutid Proboscidea at the local assemblages (specifically the Savage Canyon site) grouped as the Stewart Springs Fauna.

The Tonopah and Stewart Springs faunas share such elements as the borophagines *Paratomarctus temerarius* and *Aelurodon asthenostylus*. In addition, Tonopah has *Micro*- tomarctus conferta and Paracynarctus kelloggi; Stewart Springs has Carpocyon compressus. Both have "Merychippus" cf. intermontanus ("M. calamarius"), Peraceras supercilliosum, and Paracosoryx loxoceras. These assemblages correlate temporally and faunally with the Second Division and early Barstow faunas of the Barstow Formation.

New ⁴⁰Ar/³⁹Ar dates (Swisher 1992) refine the calibration of the mammal-bearing deposits in the Fish Lake Valley and Stewart Valley sites that were combined as the Fish Lake Valley Fauna in Tedford et al. (1987). These new dates confirm the contemporaneity of these sites within a range of 11.6–11.7 Ma. The composition of the Fish Lake Valley Fauna closely resembles those of early Clarendonian age from the northern Great Plains and stands in strong compositional contrast to late Barstovian sites in the Great Basin region, emphasizing once again the remarkable turnover at the close of the Barstovian in western North America.

Recently discovered localities in thick unnamed basin fill cropping out on the western flank of the Pine Nut Mountains in Douglas County, Nevada, near the California border, have yielded an unbroken Hemphillian-Blancan succession (Kelly 1994, 1997). A small assemblage of latest Hemphillian mammals including the leporids Hypolagus gidleyi and Lepoides lepoides, the rhino Teleoceras, the horse Dinohippus, the llama Hemiauchenia, and a cervid (Kelly 1997) make up the Washoe Local Fauna of late Hemphillian age. An ash bed near the lowest occurrence of Blancan mammals (Equus sp. and Ursus abstrusus, taxa included in the Buckeye Creek Local Fauna) gave a 4.96 Ma radiometric date (Lindsay et al. 2002). This is a slightly older date for the Hemphillian-Blancan transition than reported from the Yepómera or Rancho El Ocote faunal sequences that also include this superposition.

COLUMBIA PLATEAU

Northwestern Nevada (G) Fossil mammals occur in volcaniclastic sediments in the rhyolitic volcanic province of northern Nevada. Ash flow tuffs there facilitate the correlation of isolated sites over long distances and provide radioisotope calibration of the sequence. Especially noteworthy is the volcanic field of northwestern Nevada (Washoe and Humboldt counties) and adjacent Oregon, which contains the superposed Massacre Lake Local Fauna (late Hemingfordian), the Virgin Valley Fauna (early Barstovian), and the High Rock Lake sites (early late Barstovian). These sites document the early appearance of zygolophodont mammutids in the northwestern United States and reinforce the evidence from Oregon of a distinguishable zoogeographic province in that region.

The Massacre Lake Local Fauna lies below an ash flow tuff thought to be an outlier of the Summit Lake Tuff (Noble et al. 1970, 1973). This unit was dated by Evernden et al. (1964, who first announced discovery of the fossil mammal site) at 15.6 Ma but was later revised to 16.5 Ma by Swisher (1992), who named this local unit the Tuff of Big Basin. The Massacre Lake Local fauna has a unique mixture of Columbia Plateau Barstovian forms such as *Liodontia, Paracynarctus kelloggi, Desmatippus, Dromomeryx*, and *Ticholeptus*, with Great Plains Hemingfordian forms including *Alphagaulus, Protomarctus, Anchitherium, Parahippus*, and *Bouromeryx* and western Hemingfordian–Barstovian forms such as *Parapliohippus*. A fragment of a mammutid tooth was found at this site (Morea 1981; Woodburne and Swisher 1995).

The Virgin Valley Fauna (Merriam 1911) was obtained from the "lower member of the Virgin Valley beds" of Merriam (1910). Subsequent work recognized that the "upper member" was equivalent to his "Thousand Creek beds" of Hemphillian age, and the Virgin Valley beds were accordingly amended. The rocks containing the Virgin Valley Fauna, the Virgin Valley Formation (sensu stricto [s.s.]), interfinger with and overlie the Cañon Rhyolite, which has given an ${}^{40}\text{Ar}/{}^{39}\text{Ar}$ date of 16.28 \pm 0.07 Ma (Swisher 1992) beneath the fauna, perhaps a maximum age. The fauna is more closely bracketed by ash beds in the Virgin Valley Formation that range from 15.85 ± 0.05 to 15.18 \pm 0.03 Ma. Unlike the Massacre Lake Fauna, the Virgin Valley Fauna lacks most Great Plains elements and instead resembles Columbia Plateau equivalents. It is the type locality for such taxa as Liodontia alexandrae, Oreolagus nevadensis, Paracynarctus kelloggi, Zygolophodon merriami, Moropus? merriami, and Parablastomeryx mollis and also includes Protomarctus, Hypohippus, Desmatippus, Merychippus brevidontus, Acritohippus isonesus, and Dromomeryx.

This endemism continues into the fauna at the High Rock Lake sites (Merriam 1911; Stirton 1939), which are contained in volcaniclastic sediments bracketed below by the Soldier Meadow Tuff, best dated at 16.12 \pm 0.03 Ma (Swisher 1992) and above by a local ash dated approximately 14.5 Ma (Swisher 1992). Most of the fauna listed for the Virgin Valley continues in this assemblage, including Zygolophodon, but the equine horse "Merychippus" californicus (Downs 1961), a large oreodont, and Merycodus nevadensis (type locality) join the fauna.

Eastern Oregon (H) The historic John Day region's rich fossil deposits have been repeatedly exploited since the 1860s and made famous by collectors for Marsh (Schuchert and LeVene 1940) and Cope (1884). They

were first studied stratigraphically by Merriam and Sinclair (1907), later revised by Fisher and Rensberger (1972), and are now subject to further revision since the most important sites were incorporated into the John Day National Monument in 1980. This sequestering of fossiliferous terrain has initiated new field studies by T. Fremd and three of us (L.B.A., R.M.H., C.C.S.), in company with M. O. Woodburne. This new work is still ongoing, but a progress report (Fremd et al. 1994) compiled the fauna of intervals to produce the first biostratigraphy for major elements of the fauna, including the placement of many historic specimens. Stepleton and Hunt (1994; Hunt and Stepleton 2001) have focused on the Upper John Day Formation lithostratigraphy and biostratigraphy. Albright, Woodburne, and Swisher have initiated a magnetostratigraphic study to revise Prothero and Rensberger's (1985) pioneer effort. Swisher continues to provide 40 Ar/39 Ar single-crystal dates for the many ash beds that underpin the correlation of the magnetostratigraphy with the Geomagnetic Polarity Time Scale and provide timing for significant volcanic events. Rensberger's (1971, 1973, 1983) systematic studies of the geomyoid and aplodontid rodents are important modern contributions, but their chronology will necessarily be modified by the studies enumerated earlier. Comparable systematic work on canids (Wang 1994; Wang et al. 1999), amphicyonids (Hunt 2001 and pers. comm., 2003) and other groups are under way. Such studies are particularly important because faunas of the John Day Formation, along with comparable assemblages in the northern Rocky Mountains west of the Continental Divide, have a distinct taxonomic composition that delineates a distinctive zoogeographic region that existed there during early Arikareean time.

The middle part of the John Day Formation, above the basal Big Basin Member, is composed of the Turtle Cove Member and its partial facies, the Kimberly Member overlain disconformably by the Haystack Valley Member (sensu lato [s.l.]; Fisher and Rensberger 1972). The faunal succession is now keyed to a succession of widely traceable tuffs, most of which have been dated by 40 Ar/39 Ar on single crystals using the laser fusion method (Swisher, pers. comm., 2002). Fremd et al. (1994) have given faunal lists for the interash intervals (lithostratigraphic units A-L; see figure 6.2H) of five linked biostratigraphic sections extending along a 10-km segment of the Main Fork of the John Day River from Turtle Cove to Bone Creek in western Grant and eastern Wheeler counties, Oregon. Based on recent U.S. National Parks collecting and knowledge of the location of historical specimens, many taxa have been allocated to these intervals, yielding a biostratigraphy that contains much of the John Day "Fauna" (figure 6.2H) in a total section about 500 m thick.

Radioisotopic dates and magnetostratigraphy suggest that the sequence begins at about 30 Ma and extends to about 18 Ma. Prothero and Rensberger's (1985) magnetostratigraphy is called into question by this extended temporal range and their necessary reliance on a single date that was much too young (the Picture Gorge Ignimbrite at 26 Ma). However, their magnetostratigraphy for the Picture Gorge–Deep Creek Tuff interval can be correlated with the chron C10n–C9n interval (27–29 Ma, Berggren et al. 1995) using the new data.

In the northern Great Plains the disconformity between the White River and Arikaree Groups falls in chron C10n, but many elements of the White River Chronofauna survive into the base of the Arikaree; their extinction occurs just above the basal sands (Gering and upper Sharps formations) of the Arikaree Group. Although we see loss of some of these elements in the John Day (Eusmilus, Nimravus, Dinictis, and Perchoerus) below the Deep Creek Tuff (27.89 \pm 0.57 Ma), others survive nearly to the top of the middle John Day (Agriochoerus, Eporeodon, Hypertragulus, and Palaeolagus) and beyond (Miohippus). Some of the taxa that appear in the northern Great Plains after the extinction of White River elements, including Archaeolagus, Alwoodia, Pleurolicus, Desmatochoerus megalodon, and Oreodontoides oregonensis, are also present at the Picture Gorge Ignimbrite $(28.7 \pm 0.07 \text{ Ma})$ or below, a little earlier in the John Day Formation than in the Plains (Tedford et al. 1996). Other taxa that first appear at the Deep Creek Tuff include Entoptychus, Paroreodon, Merycoides, Hypsiops, Promerycochoerus, and Gentilicamelus. Most of these genera extend to the top of the middle John Day and some beyond into the Haystack Valley Member. Rensberger's (1971, 1973, 1983) biostratigraphy is compromised by recent work that shows that although the local range zones of Meniscomys and Entoptychus are successional, they overlap in the Deep Creek Tuff-Tin Roof Tuff interval, and the local range for Pleurolicus occurs with Meniscomys only at the base of the latter's range zone, below the Deep Creek Tuff (see local range zones in figure 6.2H). Allomys traverses the entire middle John Day. Diceratherium and Meniscomys do not extend beyond the Tin Roof Tuff (25.9 \pm 0.31 Ma), but some new elements are added in the succeeding interval ("L" in figure 6.2H: Schizodontomys, Leidymys nematodon, Phenacocoelus, Moropus, and Nexuotapirus robustus). The occurrence and succession of taxa in the John Day Formation above the Deep Creek Tuff represent a span of time that has not been clearly delineated biochronologically in the Great Plains.



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FIGURE 6.2 Correlation charts showing the chronologic sequence of rock units and contained fossil assemblages discussed in this chapter and in Tedford et al. (1987). The time scale follows figure 6.3. AZ, assemblage zone; B., Basalt; CIT, California Institute of Technology; F., Fauna; Fm., Formation; LF, Local Fauna; M. or Mbr., Member; Q, Quarry; Riv., River; S., site; SS, sandstone; V, volcanic.

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FIGURE 6.2 (continued)

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Recent work by Hunt and Stepleton (2001) has established that the fauna of the Haystack Valley Member of Fisher and Rensberger (1972) is a composite assemblage derived from at least three formation rank rock units that extend in age from the early late Arikareean to the early Hemingfordian. Merycochoerus, Moropus, Parahippus pawniensis, Mylagaulodon, and a Barbouromeryx-like dromomerycid occur in the uppermost unconformitybounded unit of the lithostratigraphic succession south of Kimberly post office (Rose Creek Member of Hunt and Stepleton in review). Several of these taxa indicate a correlation with the lower part of the Runningwater Formation of western Nebraska (Northeast of Agate Local Fauna; MacFadden and Hunt 1998, ~18.8-18.2 Ma) and suggest a greater affinity to Great Plains faunas of this age than previously believed. A fauna from the western facies of the John Day Formation on the eastern flank of the Cascade Range (Warm Springs Local Fauna of Woodburne and Robinson 1977; Dingus 1990) is of similar age.

Hunt and Stepleton (2001) limit the Haystack Valley Member to lithically homogeneous tuffs with fluvial welded tuff-bearing gravels at Haystack Valley, best exposed along Balm Creek in the type area of Fisher and Rensberger (1972). The Balm Creek outcrops of the revised member produced nearly the entire fauna attributed to the Haystack Valley Member of Fisher and Rensberger in Haystack Valley. This fauna includes the first occurrence of the peccary *Hesperhys*, the pleurolicine rodent *Schizodontomys*, and the last occurrence of *Entoptychus*, *Allomys*, and *Miohippus*. Hunt and Stepleton regard this fauna as of early late Arikareean age, supported by an ⁴⁰Ar/³⁹Ar age determination of 23.5–23.8 Ma.

It has long been known that one of the striking contrasts between the John Day faunas and approximate contemporaries from the northern Great Plains and the northern Rocky Mountains east of the Continental Divide was the absence of the leptauchenine oreodonts and protoceratids at John Day and the abundant presence of *Entoptychus* species there. Other compositional differences mark the John Day faunas, especially the presence of diverse aplodontid rodents, a largely endemic fauna of small hypocarnivorous borophagines (Wang et al. 1999), a different oreodont fauna except for the shared occurrence of *Promerycochoerus*, the presence of *Gentilicamelus* and *Paratylopus* camels, and particularly the survival of species of White River genera beyond 25 Ma.

Recently available ⁴⁰Ar/³⁹Ar dates (Swisher 1992) refine the chronologic position of the Mascall Formation sites in the John Day region and also provide better calibration of the Skull Springs Fauna of eastern Oregon. At the Mascall Formation type section, a tuff in unit 2 of Downs's (1956) measured section, 25 feet below the lower mammal-bearing unit 5, yielded plagioclase that gave a date (average of four determinations) of 15.77 ± 0.07 Ma. The Owyhee Basalt drawn by Tedford et al. (1987) beneath the Sucker Creek faunal sites actually overlies them. Its whole rock K–Ar dates, averaged to 14.7 \pm 0.3 Ma (Bottomley and York 1976), give a minimum age for the fauna. The Leslie Gulch Tuff in the Sucker Creek Formation, of unknown stratigraphic relationship to the faunal occurrence, was K-Ar dated (sanidine; Ekren et al. 1984) at 15.8 \pm 0.6 Ma, in agreement with the dates for the correlative Mascall and Skull Springs faunas. Recently a suite of tuffs in the Sucker Creek Formation were dated by ⁴⁰Ar/³⁹Ar single-crystal laser fusion methods (Downing and Swisher 1993), bracketing the fauna between 15 and 15.5 Ma.

NORTHERN ROCKY MOUNTAINS

Eastern Idaho (I) A zoogeographically important sequence of faunas is contained in strata of early Arikareean and early Hemingfordian age that crop out on the western flanks of the Beaverhead Mountains west of the Continental Divide in Lemhi County, eastern Idaho. The oldest faunal sequence occurs in outcrops along Peterson Creek, a tributary of the Lemhi River, about 10 miles northwest of Leadore. Nichols (1976, 1979) described the biostratigraphy and the contained fossils from collections made by him (at the University of Montana) and parties from the Idaho State Museum. Lagomorphs are represented by the archaeolagine Palaeolagus. Aplodontid rodents are diverse: Allomys, Niglarodon, and two stratigraphically successive Meniscomys species. The promylagauline Trilaccogaulus is present, as is the beaver Palaeocastor, the cricetid Paciculus, two stratigraphically successive Entoptychus species; the horse Miohippus, and the oreodonts Megoreodon and Mesoreodon. In the main this fauna resembles those of the Cabbage Patch sequence, the Fort Logan Formation, and Great Plains faunas of the early Arikareean, especially those from the upper Sharps and lowest Arikaree ("Monroe Creek") of South Dakota and the Gering of Nebraska. Of interest in an assemblage from west of the Continental Divide are the high-crowned Entoptychus species typical of the John Day; however, these species (E. fieldsi and the younger E. sheppardi) are, in Nichols's (1976) estimation, more primitive than E. basilaris, the earliest occurring form in the John Day Formation. The latter taxon first occurs above the Deep Creek Tuff of the John Day Formation, which is dated close to 28 Ma, in agreement with the calibration of the Great Plains early Arikareean (Tedford et al. 1996).

Charles Falkenbach of the Frick Laboratory, American Museum of Natural History (AMNH), working in the same area in 1942, discovered a younger fauna in Mollie Gulch about 5 miles southeast of Peterson Creek. These beds, also sandy clays with interbedded ash, are more than 45 m thick but seem to contain a unified fauna, mostly of large ungulates. The Frick collection includes the horse *Parahippus*; the camels *Oxydactylus* cf. *longipes, Michenia* cf. *agatense*, and *Protolabis*; the oreodont *Merychyus arenarum*; and the moschid *Blastomeryx*. All these taxa are typical of latest Arikareean assemblages of the Great Plains. Superposition of the rocks in Mollie Gulch with those in Peterson Creek has not been observed.

A younger fauna comes from strata exposed in Railroad Canyon on the high terrain at Bannock Pass. These deposits lie on pre-Tertiary basement rocks and dip eastward into the Horse Prairie Basin east of the Continental Divide in Beaverhead County, Montana. Some 300 m of clastic strata are exposed in the pass above the mid-Tertiary unconformity with sparsely fossiliferous deposits of early Miocene age. Fossil mammal remains were obtained throughout these exposures, but the largest collections made by Falkenbach, Nichols, and Barnosky come from the upper half of the sequence. Magnetostratigraphic studies (Zheng 1996) indicate that this part of the section lies in an interval bracketed by 16-13 Ma. Curiously, there is no detectable biostratigraphic change in the character of the fauna, which is an early Barstovian assemblage similar in composition to the Deep River, Madison Valley, and the lower zone at Hepburn's Mesa, Montana, which have been correlated with the early Barstovian 16.2-14.8 Ma interval. A few micromammals are known, and they significantly include Peridiomys and Cupidinimus, which range through the sequence, the former genus being unknown below early late Barstovian rocks. Horses are diverse, including Archaeohippus cf. ultimus, Hypohippus cf. osborni, Merychippus cf. insignis, and Acritohippus isonesus. The oreodonts include Merychyus (Metoreodon), Ticholeptus zygomaticus, and Brachycrus. The camels are dominated by species of Aepycamelus, but Paramiolabis cf. singularis also occurs. Ruminants include Blastomeryx, Rakomeryx cf. kinseyi, and Merycodus. Such a fauna is typical of the Great Plains and northern Rocky Mountains early Barstovian assemblages from rocks lying directly on the mid-Tertiary unconformity (base of the fourth sequence of Hanneman and Wideman 1991).

Western Montana and Adjacent Wyoming (J) In later years workers (especially Kuenzi and Fields 1971) recognized that a regional unconformity separates the Tertiary basin fill of Montana into two sequences: the older Renova Formation, volcaniclastic deposits of medial Tertiary age that range upward into the early Hemingfordian (ca. 18 Ma), and the unconformably overlying, predominantly epiclastic Six Mile Creek Formation of early Barstovian (ca. 16 Ma) and younger age. The seismic stratigraphic studies of Hanneman and Wideman (1991) reveal that most of the basins of southwestern Montana contain three sequences of unconformity-bounded later Tertiary units comparable with the White River, Arikaree, and Ogallala groups of the northern Great Plains. The Renova Formation subsumes two sequences; the Six Mile Creek Formation contains a single late Tertiary sequence.

The studies under way on the John Day faunal succession and those reviewed for the early Arikareean of the northern Great Plains again focus attention on the biostratigraphy of the similar span of time recorded in the Cabbage Patch beds in the Flint Creek and adjacent Deer Lodge basins of western Montana studied by Rasmussen (1969, 1977). This largely unpublished work is again reviewed in light of later studies in correlative regions discussed in this work. Rasmussen reconstructed the biostratigraphic succession from scattered fossiliferous outcrops largely on the basis of similarity of faunal composition. He recognized three faunal associations that could be attributed to the lower, middle, and upper part of the Cabbage Patch beds. The lowest fauna, largely from the well-known outcrops 4 km east of Drummond, contains Ocajila, Pseudotrimylus, ?Palaeolagus, Megalagus, Niglarodon, Agnotocastor, Eutypomys, Leidymys, Plesiosminthus, Cynodesmus s.s., ?Perchoerus, Megoreodon, Desmatochoerus, and Pronodens among the taxa that also occur in early Arikareean faunas of the John Day and Montana sites east of the Continental Divide (Fort Logan Formation) and those in the lower Arikaree Group of Nebraska. As Rasmussen (1977) concluded, this fauna has its closest similarity to that from the Gering Formation of Nebraska and the "Sharps Formation" (i.e., the "upper Sharps Formation" of Tedford et al. 1996). Differences are the diverse aplodontid assemblage (Downsimus, three Niglarodon species, and the endemic Fossodontia), an earlier occurrence of the heterosoricine Pseudotrimylus, and the endemic leptomerycid Pronodens in the lower Cabbage Patch beds.

The fauna of the middle part of the Cabbage Patch beds includes the first local occurrence of *Parvericius, Amphechinus, Archaeolagus, Alwoodia, Pleurolicus, Paciculus,* and *Diceratherium.* This fauna contains taxa in common with the lower Arikaree strata in South Dakota and western Nebraska. *Archaeolagus, Alwoodia,* and *Pleurolicus* also have their first appearances in strata just above the Sharps and Gering formations, there correlated with chron C9n (27–28 Ma). At approximately the same temporal position in the middle John Day, *Alwoodia* and *Pleurolicus* appear just above the Picture Gorge Ignimbrite and *Archaeolagus* somewhat below.

The upper Cabbage Patch fauna contains the first local occurrences of Stenoechinus, ?Gripholagomys, Gregorymys, Mookomys, and ?Euhapsis, taxa largely limited to the northern Rockies and Great Plains, hence affording little basis for correlation with the John Day sequence. In South Dakota Gregorymys has its first local occurrence in the correlated "Monroe Creek Formation" above the Sharps Formation (L. MacDonald 1972), as does Gripholagomys. The genotypic species of Euhapsis occurs in the upper part of the type Monroe Creek Formation of Nebraska (Martin 1987). Thus the faunal sequence in the Cabbage Patch beds seems to represent a short span during early Arikareean time from about 28.3 to perhaps 27.5 Ma, although the sparse mammal fauna of the upper Cabbage Patch beds does not constrain the sequence precisely, and it could range into significantly younger intervals.

The Blacktail Deer Creek Fauna, an isolated occurrence in Beaverhead County, east of the Continental Divide in the southwest corner of Montana, is important to mention because it contains the holotypes of two widely recognized early Arikareean genera: the beaver Neatocastor (N. hesperus Douglass 1901) and the anthracothere Arretotherium (A. acridens Douglass 1901). The outcrop from which these fossils were obtained is about 122 m thick; the anthracothere and a rhino ("?Caenopus," Douglass 1901) were found near the base of the section, and the beaver was found near the top in the alternating succession of light tan sandstones and clays. Subsequently Hibbard and Keenmon (1950) revisited the locality and added a new species, Gregorymys montanensis, and the oreodont Desmatochoerus megalodon ("Promerycochoerus (Parapromerycochoerus) barbouri," Hibbard and Keenmon 1950) from near the lower fossil occurrence. Gregorymys has its first record in the Great Plains in the "Monroe Creek" of South Dakota, and species of the genus extend only through the Arikareean. Desmatochoerus occurs in the Gering and equivalent strata but is limited to the early Arikareean. The earliest record of Arretotherium (as A. leptodus closely allied or conspecific with A. acridens) is in the "Monroe Creek" of South Dakota. This taxon is replaced in the early Hemingfordian by A. fricki. The genus is unknown in the intervening strata. Outside Montana Neatocastor hesperus curiously occurs only in faunas of early or medial Arikareean age in the Gulf Coast of Texas and Florida. These data sum to an early Arikareean age for the Blacktail Deer Creek assemblage.

The Fort Logan Formation (sensu Koerner 1940) from the Smith ("Deep") River basin, east of the Continental Divide in western Montana, has a microfauna (Black 1961; Rensberger 1979, 1981) that includes taxa (Palaeolagus hypsodus, Megalagus, Agnotocastor, and Eumys) that do not occur above the top of the Sharps and Gering formations of the Great Plains. Likewise, the occurrence of Paciculus has its earliest Great Plains occurrence in the upper Sharps Formation, and Cynodesmus does not occur above the basal Arikaree (Wang 1994). The Fort Logan oreodont fauna includes the leptauchenines Sespia and Leptauchenia and the genera Promerycochoerus, Mesoreodon, Desmatochoerus, and Merycoides. The latter four oreodonts co-occur in the lower Arikaree Group and in the John Day Formation around the level of the Deep Creek Tuff. Again the inference is that the Fort Logan Formation contains faunas basically of early Arikareean age. As in the case of the Cabbage Patch sequence, the presence of younger Arikareean assemblages is not evident.

Imprecise mapping of the contact between the Fort Logan and Deep River formations by Koerner (1940) failed to remove the confusion regarding the faunal content of these units, especially the assignment of clearly Arikareean oreodonts (the leptauchenines, Desmatochoerus, Merycoides, and Promerycochoerus) to the Deep River, which otherwise bears a Barstovian fauna. Because the fauna of the Deep River Formation was one of the earliest early Barstovian assemblages (along with Mascall) to be described (by Cope and Scott in the nineteenth century), much of the faunal list represents specific and generic holotypes. Therefore it stood as a singular geochronologic reference fauna into the early twentieth century. Included are the erinaceid insectivores Brachyerix and a late occurrence of Parvericius and the last occurrence of the Proscalopidae (Mesoscalops). The last occurrences of the mylagaulid Mesogaulus, the heteromyine Harrymys, and the marmotine Protospermophilus are in this and correlative faunas. The Mammutidae are present (Zygolophodon brevidens; Lambert and Shoshani 1998), as are the horses Desmatippus crenidens (Scott 1893), Hypohippus equinus (Scott 1893), and Acritohippus isonesus; the oreodont Ticholeptus zygomaticus (Cope 1875); the camel Aepycamelus; and the dromomerycids Subdromomeryx antilopinus (Scott 1893), Dromomeryx borealis (Cope 1878), and Rakomeryx kinseyi (Frick 1937). The presence of a mammutid proboscidean is noteworthy in this early Barstovian site, adding credence to other records of the group in deposits of similar age elsewhere in North America.

Although fossil mammal remains had been noted by early geologists (Hayden and especially Peale 1896) in the bluffs of the lower Madison River where it crosses Tertiary deposits of the Three Forks Basin (Robinson 1961, 1963; Dorr 1956), Earl Douglass was the first to make collections in this region beginning in 1894 and reported in his University of Montana thesis of 1899. The greater part of the fauna was described by him in that and subsequent works, later revisions of some taxa have been made, but few additions to the faunal list have resulted from fieldwork in the twentieth century.

Douglass (1899) gives a stratigraphic section of the Madison River bluffs that stretch along the east side of the river south of Three Forks and Logan in Gallatin County, Montana. Initially, he referred to the fossil mammal-bearing rocks as the "Loup Fork beds" or the "Loup Fork Epoch," further noting, "The beds overlie the White River and occupy the top of the triangular bench between the Madison and Gallatin rivers from the vicinity of Logan on the north, nearly to Elk Creek on the south; also the tops of the high bench west of the Madison River" (1899:155). Dorr (1956) proposed a type section for the Madison Valley Formation in the northern part of the outcrop belt described by Douglass but included in its base rocks referred to the White River beds by Douglass. It is clear from Dorr's figures and description that the "Madison Valley beds" of Douglass include only the conglomerates containing fossil wood and intercalated sands and clays equivalent to the "fossil wood conglomerate" at the top of Dorr's section.

Douglass (1899, 1903) and Robinson (1963) report the occurrence of "mastodon" remains in high gravels in the Three Forks basin, but only one of these, a juvenile ramus, ascribed to the "Madison Valley beds" by Douglass (1903), has been described. Without a figure it is difficult to make comparisons, but the remains seem to be compatible with those of Zygolophodon, perhaps like Z. brevidens of Cope. In any event, the remarks definitely put such Proboscidea in the fauna of the "Madison Valley beds." The remainder of the assemblage resembles that of the Deep River with some exceptions that may denote either environmental or temporal differences. Douglass reviewed the content of the fauna in 1903, and we follow this list and the work of later authors for the taxa contained in the Madison Valley beds. The rodent fauna is dominated by sciurids: Spermophilus (Otospermophilus) primitivus (Bryant 1945), the marmotines Arctomyoides and Palaeoarctomys, and the mylagaulid Alphagaulus pristinus are present. The carnivores Aelurodon cf. asthenostylus, Miomustela madisonae, and Pliocyon ossifragus; the horses Archaeohippus minimus, Acritohippus isonesus, and "Protohippus"; the rhino Peraceras superciliosum; the oreodonts Brachycrus rusticus and Ticholeptus zygomaticus; the camels Miolabis montanus, Procamelus lacustris, Aepycamelus elrodi, and Aepycamelus madisonensis; the moschid Blastomeryx gemmifer; the dromomerycids Dromomeryx borealis, Bouromeryx americanus, and Rakomeryx kinseyi; and the antilocaprids Merycodus ?agilis and Paracosoryx furcatus complete the known fauna.

Like the fauna of the Deep River Formation, the Madison Valley also seems to be of early Barstovian age principally on the biochrons of its wider-ranging horses, oreodonts, and camels as seen in the Great Plains. A strong local element is present in the rodents and dromomerycids.

Dorr (1956) and Sutton and Korth (1995) described the Anceney Local Fauna collected topographically high in the southernmost part of the Madison Valley Formation outcrop. They suggest that this site lies stratigraphically above the part of the section containing the classic fauna. This sample was obtained from a road cut and represents a coeval assemblage. It is strongly biased toward the microfauna, which includes the hedgehog Brachyerix; the soricids Limnoecus and Angustidens (its last occurrence); the talpid Domninoides; the lagomorphs Oreolagus nevadensis and Hypolagus; the last promylagauline, Gabreathia; the mylagauline Alphagaulus; the castorid Euroxenomys; the sciurids Tamias, Spermophilus (Otospermophilus), and Cynomyoides (Korth 1996b); diverse geomyids Mookomys, Peridiomys, Perognathus, Cupidinimus, and Phelosaccomys; the cricetid Copemys nebrascensis; the borophagine canids Paratomarctus temerarius and Aelurodon cf. asthenostylus; the mustelids Leptarctus primus, Plionictis, and Martes; the horses Hypohippus cf. osborni and Acritohippus stylodontus (Evander 1996; "Merychippus cf. M. intermontanus" of Dorr 1956); the rhino Peraceras superciliosum; the moschid Blastomeryx cf. elegans; the camel Aepycamelus elrodi; and the antilocaprid Merycodus cf. M. necatus.

Even considering the differences in manner of collection, there are many comparable taxa between the Anceney Local Fauna and the classic fauna of the Madison Valley beds. Like the latter, the assemblage agrees best with assemblages of early Barstovian age, especially the co-occurrence of the mylagaulids *Galbreathia* and *Alphagaulus*, the heteromyids *Mookomys* and *Peridiomys*, the *Cupidinimus* species, and the ochotonid *Oreolagus*. Zoogeographically the relationship of this assemblage lies largely with the Great Plains.

South of the Three Forks Basin in the Yellowstone River valley, just north of the National Park, outcrops on the eastern side of the river called the Chalk Cliffs have yielded an important Barstovian faunal sequence from the Hepburn's Mesa Formation (Barnosky and Labar 1989). A magnetostratigraphy (Burbank and Barnosky 1990) for this sequence places it more securely in time than the assemblages discussed earlier. The fossiliferous sequence extends from chron C5Br into chron C5ADn. The biostratigraphy has been generalized to two zones, and the taxa (at the generic level) have been assigned to a Peridiomys/Parahippus zone older than 14.8 Ma and a Lignimus/Tardontia zone extending from 14.8 to about 14 Ma (the top of the exposed section). The lower zone contains Alphagaulus (A. douglassi; McKenna 1955), Peridiomys, Oreolagus, Hypolagus, "Merychippus," "Parahippus" (including Desmatippus), Blastomeryx, Dromomeryx, and Merycodus, all of which also occur in the Madison Valley and Deep River faunas. The limited occurrence of the rodents and Desmatippus indicates an early Barstovian age, as does the calibration of this part of the sequence (older than 14.8 Ma).

The upper zone is defined by micromammals from collections at the top and bottom of the zone. Of particular significance is the occurrence of the aplodontid rodent Tardontia, the geomyids Diprionomys and Lignimus, the zapodid Pseudadjidaumo, and the sciurid Spermophilus. Some of these taxa characterize an assemblage zone (Lindsay 1972) low in the younger part of the Barstow Formation that dates at about 14.8 Ma, as at Hepburn's Mesa. The survival of other taxa, namely Mesoscalops and Alphagaulus, into the lower part of the upper zone indicates that some otherwise early Barstovian forms lingered into the earliest late Barstovian in the northern Rocky Mountains. Although these microfaunas mainly have zoogeographic affinities with the Great Plains (Lignimius, Schaubeumys), there are some western taxa (Tardontia, Pseudadjidaumo, Pseudotheridiomys, and Mojavemys) as well (see discussion in Barnosky 1986a), in contrast with the Anceney Local Fauna, which lacks late Barstovian rodent taxa.

The Colter Formation crops out in Jackson Hole, Teton County, Wyoming, just south of Yellowstone Park and within 130 km of the Chalk Cliffs (Hepburn's Mesa) north of the park. This unit is 1500 m thick and contains an intermittent faunal succession (Barnosky 1986a) that helps fill some gaps in our knowledge of mammalian history in the northern Rocky Mountains. Near the base of the formation tuffaceous sediments produce a small collection of taxa, the Emerald Lake Fauna, that includes the aplodontids Niglarodon cf. blacki and Alwoodia cristabrevis, the leporid Archaeolagus emeraldensis, and the oreodont Promerycochoerus superbus ("Desmatochoerus leidyi," Barnosky 1986a:45; M. Stevens, pers. comm., 2002). Such an assemblage finds equivalents at the generic level in the early Arikareean (Ar2) of Montana (Fort Logan Fauna) and in the "Monroe Creek-Harrison" interval in

southwestern South Dakota. More than 50 m higher in the Crater Tuff–Breccia Member, two local faunas separated by about 250 m were grouped by Barnosky (1986a) as the East Pilgrim Assemblage. The lowest local fauna, East Pilgrim 11, is represented by a single taxon, the oreodont *Merychyus arenarum*, whose range is confined to Upper Harrison strata (latest Arikareean) in the Great Plains. The upper local fauna, East Pilgrim 5, contains the equid *Parahippus tyleri* and oreodont *Merycochoerus magnus*, both of which occur in the Runningwater Formation of Nebraska (early Hemingfordian).

Nearly 400 m higher in the Colter Formation, in the Pilgrim Conglomerate Member, Barstovian mammals, the Cunningham Hill Fauna, appear and are represented by a more diverse array of taxa, especially microfauna. The greatest resemblance of the rodent fauna is with early late Barstovian faunas such as the Lignimus/Tardontia zone assemblage in the upper part of the Hepburn's Mesa Formation (Burbank and Barnosky 1990) and specifically with the Norden Bridge and Railway Quarries (Crookston Bridge Member, Valentine Formation) of north-central Nebraska in the joint occurrence of Oregonomys agrarius (sensu Voorhies 1990a), Copemys kelloggae, Cupidinimus (as C. whitlocki Barnosky 1986b close to C. nebrascensis), and Lignimus (L. transversus Barnosky 1986a, closely related to Norden Bridge L. cf. montis, Voorhies 1990b). The few larger mammals do not materially contribute to the age determination other than the little worn hipparionine p4, which resembles Cormohipparion quinni ("Neohipparion republicanus" of Voorhies 1990a).

NORTH GREAT PLAINS

Saskatchewan (K) Scattered outcrops are all that remain of the once continuous Tertiary blanket of the northern Great Plains in Canada. Profound preglacial erosion, occurring in the late Miocene and Pliocene, has removed most of this record. The Hand Hills of southeastern Alberta preserve limited ?Barstovian (Storer 1978) and late Hemingfordian (Burns and Young 1988) assemblages, and the former record is the youngest in the uplands of the region. Some upland surfaces in the Cypress Hills Plateau have been dated as late Miocene (Barendregt et al. 1997), and in that part of the region up to 150 m of erosion may have occurred since that time. The Wellsch Valley Local Fauna of Saskatchewan (Stalker and Churcher 1972; Harrington 1978) appears to correlate most reasonably as early Pleistocene (?early Irvingtonian), and as the earliest low-elevation assemblage in the area, it may provide a constraint for the end of downcutting.

Informative faunas occur in the southern plateaus of Saskatchewan, just north of the U.S.–Canada border in two areas: The Cypress Hills Plateau has a notable post–White River record (Skwara 1988; Storer 1993, 1996; Storer and Bryant 1993), and the Wood Mountain Plateau has an important late Barstovian fauna, the Wood Mountain Fauna (Storer 1975).

Fossil mammal remains have been collected from the sands and gravels of the Cypress Hills Formation outcrops for more than 100 years, but only recently have faunas markedly younger than Eocene (Chadronian) been acknowledged. Now the formation is known to contain faunas spanning the Arikareean to Hemingfordian interval from scattered localities in the southeastern part of the Cypress Hills Plateau (Storer 1993, 1996). The Kealey Springs Local Fauna, northwest of Anxiety Butte, has White River taxa such as Centetodon, Eutypomys, Scottimus, Leptomeryx, and Elomeryx associated with Parvericius, Crucimys, Parallomys, Downsimus, Pseudotheridomys, Schizodontomys, Geringia, Archaeolagus, Promerycochoerus, and Sespia (Storer 2002), suggesting correlation with lower Arikaree sites in western Nebraska. Recently Williams and Storer (1998) reviewed the cricetid rodents and Pseudotheridomys and correlated the Kealey Springs Local Fauna with assemblages from the Monroe Creek of the central Great Plains.

Some fragmentary remains from Anxiety Butte suggest that late Arikareean faunas may be present (Storer 1993), but the definitive presence of early Hemingfordian assemblages at that locality was demonstrated by Storer and Bryant (1993). Two sites on the southern edge of the butte, and at approximately equivalent elevations, yielded Archaeohippus stenolophus (Lambe 1905, including "Mesohippus" planidens Lambe 1905) associated with Parahippus, Diceratherium, Arretotherium cf. fricki, Merycochoerus cf. proprius, Michenia, ?Pseudoparablastomeryx, and Blastomeryx. This suite of taxa is comparable with forms from the basal Ogallala strata (Runningwater Formation) of Nebraska. A larger Hemingfordian fauna, the Topham Local Fauna (Skwara 1988), is the youngest fauna obtained from the Cypress Hills Formation. It was found west of Anxiety Butte and includes Oreolagus, Megalagus, Mylagaulodon, Protospermophilus, Miospermophilus, Leidymys, Schaubeumys, Pseudotheridomys, Leptodontomys, Heliscomys, Proheteromys (three species), Parahippus, Hypohippus, entelodonts, Blastomeryx, Parablastomeryx, dromomerycids, Michenia, and Merychyus, all of which compare best with Great Plains early Hemingfordian faunas, especially those rich in micromammals (e.g., Quarry A; Wilson 1960).

The Wood Mountain gravels and sands cap the plateau in southernmost Saskatchewan near the international

boundary, 200 km southeast of the Cypress Hills Plateau. More than 30 m of these deposits yield a number of local faunas that are sufficiently alike compositionally to be grouped as the Wood Mountain Fauna (Storer 1975, 1978, 1993). This assemblage of more than 55 species includes the following taxa important in correlation: *Brachyerix*, Megasminthus, Leptodontomys, Lignimus, Copemys, Anchitheriomys, Monosaulax, Hesperolagomys, Russellagus, Paratomarctus (not Tomarctus of Storer 1975), Aelurodon cf. ferox (not "A. cf. saevus" of Storer 1975), Amphicyon, Ursavus, Hemicyon, Zygolophodon proavus (in Madden and Storer 1985), Hypohippus osborni, Archaeohippus, Acritohippus cf. isonesus, Hipparion, Calippus ("Equidae gen et sp. indet.," Storer 1975), Ticholeptus, Blastomeryx, Procranioceras cf. skinneri, Merycodus necatus, M. sabulonus, and Paracosoryx cf. alticornis. As Storer (1975:126–127) pointed out, this fauna, though retaining early Barstovian elements, includes a number of taxa common to the earliest Valentine Formation assemblages (later or medial Barstovian) of Nebraska such as Russellagus, Megasminthus, Lignimus, Paratomarctus, Aelurodon cf. ferox, Ursavus, Hemicyon, Hipparion, Calippus, and Procranioceras. This suite of taxa includes genera that also characterize the Keota Fauna in the Pawnee Creek Formation of northeastern Colorado, where geochronologic evidence supports a pre-Valentine position for a comparable assemblage.

The only Canadian Miocene fauna outside the Great Plains is preserved in sediment filling the Haughton Astrobleme on Devon Island in the Canadian Arctic Islands above the Arctic Circle at 75°22'N latitude (Omar et al. 1987; Hickey et al. 1988; Whitlock and Dawson 1990). Fission-track dating of apatite grains (Omar et al. 1987) from the gneiss shocked by impact gives a 22.4 \pm 1.4 Ma date for that event and a maximum age for the fauna contained in the sediments infilling the crater. This undescribed assemblage is of great zoogeographic interest. It contains a heterosoricine shrew, cf. *Domnina*; an ochotonid, cf. *Desmatolagus*; a rhino; and an artiodactyl of "uncertain affinities," none of which are exclusively North American groups.

Nebraska and Wyoming (L) Since the previous review (Tedford et al. 1987) a number of new studies have focused on the biochronology of parts of the Nebraskan record, particularly the early and late Arikareean, early Hemingfordian, and early late Barstovian, all of which provide new insights and information on the mammal ages classically typified by evidence from Nebraska. These studies have met the challenge of our previous review, which called for improvement of biostratigraphic knowledge above that of just the composite faunal content of whole lithostratigraphic units.

Continued interest in the White River–Arikaree Group contact has focused on the lithostratigraphy of the bracketing units, their biostratigraphy and magnetostratigraphy, coupled with radioisotopic dating of the contained ash beds. These studies have led to a closer look at an important interval on the northern Great Plains, one broken by faunal turnover at and after the demise of the White River Chronofauna. This subject was explored in a preliminary way by Tedford et al. (1985), and the results were incorporated in Tedford et al. (1987). A more comprehensive treatment resulted in Tedford et al. (1996), which provides the substance for the following summary.

Tedford et al. (1996) abandoned the lithostratigraphy of Vondra (1963), with its downward extension of Darton's (1899) Gering Formation into White River Group strata. The latter rocks were subsequently recognized as the "Brown Siltstone beds" by Swinehart et al. (1985), who considered the upper member of the Brule Formation to represent an upward and gradational coarsening of the White River Group conformably above the Whitney Member. The Brown Siltstone beds contain many new taxa coexisting with forms typical of the White River Chronofauna, and these new taxa define and characterize the beginning of Arikareean time in the Great Plains. In a closer look at the stratigraphy of this interval, Tedford et al. (1996, figure 9) show that, of the immigrant taxa previously used to define the beginning of the Arikareean (Ocajila, Talpinae, Plesiosminthus, and "Allomys" = Alwoodia), only the zapodid Plesiosminthus occurs near the base of the Brown Siltstone. The other immigrant taxa have first stratigraphic occurrences as high as the basal Arikaree strata, where the local extinction of White River chronofaunal elements has been completed and a new fauna appears. This turnover episode is an important feature of the Great Plains faunal succession. We noted earlier that the other classic biostratigraphic record of this interval, that in the John Day Formation of Oregon, also shows a turnover, beginning slightly earlier, but the new fauna is characterized by persistent co-occurrence of some White River taxa into much younger deposits.

The new fauna that occurs in the lower Arikaree strata is biased by the dominance of aeolian facies, so the record is composed largely of oreodonts and a few horses, camels, and rhinos. Burrowing rodents were not common, and the beavers so conspicuous in younger Arikaree rocks were just beginning their diversification. Local fluviatile settings provide most of our knowledge of mammalian diversity of this span. For these reasons it has been difficult to acquire a biostratigraphy for the Monroe Creek and undifferentiated lower Arikaree rocks in Nebraska. The classic work by Peterson (1907) remains largely unchallenged. Hunt (1985) reinvestigated the stratigraphic allocation of Peterson's collection from the type area of the Monroe Creek Formation, north of Harrison, Nebraska, and reaffirmed the assignment of *Leptauchenia, Desmatochoerus megalodon*, and *Diceratherium* to the lower part of the unit.

In an effort to provide a magnetostratigraphy for the lower part of the Arikaree Group, including Hatcher's (1902) Monroe Creek Formation, MacFadden and Hunt (1998) chose a section at Pants Butte, 8 km east of Monroe Creek Canyon, to avoid faulting. Only the lowermost 98 m of the Arikaree Group is exposed at Pants Butte (compared with 200-215 m at Monroe Creek Canyon). The Pants Butte section was correlated with chron C9r-C9n, probably continuing into chron C8r-C8n, and possibly to C7Ar or C7r, suggesting that the entire section at Pants Butte is older than 25 Ma (Berggren et al. 1995). The lack of faunal control at Pants Butte makes it uncertain where the "lower Monroe Creek Fauna" would occur in this section. Biochronologic data from the Platte Valley do not constrain the upper part of the ranges of the three lower Monroe Creek taxa.

An important insight into the nature of the small mammals of the lower Monroe Creek interval is the collections described by Korth (1992) from exposures along the north side of the Niobrara River near the mouth of McCann Canyon in eastern Cherry County, Nebraska. The McCann Canyon Local Fauna was taken from strata referred to the Harrison Formation that are unconformably overlain by the Valentine Formation (Skinner and Johnson 1984:229). However, as Korth concluded, the systematic relationships of this assemblage lie most closely with those described by J. R. Macdonald (1963, 1970) and L. J. Macdonald (1972) from strata referred to the Monroe Creek Formation in the Pine Ridge Reservation just north of the border in South Dakota. Taxa in common include Alwoodia, Parallomys, Trilaccogaulus, Gregorymys, Pseudotheridomys, Plesiosminthus, and Archaeolagus, all taxa that characterize the lower Arikaree Group deposits above the basal strata (Gering, Sharps formations) and thus younger than 28 Ma. (Tedford et al. 1996). In addition, the McCann Canyon Local Fauna contains such White River holdovers as Domnina, Centetodon, and the yoderomyine Arikareeomys but lacks Palaeolagus. The presence of a low-crowned species of Entoptychus (E. grandiplanus) is the only wellrepresented occurrence of the genus in the Great Plains (see Korth 1992 for discussion).

Hunt (1985) also affirmed that the upper part of the Monroe Creek Formation of Hatcher (1902) contained

194 Richard H. Tedford, et al.

the type specimens of Peterson's (1907) taxa: Promerycochoerus carrikeri, Phenacocoelus typus, and Euhapsis platyceps. These taxa also occur in the overlying Harrison Formation, where they are joined by a diverse and clearly new fauna, indicating that a turnover event took place between the Monroe Creek and Harrison formations. MacFadden and Hunt (1998, figures 15 and 16) were aware that their magnetostratigraphic study of the Arikaree Group at Pine Ridge in northwest Nebraska sampled only the lower part of the Arikaree Group at Pants Butte and the uppermost part at Eagle Crag. Therefore their magnetostratigraphy contained a hiatus in the middle part of the Arikaree section. This lacuna can be filled, at least in part, by rocks of the Monroe Creek Canyon section. A magnetostratigraphic study of that section by Glynn Hayes and R. M. Hunt is in progress. However, one or more hiatuses appear to be widespread in the Arikaree Group of the northern Great Plains, so we lack biostratigraphic characterization of the important turnover event or events that occur somewhere in this span.

The Harrison is primarily an aeolian deposit with local fluviatile facies near the base of the 50-m-thick unit. The latter facies produce a sufficiently varied mammal fauna to typify this interval biochronologically as previously described (Tedford et al. 1987). MacFadden and Hunt (1998) correlated the upper part of the Harrison Formation at Monroe Creek Canyon with the long chron C6n, although the lower part of the formation in the Niobrara River valley at Agate National Monument, limited by a 22.9-Ma K-Ar date on the Agate Ash (Izett and Obradovich 2001), ranges downward into earlier chrons. The top of the Harrison Formation is limited by the zircon fission-track date on the Eagle Crag Ash (Hunt et al. 1983), which occurs at the base of the disconformably overlying Upper Harrison beds. Few details of the biostratigraphy in the Harrison Formation have been recognized, but exposures in the Niobrara Valley near Agate and in the type area of the formation along the Pine Ridge in Sioux County, Nebraska, and adjacent Niobrara County, Wyoming, contain most of the fauna listed.

MacFadden and Hunt (1998) postulated a very short span for the volcaniclastic loess of the Upper Harrison beds (Peterson 1907, 1909), which lies on the Harrison in a deeply dissected surface. The Eagle Crag Ash broadly constrains the age of its base (19.2 \pm 0.5 Ma). The 60-mthick unit lies mostly in a reversed interval that was correlated with part of chron C5Er, its base at the top of chron C6n, a 400-k.y. interval spanning 19.2–18.8 Ma. Again, fluviatile lithofacies such as that containing the Agate Bone Bed at the base of the dominantly aeolian unit contain most of the faunal typification of the lower part of the interval. The upper part yields a fauna from aeolian volcaniclastic loess of more advanced character. This composite fauna shows a strong resemblance to that of the preceding Harrison assemblages but includes new elements that are phylogenetically exotic to the North American fauna and are therefore regarded as immigrants at the middle latitudes. Hunt (2002) recently proposed a replacement name, *Anderson Ranch Formation*, for the Upper Harrison beds, based on the type exposures in the Niobrara Canyon, Sioux County, Nebraska, where O. A. Peterson (1909) first defined the formation.

Rocks correlated with the Runningwater Formation fill a shallow paleovalley cut into the Upper Harrison in the region northeast of the Agate Post Office in Sioux County. These are epiclastic and volcaniclastic fluvial sandstones and loessic deposits about 30 m thick. The lower 20 m were found to lie in a mixed-polarity interval (MacFadden and Hunt 1998, figure 14) correlated with chron C5E and the base of C5Dr, the base at 18.8 Ma and the local top at 18.2 Ma, possibly extending to 18.0 Ma. The fauna from these deposits occurs as scattered specimens and has not been fully described. It represents a continuation of the chronofauna first seen in the Harrison Formation, but it differs from the Runningwater Local Fauna from the type section to the east of the Agate area in that Syndyoceras continues from the Harrison but not into the type Runningwater; Merycochoerus magnus replaces M. matthewi and is replaced by *M.proprius* in the younger part of the Runningwater.

In the Niobrara River area of northwestern Nebraska, the Runningwater Formation represents the basal unit of the principally epiclastic Ogallala Group. These fluviatile strata cut across and may remove deposits of the underlying volcaniclastic Arikaree and White River groups. This episode marks a profound change in depositional style from broad sheetlike bodies with prominent aeolian facies to local valley filling, principally epiclastic fluviatile units, lying in a dissected terrain. This regional shift in depositional style is not immediately reflected in biological change, but local stream channel deposits referred to the Box Butte and Sheep Creek formations in western Nebraska contain faunas that indicate that a significant event involving extinction and evolution ensued during early Ogallala time. This turnover initiated an early phase of one of the more enduring chronofaunas of the midcontinent late Cenozoic. This event cannot be precisely pinpointed in time but must have occurred rapidly between 17 and 17.5 Ma. Prominent among the many changes are the origin and initial diversification of equine horses (MacFadden and Hulbert 1988; Hulbert and MacFadden 1991); the diversification of mylagauline rodents (Korth

2000) and dromomerycids; antilocaprids, advanced camelids, and the rise of advanced borophagine canids (early cynarctines, aelurodontines, and borophagines; Wang et al. 1999); the first occurrence of immigrant rhinos (*Aphelops* and *Teleoceras*) and felids; and the loss of entelodonts, many oreodonts, early amphicyonids, most hesperocyonine canids (Wang 1994), and *Menoceras* (Tedford et al. 1987). Because of the manner in which the Hemingfordian was initially proposed, this natural biochronologic event is used only to divide the Hemingfordian into two parts, with the turnover defining the late Hemingfordian.

In recent years there has been increased interest in faunas that lie at the base of the Valentine Formation and equivalent units in Nebraska. They record a significant step in the evolution of the chronofauna that leads to assemblages of maximum diversity by the close of the medial Miocene. Voorhies (1990a, 1990b) and associates have described the local faunas of the closely associated Norden Bridge, Egelhoff, and Carrot Top quarries (Voorhies 1990b) from the basal part of the Valentine Formation (Cornell Dam Member of Skinner and Johnson 1984) in north-central Nebraska. The presence of gomphotheriid proboscideans in these sites records a significant expansion of range of these animals into the midcontinent; this appearance is used to define the beginning of the late (or medial, Voorhies 1990a) Barstovian time. However, in the case of the Nebraska sequence, the profound disconformity beneath the Valentine strata truncates the actual first occurrence of these proboscideans in that area. We must turn to evidence from the more complete stratigraphic sequence in the Pawnee Creek Formation, northeastern Colorado, for the first local appearance of the gomphotheriids. The Hurlbut Ash near the base of the Valentine Formation has been fission-track dated 13.6 \pm 1.3 Ma (Boellstorff and Skinner 1977), and the date is now confirmed at 13.55 \pm 0.09 Ma by ⁴⁰K-⁴⁰Ar dating of glass shards (Swisher 1992) and at 13.5 \pm 0.1 Ma by identification of the element composition of the Hurlbut Ash with its source in an eruptive center in northern Nevada (Perkins and Nash 2002, table DR2).

Voorhies's review (1990b) shows that the faunas of the Cornell Dam Member record an early phase of organization of the Miocene Chronofauna of the Great Plains. Cornell Dam representatives of long-ranging genera typical of this chronofauna in addition to Proboscidea are the beaver *Eucastor*; such borophagine dogs as *Paratomarctus, Aelurodon, Carpocyon,* and *Cynarctus* (Wang et al. 1999); the canine *Leptocyon*; the mustelid *Leptarctus*; such horses as *Cormohipparion* ("*Neohipparion*"), *Protohippus,* and *Calippus*; the rhinos *Aphelops,* Teleoceras, and Peraceras; the oreodont Ustatochoerus; camels such as Aepycamelus, Procamelus, and Protolabis; and diverse merycodontine antilocaprids. This early fauna contains many taxa such as the beavers Anchitheriomys and Monosaulax, the aplodontid Allomys, the horses Anchitherium and Archaeohippus, the protoceratid Prosynthetoceras, the dromomerycid Dromomeryx, the merycodonts Ramoceros and Submeryceros, and the oreodont Ticholeptus that reach the limit of their geologic ranges at this time, giving rise to an extinction event that continues into the faunas of the overlying Crookston Bridge and Devil's Gulch members.

At the family level such venerable groups as aplodontids, chalicotheres, and leptomerycids make their final appearances in the Great Plains before the Burge Member. This extinction, along with continued evolution (much of it anagenetic) in surviving groups, but little immigration, shapes the faunas of the succeeding Burge and Ash Hollow strata. Unfortunately we have little evidence for the timing of these events beyond the knowledge of the approximate initiation of Valentine sedimentation (13.6 Ma) and an ⁴⁰Ar/³⁹Ar age for vitric ash in the lower part of the overlying Ash Hollow Formation (12.18 \pm 0.12 Ma, Swallow Ash; Swisher 1992). Because there are regional disconformities at the base of the Burge Member of the Valentine and at the base of the Ash Hollow, these data imply that the depositional span of the Valentine must be less than 1 m.y.

New ⁴⁰Ar/³⁹Ar dates obtained from glass shards in the Swallow and Davis ashes allow calibration of the lower part of the Ash Hollow Formation of north-central Nebraska (Swisher 1992) to 11.5–12.2 Ma. Faunas from the upper part of this unit indicate that it must reach nearly to the Clarendonian–Hemphillian boundary. Younger Ash Hollow faunas (including the Feltz Ranch, Oshkosh, and Uptegrove faunas in the type area of that unit) are compositionally medial and later Hemphillian assemblages, as supported by bracketing dates. The Santee Local Fauna, the youngest Nebraska Hemphillian fauna, occurs just below a vitric tuff (Santee Ash) fission-track dated to 5.0 ± 0.2 Ma (Boellstorff 1978).

An important record of later Hemingfordian faunas is contained in the Split Rock Formation (as restricted by Munthe 1979b) of central Wyoming. These rocks were deposited in the Granite Mountains Basin formed by mid-Tertiary subsidence and folding (Love 1970) along the Split Rock syncline. Older faunas occur along the northern flank of the basin that yield scattered remains including *Oxydactylus* cf. *longipes, Paracynarctus kelloggi,* and *Merychyus* (Munthe 1979b) of early Hemingfordian age. A concentration of remains scattered through 130 m

196 Richard H. Tedford, et al.

of the section exposed in Fremont and adjoining Natrona counties near their common junction with Carbon County seems to represent a taxonomically unified assemblage called the Split Rock Fauna here ("local fauna" in Munthe 1979b, 1988). An ash in the faunal sequence produced a radiometric date of 17.4 ± 0.08 Ma (Izett and Obradovich 2001). The fauna includes a diverse lower vertebrate assemblage and 45 mammalian taxa, among which are the erinaceid insectivores *Brachyerix* and *Parvericus*; the mole Mesoscalops; the ochotonids ?Desmatolagus schizopetrus and Oreolagus nebrascensis; the mylagaulids Galbreathia and Alphagaulus; the squirrels Protospermophilus and Miospermophilus; the geomyoids Harrymys, Schizodontomys, Proheteromys, and Peridiomys; the zapodid Plesiosminthus; the borophagine canids Protomarctus, Metatomarctus, Paracynarctus, and Cynarctoides; the equids Hypohippus and "Merychippus" primus; the domeheaded chalicothere Tylocephalonyx; the oreodont Brachycrus; the camels Protolabis and Blickomylus; the dromomerycids Bouromeryx and possibly Barbouromeryx; and the antilocaprids Merycodus and Paracosoryx. This assemblage clearly is a late Hemingfordian fauna with strong affinities to assemblages in adjacent Nebraska. Several genera do not range into the Barstovian (Prototomarctus, Metatomarctus, Tylocephalonyx, and Blickomylus), and others do not occur in earlier Hemingfordian assemblages (Galbreathia, Alphagaulus, Hypohippus, "Merychippus" primus, and Brachycrus). In the northwestern Albuquerque Basin Blickomylus occurs in the red mudstones of Canvada Pilares Member of the Zia Formation in strata as young as the base of chron C5Cn (Tedford and Barghoorn 1999), calibrated at 16.7 Ma, a date comparable with that determined from the ash in the Split Rock faunal span.

Southwestern South Dakota (M) A recent review (Tedford et al. 1996) of the Whitneyan-Arikareean transition in southwestern South Dakota gives further substance to the reconstruction proposed in Tedford et al. (1987) for the Sharps Formation. Lithologically this unit lies astride the boundary between the White River and Arikaree groups. The lower part is lithologically identical to the Brown Siltstone beds of the Brule Formation in adjacent Nebraska, including the correlative Rockyford and Nonpareil ash beds. Like the Arikaree regionally, the disconformably overlying upper part of the unit has a basal channel filling sandstone that grades upward into massive silts and fine sands of typical Arikaree lithologies. The Wounded Knee-Sharps Fauna of Macdonald (1963, 1970), from the upper part of the Sharps Formation, contains a mixture of relictual White River taxa and new records, including the introduction of taxa typical of the Arikaree.

Our lack of knowledge of the biostratigraphy of the younger levels in the Arikaree Group of the Great Plains has already been discussed in connection with the work of Hunt (1985) and MacFadden and Hunt (1998) in the Monroe Creek-Harrison region of northwestern Nebraska. When traced northeastward toward South Dakota, the Monroe Creek and Harrison formations are truncated by the disconformity at the base of the Anderson Ranch Formation (former Upper Harrison beds; Hunt 2002) so that around Chadron, Nebraska, the Pine Ridge Escarpment shows the Anderson Ranch resting directly on lower Arikaree rocks that contains a Wounded Knee-Sharps like fauna (Tedford et al. 1996). Northeast at the Beaver Wall in Nebraska and the adjacent Slim Buttes in South Dakota the intervening strata reemerge. At Slim Buttes, just east of the White Clay Fault Zone, the lithic sequence seems similar to that in the classic "Rosebud" outcrops along Porcupine Creek, further east in South Dakota. In the latter area, the nodular, massive to thick-bedded, silty sandstones of the upper part of the Sharps Formation are gradationally overlain by nodular, massive, pink sandy siltstones that form vertical outcrops (usually called "Lower Rosebud" or "Monroe Creek"; Harksen 1969; Macdonald 1963). At Bear Creek Bluff, at the entrance of Porcupine Creek Canyon, these rocks contain an upward extension of the Sharps oreodonts Mesoreodon ?minor, Desmatochoerus megalodon, Megoreodon grandis, and Leptauchenia (Sespia is absent). New taxa appearing in the "Monroe Creek" Formation in southwestern South Dakota include Amphechinus, Archaeolagus, ?Gripholagomys, ?Desmatolagus, Fossorcastor, Alwoodia, Pleurolicus, Gregorymys, Pseudotheridomys, Mammacyon, Nexuotapirus, and Oreodontoides along with immigrant carnivores Promartes and ?Plesictis (J. R. Macdonald 1963, 1970; L. J. Macdonald 1972; Tedford et al. 1996). These strata record the last Great Plains occurrence of some White River taxa: Proscalops, Geolabis, Palaeolagus, Palaeocastor, Eutypomys, Heliscomys, and possibly Nimravus and the leptauchinine oreodonts.

The Turtle Butte Formation, which crops out 163 km southeast of the classic Pine Ridge Reservation region, contains a fauna of large mammals, the Wewela Fauna of Skinner et al. (1968), similar in character to those found in the lower Arikaree (faunas of the "Lower Rosebud" or "Monroe Creek" formations) of western South Dakota and adjacent Nebraska. The following forms (taxonomy revised) are present: the canine *Leptocyon*; the hesperocyonine *Enhydrocyon pahinsintewakpa* (Wang 1994); a large nimravid carnivore, possibly *Hoplophoneus occiden*-
talis; the horse *Miohippus equinanus;* the giant entelodont *Archaeotherium trippensis* (cf. "*Dinohyus*" *minimus;* Schlaikjer 1935); the camel *Miotylopus;* and the oreodonts *Megoreodon grandis* and *Paramerychyus* cf. *harrisonensis* (Stevens, pers. comm., 2002).

In the Porcupine Creek outcrops, massive buff to gray sandstones with slabby cemented zones (often referred to the "Harrison" Formation; Harksen 1969; Macdonald 1963, 1970) conformably overlie the "Monroe Creek" siltstones and introduce a different oreodont fauna with Promerycochoerus superbus, Promerycochoerus cf. carrickeri, and ?Hypsiops latidens; Oreodontoides oregonensis and Desmatochoerus megalodon continue, but the leptauchenines appear to be absent; neither Paramerychyus nor Merychyus is recorded. Additional first appearances at these levels include Pseudopalaeocastor, Parenhydrocyon, Parahippus, and Arretotherium, but in general the "Monroe Creek" and "Harrison" formation mammal faunas retain several genera (and even species) in common, such as Fossorcastor, Gregorymys, Enhydrocyon, Miohippus, Diceratherium, Desmatochoerus, Oreodontoides, and Nanotragulus. At Slim Buttes, strata with such a fauna are strongly disconformable on the lower Arikaree. In turn these rocks are disconformably overlain by the "Upper Rosebud" (= Anderson Ranch Formation) strata in the upper part of the Porcupine Creek drainage. This is a frustratingly limited view of a critical faunal transition, biased by faunal facies and the imposition of disconformities with ostensibly large hiatuses. The post-Sharps faunal succession resembles that in the type Monroe Creek described by Peterson (1907) and reviewed by Hunt (1985).

Northeastern Colorado (N) The lithostratigraphy and biostratigraphy of the Pawnee Creek Formation and younger Ogallala rocks were presented in Tedford et al. (1987). They accepted the lectotype of the Pawnee Creek Formation proposed by Galbreath (1953), removing only the capping gravels of the type section as undivided upper Ogallala beds. The Pawnee Creek Formation, as emended, fills the course of a single river valley that follows a broadly sinuous path through the Pawnee Buttes area, 7-20 km east of Grover, Weld County, Colorado (Tedford 1999, figures 16 and 19). Dated ash beds (Swisher in Tedford 1999) in this unit show that the Pawnee Creek Formation spans the interval between 14 and 14.5 Ma. Temporally and biochronologically it lies between the older Olcott (15–16 Ma) and younger (less than 14 Ma) Valentine formations of adjacent Nebraska and their abundant faunas and thus fills an important hiatus in the classic Nebraska sequence. Significantly, the capping gravels of the Pawnee Creek type section are part of the overlying upper Ogallala rocks containing local faunas (Kennesaw, Vim-Peetz, and Sand Canyon; Galbreath 1953) that readily correlate with those from the lower Valentine of Nebraska. The deposition of the Pawnee Creek Formation, as now restricted, took sufficient time so that there are some differences in the local range zones of certain taxa. Galbreath (1953) used the term Eubanks Fauna for the assemblage from the lower part of the section. This fauna is a mixture of survivors from the early Barstovian (e.g., Microtomarctus, Leptarctus primus, Desmatippus, Merychippus insignis, Ticholeptus, and Brachycrus), derived members of early Barstovian clades (e.g., Hypohippus osborni vs. Hypohippus pertinax), and new genera that assume an important role in the gathering Miocene Chronofauna (i.e., Aelurodon, Calippus, Protohippus, Megahippus, Ustatochoerus, and Cranioceras). The fauna of the upper part of the Pawnee Creek Formation, the Keota Fauna of Tedford (1999), is typified by the local fauna of the Horse and Mastodon Quarry. This assemblage is marked by the first appearance of Proboscidea, both mammutids (Zygolophodon) and gomphotheriids (Gomphotherium) just above an ash whose glass ⁴⁰Ar/³⁹Ar age is 14.4 \pm 0.02 Ma (Swisher in Tedford 1999). The accompanying fauna differs little from that of the Eubanks Fauna except for the appearance of Carpocyon compressus and Cormohipparion paniense and the loss of the holdover taxa listed earlier. The continued coexistence of Ticholeptus with Ustatochoerus medius, Dromomeryx pawniensis with Procranioceras pawniensis, and Paracosoryx with Cosoryx gives the Keota Fauna a significant biostratigraphic signature compared with assemblages from the lower part of the Valentine Formation. A hiatus of nearly 1 m.y. may separate the Keota and Norden Bridge faunas judging from ash dates now available.

Texas Panhandle, Adjacent Oklahoma and Kansas (O) The importance of the southern Great Plains region in establishing a biostratigraphic sequence of faunas was emphasized by Tedford et al. (1987:175) and by Schultz's (1990) excellent review. This sequence has gained in value in recent years with the addition of microfaunal elements to the better-known large mammal assemblages through the work of the late Walter Dalquest and his colleagues.

A case in point are the Beaver County, Oklahoma, Clarendonian sites, known since the nineteenth century. Hesse (1936) gave the first review of the Beaver County sites, adding new information from the collections of the universities of Kansas and California. Three sites in the Laverne Formation produce locally abundant fossil mammals. These sites are grouped as the Beaver Fauna

because they are identical taxonomically. They are spread through many meters stratigraphically and distributed from near the town of Beaver east almost to Laverne (Harper County), a distance of some 30 km. The remains occur in locally deformed fine sands and interbedded diatomites that lie unconformably beneath younger Ogallala strata (containing the Biorbia fossil seed assemblage). The Whisenhunt Quarry Local Fauna (Dalquest et al. 1996) supplies most of the microfaunal material; the classic Cragin Quarry and Beaver Quarry local faunas (Hesse 1936) supply the macromammals. Biochronologically important elements of this fauna include the hedgehog Untermannerix, the mole Domninoides, the endemic ochotonid Oklahomalagus, an early leporine Pronotolagus, a late occurrence of the marmotine Miospermophilus, the beaver Eucastor planus, the zapodid Macrognathomys, and the cricetids Tregomys and Copemys lindsayi. Large mammals include the borophagine canid Aelurodon taxoides and the horses Calippus (Grammohippus) martini, Pseudhipparion gratum, Hipparion cf. tehonense, and Cormohipparion occidentale, whose overlapping range zones indicate a medial Clarendonian age. The Wakeeny Local Fauna from western Kansas (R. L. Wilson 1968) represents a closely similar fauna and ecology with beavers, cricetids, and rare geomyoids.

Thirteen kilometers north of the Beaver local faunal site on the south bank of the Cimarron River, the upper part of the Ogallala Formation lies in a solution collapse basin developed in the Permian gypsum. These sediments are capped by a caliche and contain a late Hemphillian fauna, the Buis Ranch Local Fauna (Hibbard 1954, 1963; Stevens 1966). This assemblage includes the following taxa: the talpid *Hesperoscalops*; the ground squirrel *Spermophilus* (*Buiscitellus*) *dotti*; the geomyoids *Perognathus*, *Prodipodomys*, and *Pliogeomys*; the skunk *Buisnictis* and fox *Vulpes*; the horse *Nannippus aztecus*; the rhino *Teleoceras*; and the llama *Hemiauchenia*.

Microfaunas associated with the well-known early and late Hemphillian sites in the Texas Panhandle fill the gap between the Oklahoma assemblages discussed earlier. Dalquest and Patrick (1989) described a microfauna from Sebits Ranch Site 24B, from which most of the early Hemphillian Higgins Local Fauna was collected. It curiously lacks cricetid rodents but yields the eomyid *Kansasimys dubius*, the geomyoids *Perognathus* and *Pliosaccomys*, a ground squirrel *Spermophilus*, and the archaeolagine rabbit *Hypolagus vetus*. In contrast, the Coffee Ranch Quarry site produced a larger fauna of late Hemphillian age (Dalquest 1983; Dalquest and Patrick 1989) with *Hypolagus* cf. *vetus*; the eomyid *Comancheomys*; the ground squirrel *Spermophilus*; diverse geomyoids *Progeomys, Perognathus, Cupidinimus,* and *Prodipodomys;* and the cricetids *Calomys (Bensonomys), Prosigmodon, Peromyscus,* and *Neotoma (Paraneotoma).* This fauna resembles the Buis Ranch and Saw Rock Canyon local faunas at the generic level but not at the specific. It also lacks the primitive arvicoline present at Saw Rock Canyon.

SOUTHERN GREAT BASIN

Rio Grande Rift, New Mexico (P) The Española and adjacent Albuquerque basins contain important superposed sequences of faunas of late Oligocene through Miocene age. Cope discovered the faunas of the "Santa Fe Marls," but the decades of collecting and stratigraphic study by the Frick Laboratory have proven the great value of these areas to biochronology. Galusha and Blick (1971) and Galusha (1966) laid out the lithostratigraphy for both basins. Barghoorn (1981) provided a magnetostratigraphy for both basins (Tedford and Barghoorn 1993, 1999), which was constrained by ash dating. The fauna was initially described by Cope (1874, 1875), and the newer collections were informally reviewed by Tedford (1981) and Tedford and Barghoorn (1997). The faunal sequence in both basins is partially overlapping; that in the Española Basin is the longest.

The oldest assemblages are best represented in the northern Albuquerque Basin at Standing Rock Quarry in the base of the Piedra Parada Member of the Zia Formation. This local fauna includes the leporid Archaeolagus; the heteromyids Ziamys and Proheteromys; the carnivores Cynarctoides, Promartes, Daphoenodon, and Cephalogale; and the camel Stenomylus. These taxa are comparable with assemblages from the Anderson Ranch Formation (formerly Upper Harrison beds; Hunt 2002) of Nebraska. The Piedra Parada Member is a volcaniclastic dune sand, including interdune pond and fluviatile facies in its lower part (Gawne 1981). These deposits yield additional taxa from the northwestern part of the basin that are approximately contemporaneous with those from the Standing Rock Quarry (Diceratherium, Merychyus cf. arenarum, Oxydactylus, and Michenia cf. agatense) that confirm the correlation of these faunas with those from the Upper Harrison beds of Nebraska.

The Chamisa Mesa Member of the Zia Formation lies conformably above the Piedra Parada dunefield and represents a transitional environment from aeolian dominated to mixed aeolian–fluviatile deposits (Gawne 1981). In its type area in the northernmost Albuquerque Basin there is a sequence of superposed fossil concentrations ("quarries") that appear to span most of the Hemingfordian. These sites are dominated by the stenomyline camel Blickomylus. In the lowest site (Blick Quarry) it occurs with Stenomylus, Archaeolagus, Oreolagus, Pleurolicus, Cynarctoides, and Protomarctus optatus. At an intermediate stratigraphic level (Jeep Quarry) Blickomylus occurs with Alphagaulus, Archaeolagus, Cynarctoides, Desmocyon thomsoni, Metatomarctus canavus, Promartes, Amphicyon, Menoceras, Michenia, Protolabis, Nothotylopus, and Merycodus. Five meters higher in the conformable section at Mesa Prospect, Parahippus cf. tyleri and "Merychippus" sp. (cement bearing, hypsodont cheek teeth) join the artiodactyl fauna seen at Jeep Quarry. The endemic rodents, very rare oreodonts, diverse camelids, and the peculiarly limited distribution of a very derived stenomyline places a distinctive zoogeographic stamp on a faunal sequence that otherwise resembles that of the Runningwater to Sheep Creek interval in Nebraska. Magnetostratigraphic work in correlative rocks along the northwestern side of the Albuquerque Basin (Tedford and Barghoorn 1999) indicates that the Zia Formation (including the local Canyada Pilares Member of Gawne 1981 at the top) extends to chron C5Cn close to 16.0 Ma. Unfortunately there are few fossils other than the camels Michenia and Protolabis cf. barstowensis at the top of the section in that area.

A regional disconformity occupies the span of the early Barstovian in the Albuquerque Basin, but this interval and the late Hemingfordian are represented in the Española Basin. In the latter basin, the upper part of the Nambé Member of the Tesuque Formation has a more diverse fauna than the Zia Formation, including the horses Archaeohippus, Acritohippus isonesus, and Protohippus; the rhino Aphelops; the camels Aepycamelus, Nothotylopus, Michenia, and Paramiolabis (but no stenomylines); the borophagines Cynarctoides, Paracynarctus (also present in the Canyada Pilares Member, Zia Formation), and Microtomarctus conferta; and the immigrant felid Pseudaelurus. This fauna comes from rocks that lie in the normal interval at the top of chron C5C and seems more derived than the youngest well-represented assemblage from the Zia Formation.

The rich fauna of the overlying Skull Ridge Member of the Tesuque Formation was unknown to Cope but was discovered and well sampled by the Frick Laboratory. Surprisingly, a very derived stenomyline, *Rakomylus*, reappears but is nevertheless a very rare taxon. The camel fauna of this unit is diverse and includes species of *Miolabis*, *Paramiolabis*, *Nothotylopus*, *Australocamelus*, *Aepycamelus*, *Protolabis*, and *Michenia*. The horses are rare but include "Merychippus" cf. intermontanus, Acritohippus isonesus, Anchitherium, and Hypohippus; Megahippus makes its earliest occurrence. The rhinos are Teleoceras and Peraceras. The arctoids Hemicvon and Amphicvon cf. ingens are present, and the borophagine canid fauna closely resembles that of the Lower Snake Creek Fauna of western Nebraska, with Cynarctoides, Paracynarctus, Psalidocyon, Microtomarctus, Tomarctus hippophaga, and Tomarctus brevirostris (Wang et al. 1999) and the last hesperocyonine, Osbornodon. The oreodonts Merychyus and Brachycrus, the antilocaprid Merycodus, and the dromomerycid Rakomeryx complete the known fauna. Magnetostratigraphic work (Barghoorn 1981; Tedford and Barghoorn 1993) and ash dating show that the Skull Ridge Member spans nearly all of chron C5B (16.0-14.9 Ma; Berggren et al. 1995). Sanidine 40 Ar/ 39 Ar dates of 15.42 ± 0.06 Ma (McIntosh and Quade 1995) and 15.3 \pm 0.05 Ma (Izett and Obradovich 2001) were obtained on the White Ash No. 4 near the top of the Skull Ridge Member, in agreement with the magnetostratigraphic results.

Compared with the approximately contemporaneous assemblages from the northern Great Plains (Sheep Creek through Lower Snake Creek interval), the Nambe and Skull Ridge faunas have greater numbers and diversity of camels and fewer horses, antilocaprids, moschids, and dromomerycids. The canid and amphicyonid fauna is largely the same, but oreodonts are rare in New Mexico during this span. These compositional differences probably reflect ecological contrasts, resulting in some endemism (*Rakomylus*), but fundamentally the New Mexican faunas represent zoogeographic outliers of those of the Great Plains. Farther west in the Great Basin faunal diversity declines markedly during this interval.

In the Española Basin, as in the Albuquerque Basin, a regional hiatus breaks stratigraphic continuity beneath the Pojoaque Member of the Tesuque Formation. This hiatus removes the record of most of chron C5AD so that the Pojoaque Member deposition begins in late C5ADn at about 14.3 Ma and extends into chron C5An2 at approximately 12 Ma. This was the unit that yielded nearly all of Cope's collection of 1874. The most fossiliferous interval is the lower 120 m of the unit, which produced the following taxa important in correlation: Monosaulax pansus (Cope 1874, now clearly differentiated from Eucastor tortus; Korth 1999c), Copemys loxodon (Cope 1874), "Mylagaulus," Hesperolagomys, Russellagus, Panolax santae*fidei* (Cope 1874), and *Hypolagus*; the borophagine canids (Wang et al. 1999) Microtomarctus, Aelurodon (Strobodon) stirtoni, A. ferox (= A. wheelerianus; Cope 1877), Paratomarctus, Carpocyon, and the canine Leptocyon; Hemicyon ursinus (Cope 1875); the horses Hipparion sanfondensis (Frick 1933; Hippotherium speciosum of Cope 1877), Neohipparion coloradense (MacFadden 1984), Protohippus, Dinohippus, and Pliohippus, associated with the large and primitive *Merychippus calamarius* (Cope 1875) and the anchitherines *Hypohippus* and *Megahippus* cf. mckennai; the rhinos Teleoceras, Aphelops, and Peraceras. The camel Procamelus makes its first appearance, and the genera Aepycamelus, Paramiolabis, Miolabis, Nothotylopus, Protolabis, Michenia, and Australocamelus continue from the Skull Ridge. The merycodonts are more diverse, including species of Meryceros, Cosoryx, and Ramoceros. The moschids, tragulids, a surviving leptomerycid, and Cranioceras teres (Cope 1874) are present; Ustatochoerus medius is the only oreodont. Significantly, gomphotheriid proboscideans are common, with all the morphological diversity grouped into a single taxon, Gomphotherium productum (Cope 1874), by Tobien (1972, 1973). This diverse fauna has a strong systematic relationship with faunas of the Valentine Formation of Nebraska and other early late Barstovian faunas of the northern Great Plains. Most of the Pojoaque taxa co-occur in the chron C5AC and C5AB interval (Barghoorn 1981; Tedford and Barghoorn 1993), 14.3 to 13.3 Ma, and biotite from a thin white ash about 170 m above the base of the Pojoaque Member gave an 4° Ar/ 3^{9} Ar date of 13.7 ± 0.18 Ma (Izett and Obradovich 2001, mean of four determinations). The fauna of this interval is thus temporally correlative with the basal Valentine Norden Bridge to Railway Quarry local faunas in agreement with the age of the Hurlbut Ash, 13.6 ± 0.2 Ma (Swisher 1992).

Poorly fossiliferous, structurally disturbed, and unfavorable lithofacies (dune sands, Ojo Caliente Member, Tesuque Formation) limit the biostratigraphy of the Pojoaque to its lower levels. The record reemerges at the base of the overlying Chamita Formation, where Round Mountain Quarry yields an early Clarendonian assemblage: Epicyonsaevus has its first local occurrence with Aelurodon taxoides (Wang et al. 1999); the horses include Megahippus cf. matthewi, Pliohippus cf. pernix, and Pseudhipparion gratum; the merycodonts Cosoryx and Paramoceros, the gelocid Pseudoceras, and camel Hemiauchenia are represented at the quarry; and correlative sediments in the vicinity add Epicyon haydeni, Dinohippus, Cormohipparion occidentale (MacFadden 1984), Aphelops jemezanus (Cope 1875), Teleoceras, Peraceros, Gomphotherium productum, Megatylopus, Ustatochoerus major, Longirostromeryx, Blastomeryx, and Plioceras. These taxa also occur together in the classic Clarendonian sites in the Great Plains. A basalt flow higher in the local section gives a whole rock date of 9.6 \pm 0.2 Ma (Aldrich and Dethier 1990) as minimum age for the Round Mountain and stratigraphically associated fauna.

In the type section of the Chamita Formation, Mac-Fadden's (1977) magnetostratigraphy for the incomplete 500-m-thick section extends from the top of chron C5n to the base of chron C3r, 9.7-5.8 Ma. Scattered mammal remains occur in the lower part of the section including the sloth *Pliometanastes*, the canid *Epicyon* cf. *haydeni*, the camel Megatylopus, and the antilocaprine Plioceros sp.; the first two taxa co-occur in the Great Plains only in strata of early Hemphillian age, 8-7 Ma. Thus the exposed base of the Chamita type section probably overlaps the top of the referred exposures in the vicinity of Round Mountain Quarry. A late Hemphillian fauna occurs in the upper tuffaceous zone of the type Chamita at the approximately contemporaneous San Juan and Rak Camel quarries. The composite assemblage would come from "chron 6N" (Lindsay et al. 1987, now chron C3Bn, about 7 Ma, Berggren et al. 1995), early in the late Hemphillian as calibrated here. Sanidine from the upper tuffaceous zone at the level of the quarries yielded a 40 Ar/ 39 Ar date of 6.9 \pm 0.03 Ma (Izett and Obradovich 2001). The fauna includes Dipoides williamsi, Eucyon davisi, Plesiogulo, Astrohippus ansae, Dinohippus interpolatus, Hemiauchenia, and Megatylopus matthewi and has a clear taxic relationship to broadly comparable assemblages from the Hemphill beds of the Texas Panhandle.

Yepómera, Northern Chihuahua, Mexico (Q) Flatlying, fine-grained sediments exposed in the valley of the Rio Papagochic, 200 km west of Chihuahua City, yield a very late Hemphillian (Yepómera Fauna) through earliest Blancan (Concha Fauna) succession calibrated magnetostratigraphically (Lundelius et al. 1987). The composition of the Yepómera Fauna is similar to that of latest Hemphillian faunas of the Texas Panhandle and adjacent Oklahoma (Axtel and Buis Ranch local faunas) that are contained in rocks superposed on the Hemphill beds carrying the well-known Coffee Ranch Local Fauna. The Yepómera Fauna (composite of several sites; Lindsay and Jacobs 1985) includes Notolagus*, Paenemarmota*, Prodipodomys, Pliogeomys*, Copemys[†], Calomys (Bensonomys), Baiomys, Prosigmodon*, Eucyon davisi[†], Vulpes stenognathus[†], Agriotherium, Taxidea^{*}, Machairodus[†], Astrohippus stocki[†], Dinohippus mexicanus[†], Neohipparion eurystyle[†] (MacFadden 1984), Nannipus aztecus[†], Teleoceras[†], Prosthennops, Megatylopus, Hemiauchenia, and Hexobelomeryx[†] (asterisks denote earliest appearance of taxon, daggers indicate last appearance). The notations indicate the nature of this turnover fauna, which is placed magnetically just straddling the Sidufjall subchron of the Gilbert chron with a terminal date for the fauna, and the

Hemphillian mammal age, at about 4.8 Ma in earliest Pliocene time.

This fauna is one of a series of sites of Hemphillian age stretching south from the Southern Great Plains of western Texas into the Chihuahua–Coahuila Plateaus and Range (Yepómera), the Trans-Mexican Volcanic Belt (Rancho El Ocote), and into Central America (e.g., the Gracias and Corinto local faunas). All have taxonomically similar ungulate components implying broad environmental similarity deep into the modern Neotropics in the late Miocene.

Big Bend, Texas (R) Basin-forming extensional tectonics of the Big Bend, Presidio County, Texas, roughly corresponds in time with those of the rest of the Chihuahua-Coahuila Plateaus and Ranges Province and gave rise to a series of small basins, among which are the Delaho and, to the west, the Santana graben. Both are filled with coarse clastic debris and contain mammal faunas of similar composition. An interbedded basalt in the base of the lower member of the Delaho Formation underlying the Castolon Fauna yields a whole rock K-Ar date of 23 Ma (Stevens et al. 1969; Stevens and Stevens 1989). Rocks (Closed Canyon Formation [Henry et al. 1998], formerly member 9 of the Rawls Formation) containing the Santana Mesa Fauna are bracketed by flows and dikes dated at 23.3-22.5 Ma. The Castolon Fauna (Stevens et al. 1969) contains (taxa denoted with an asterisk are unique to the Big Bend) Archaeolagus, Gregorymys, Similosciurus*, Phlaocyon annectens (Wang et al. 1999), Parenhydrocyon wallovianus (Wang 1994), Moschoedestes delahoesis*, Merychyus cf. calaminthus, Ustatochoerus leptoscelos*, Priscocamelus wilsoni*, Michenia, Stenomylus, Aguascalientia, Delahomeryx*, and Nanotragulus ordinatus. The Santana Mesa Fauna does not extend this list, and Aguascalientia is shared with the Zoyotal Fauna of central Mexico. The level of endemicity of this assemblage poses problems in correlation, but the basalt dates agree with an early late Arikareean age that is close to the age of the base of the Harrison Formation of Nebraska.

The Closed Canyon Formation also has been mapped in a small graben that is not continuous with the Santana Bolson. This site contains the Arenosa (formerly Hodoo) site with *Merychyus elegans* and indeterminate camelid material (Stevens and Stevens 1989:77) indicating an early Hemingfordian age for that rock body. The unfossiliferous Smokey Creek Member of the Delaho Formation probably is of similar age because the histories of these basins seem roughly concurrent.

CENTRAL MEXICO

Aguascalientes (S) In Mexico, 800 km south of the Big Bend, near the city of Aguascalientes, rhvolitic tuff and interbedded tuffaceous sandstones (Zoyatal Tuff of Hernandez 1981) quarried for building material contain the Zoyotal Fauna (Dalquest and Mooser 1974). Only four taxa represent this assemblage: the oreodont Merychyus cf. elegans, the floridatragulid camel Aguascalientia wilsoni, a peccary referred to Dyseohyus, and the rhino Menoceras (Ferrusquia-Villafranca 1990). The oreodont is a common early Hemingfordian taxon, and the floridatraguline is more derived than the Aguascalientia sp. from the Castalon Fauna (Stevens 1977). Although younger than the Castolon and Santana Mesa faunas of Texas, the Zoyotal is dominated by similar elements, suggesting that northern Mexico and adjacent Texas shared environmental features (Stevens 1977), in the early Miocene.

Guanajuato (T) In the Trans-Mexican Volcanic Belt several sites occur in fine-grained sediments deposited in a local fault-bounded basin just north of the city of San Miguel de Allende and 1100 km southeast of the temporally and biologically closely allied Yepómera Fauna of Chihuahua. Late Hemphillian fossils occur in the lower 10 m of the exposed basin fill, and at the better-known Rancho El Ocote site they have been divided into two levels. However, the faunas differ mainly in the distribution of large (lower) and small (upper level) taxa, and they are treated as essentially coeval in this work (Carranza-Castañeda and Walton 1992, table 1). The carnivore and ungulate faunas are similar to those at Yepómera at the species level despite the efforts of earlier authors (Dalquest and Mooser 1980) to see the horses, in particular, of the "Ocoté Local Fauna" as "slightly advanced" over those at Yepómera and hence needing taxonomic separation (see MacFadden 1984 for the different opinion followed here). Significant differences with regard to Yepómera are the presence of a sloth identified as Glossotherium that, if verified as to genus, would be an earlier occurrence than previously documented in the United States (late Blancan); the slightly greater species diversity of sigmodontine rodents; and the lack of the geomyids and heteromyids present at Yepómera. These differences probably reflect ecological contrasts between the widely separated sites, but they do not mask the close similarity of these faunas. A fission-track date on an ash in the upper part of the beds of Hemphillian age (Kowallis et al. 1986) gave an age of 4.6 Ma, remarkably close to that

woodburne 06

2/1//04 1:36 PM Page 202

inferred from magnetostratigraphy for comparable strata at Yepómera.

SOUTHEASTERN MEXICO

Oaxaca (U) In Oaxaca the continental Tertiary deposits are largely preserved in narrow northwest-southwest trending grabens such as the Valle de Oaxaca, in the center of the state. Surrounded by horsts of pre-Tertiary rocks, the Cenozoic graben fill includes Paleogene conglomerates and andesitic flows unconformably overlain in the northern part of the graben by the Miocene Suchilquitongo Formation of Wilson and Clabaugh (1970), unconformably overlain by Plio-Pleistocene deposits. The Suchilquitongo Formation is a fluviolacustrine sequence with an interbedded rhyolitic tuff, the Etla Member, that yielded biotite and plagioclase K-Ar ages of 19.3 \pm 0.3 and 20.6 \pm 0.3 Ma, respectively (Ferrusquia-Villafranca 1992). The Suchilquitongo Local Fauna was obtained 80 m above the Etla Tuff and includes the oreodont Merychyus minimus, Merychippus sp., and a new kyptoceratine protoceratid larger and more hypsodont than Syndyoceras cooki (Ferrusquia-Villafranca 1990). This local fauna is best regarded as an early late Hemingfordian assemblage. However, the occurrence of hypsodont equines with a limiting date established for such taxa at 17.5 Ma, that is, younger than the Etla Tuff, may indicate a younger age for the fauna or the need to extend the range of hypsodont equines beyond this limiting date.

In the southeastern part of the Valle de Oaxaca Graben the Tertiary deposits include an extensive pyroclastic sheet partly intertongued and overlain by a tuffaceous fluviolacustrine unit that crops out in the vicinity of Matatlán, 40 km southeast of Oaxaca City. The pyroclastics were K-Ar dated (Ferrusquia-Villafranca 1992) at 15.3 \pm 0.8 (biotite) and 16.0 \pm 0.8 Ma (plagioclase). The Matatlán Local Fauna (Ferrusquia-Villafranca 1990) was obtained from epiclastic strata overlying the dated pyroclastics, and although represented by fragmentary remains it appears to be Barstovian in age. The horses are diverse and suggest an early late Barstovian age. Continued study of the site by Ferrusquia-Villafranca and associates produced remains of Leptarctus, a felid (cf. Pseudaelurus), "Merychippus" s.l. (both hipparionine and equine forms), a rhino, the camel Protolabis, and a leptomerycid (cf. Pseudoparablastomeryx).

The first site discovered in Oaxaca was at El Gramal, along the Pan-American Highway in the Nejapa Valley near the Rio Tehuantepec, about 95 km southeast of Oaxaca City. Stirton (1954) reported the discovery, in gently dipping volcaniclastic sediments, of part of a palate and skeletal fragments of "*Merychippus*" associated in the same concretion with part of an unfused cannonbone of a small camelid identified as "*Oxydactylus*." The fauna was named El Gramal. Subsequent work in the vicinity of the type locality by J. A. Wilson (1967) and colleagues yielded a broken M₃ of "*Meychippus*" sp., a fragment of a gomphothere tusk (with enamel band), and an upper tooth fragment of a protoceratid. Later collecting by Ferrusquia-Villafranca (1975, 1990) and associates yields the following composite list for the El Gramal Fauna: *Gomphotherium* sp., "*Merychippus*" sp., cf. *Miolabis*, cf. *Protolabis*, and a protoceratid. Two additional horses are represented in the collection, one a small hipparionine similar in size and morphology to *Hipparion shirleyi* and the other a small protohippine, perhaps *Calippus*.

Continued geologic study in the Nejapa area by Ferrusquia-Villafranca and associates has shown that the fossiliferous deposits, the tuffaceous fluviolacustrine El Cameron Formation, overlies and partly intertongues with a sheet of felsic tuff, the Yautepec Tuff, for which K–Ar determinations (Ferrusquia-Villafranca 1992) indicate an age between 15.0 \pm 0.8 (biotite) and 16.7 \pm 0.71 Ma (plagioclase). The Yautepec Tuff is younger than the Etla Tuff, underlying the Suchilquitongo Formation, and its contained fauna. The El Camaron Formation, contained in a small graben, can be divided into two informal units: a fine-grained lower member and a coarse-grained upper member. The lower member has yielded fossil mammals at a number of localities in the vicinity of El Gramal.

At El Camaron, 7 km south of El Gramal, correlative rocks (Ferrusquia-Villafranca 1990) yield *Plionictis oaxacaensis*, a gomphotheriid, a small protohippine, and a merycodont. Further exploration (Ferrusquia-Villafranca 1990:109) 7 km north-northeast of El Gramal, near the village of La Mancornada, produced *Gomphotherium*, two equids (one referred to the El Gramal hipparionine, the other like the Camaron protohippine), a small and medium-sized camel, and carnivores referred to Canidae and Felidae.

Despite the fragmentary nature of the evidence, the taxonomic similarity in all these Nejapa sites suggests a fauna of broadly late early Barstovian age. The composite fauna is similar to contemporary assemblages of the Great Plains and contains no recognizable Gulf Coast endemics beyond perhaps the protoceratid, depending on its precise identity.

Central-West Chiapas (U') This site has yielded the southeasternmost Tertiary mammal fauna of Mexico; it comes from the thick marine and terrestrial sequence preserved in the Ixtapa Graben, located 25 km east-

northeast of Tuxtla Gutierrez, the state capital. The fossilbearing unit is the Middle Miocene Ixtapa Formation (redefined, Ferrusquia-Villafranca 1996), which is a 3000to 3500-m-thick calclithitic conglomerate, tuffaceous sandstone, and siltstone sequence interbedded with felsic tuffs, which have yielded biotite and plagioclase K–Ar ages of 15.02 ± 0.35 and 16.02 ± 0.53 Ma in the lower part and 12.12 ± 0.19 and 12.24 ± 0.19 Ma in the middle part (Ferrusquia-Villafranca 1992, 1996).

The small but significant mammal assemblage that forms the Ixtapa Local Fauna (Ferrusquia-Villafranca 1990) was collected from epiclastic beds in the lower part of the formation, located some 200 m below the older dated tuff. The fauna includes the equid *Cormohipparion*, the rhino cf. *Teleoceras*, and the proboscidean *Gomphotherium*.

The equid is close in degree of hypsodonty and occlusal pattern to Cormohipparion quinni, known from the late Barstovian (MacFadden 1998 and references therein). Teleoceras and Gomphotherium are long-lived and widespread genera in temperate North America; however, the latter is represented in Chiapas by a species reminiscent in molar size and occlusal pattern to the Barstovian G. obscurum, the most primitive North American species of this genus (Lambert and Shoshani 1998). On this basis, the age of the Ixtapa Local Fauna probably would fall in the late early Barstovian. The stratigraphic position of the fossiliferous beds (about 200 m below the older dated tuff strata, 15-16 Ma), constrains the age to the early Barstovian. This datum is significant on two counts. First, the Ixtapa *Cormohipparion* record antedates by 1 Ma that of C. quinni, probably its closest North American sister species. Second, the Ixtapa gomphothere is practically coeval with the possible earliest record of Gomphotherium in the United States (North Coalinga Local Fauna from the California Coast Ranges; Bode 1935a; Tedford et al. 1987:156) and somewhat older than the earliest widespread appearance of undisputed gomphotheriid remains across the United States, an event that occurred circa 14.5-14.8 Ma (Tedford et al. 1987).

CENTRAL AMERICA

Honduras and Adjacent El Salvador (V) Small basins faulted into the ignimbrite plateau of Pacific coastal Honduras and adjacent El Salvador have produced late Miocene faunas resembling those of midlatitude North America. The best known assemblage is the Gracias Fauna of central southern Honduras (reviewed in Webb and Perrigo 1984) and the more recently obtained Corinto Fauna of northeastern El Salvador (Webb and Perrigo 1984). These sites are about 75 km apart and have similar geologic settings: volcaniclastic fine to coarse debris with interbedded ash beds resting on the widespread ignimbrites. The composite fauna includes Borophagus secundus, Rhynchotherium blicki (type locality), Hipparion plicatile, Cormohipparion cf. occidentale, Calippus hondurensis (type locality), Prosthennops cf. serus, Protolabis cf. heterodontus, Procamelus cf. grandis, and Pseudoceras skinneri. The distribution of these taxa in northern faunas implies an early Hemphillian age, marked in Central America by the earliest record of Rhynchotherium and a Calippus species limited to Florida sites of similar age. The other taxa have wider distributions into the Great Plains. In any event, this is a fauna of midlatitude character at 14°N latitude, 1700 km south of the Gulf Coast of the United States.

Panama (W) In 1962 fossil mammals were found in the Cucaracha Formation, exposed in the Gaillard Cut of the Panama Canal by R. H. Stewart, a Canal Zone geologist. The fragmentary remains occurred in bentonitic clay and siltstone in several horizons 1.2-1.5 m thick through a stratigraphic thickness of 45 m of the 90-m-thick unit. The Cucaracha Formation is interbedded with fossiliferous marine beds that are usually assigned an early Miocene age. Whitmore and Stewart (1965) gave a preliminary report on the fauna but never fully described the assemblage. In 1977 Bob Slaughter washed a large volume of matrix from this unit and recovered some rodent remains that represented four taxa, one assigned to a new species of the geomyoid Texomys, T. stewarti; the other three include two genera that "belong to known North American forms and a third [that] is new to science" (Slaughter 1981:711), which have not been described. The faunal list known so far is Texomys stewarti, Archaeohippus, Anchitherium, ?Diceratherium, Brachycrus (Schultz and Falkenbach 1949 and M. S. Stevens, pers. comm., 2002 all concur with this identification made from the specimens and casts), and Paratoceras. Such a collection of taxa is familiar in early Barstovian faunas (e.g., Trinity River Local Fauna) of the Gulf Coast of North America. Texomys and Paratoceras are geographically limited to Panama and the Gulf Coast. The presence of the peculiar oreodont Brachycrus represents a major extension (4000 km) in geographic range from its southwestern United States records. Thus this early Miocene fauna has a composition, like those of the late Miocene faunas of Central America (Gracias, Corinto), consisting of wide-ranging (20° of latitude) forms and Gulf Coast endemics demonstrating the breadth of Miocene faunal provinces and, by inference, comparable ecological regions.

GULF COAST, NORTH AMERICA

Texas Coastal Plain (X) A substantial addition to our knowledge of the earliest known faunas of the Gulf Coastal Plain of Texas comes from Albright's description and analysis (1994, 1996, 1998a, 1998b, 1999b) of the Toledo Bend Local Fauna of easternmost Texas and his review of Arikareean assemblages of Texas and Florida (Albright 1998a). The composition of the Toledo Bend mammal fauna, particularly the lower vertebrate component (Albright 1994), clearly indicates a forested subtropical to tropical coastal lowland paleoenvironment. This affords a rare view of an Arikareean environment that is almost the antithesis of the dry upland ecologies represented by the Great Plains assemblages historically used to typify the Arikareean. Similar settings are indicated for the Florida Arikareean, which may have been subjected to additional endemism by isolation from the mainland by the Gulf Trough. An additional difficulty in placing these assemblages chronologically is the lack of biostratigraphic typification of the medial part of the Arikareean in the Great Plains, a topic we have raised elsewhere that is also discussed later in this chapter. For these reasons correlation of Gulf Coast assemblages with typical Arikareean faunas has been uncertain. However, some taxa in these faunas have broader ecological tolerances and hence larger geographic ranges that provide points of comparison with the midcontinent.

The Cedar Run Local Fauna, previously discussed by Tedford et al. (1987:176) and revised by Albright (1998a), contains Palaeolagus, Palaeocastor, Pseudopalaeocastor, Daphoenodon notionastes, ?Anchippus, ?Miohippus ("Archaeohippus"), Nexuotapirus, Diceratherium, and two species assigned to Prosynthetoceras, as in the Toledo Bend Local Fauna. In addition, Wang et al. (1999:66) found Phlaocyon minor at Cedar Run. In the Great Plains comparable genera occur in the correlated "Monroe Creek" and "Harrison" formation sites in southwestern South Dakota, with first occurrences of Pseudopalaeocastor (Martin 1987, for P. barbouri Peterson 1905) in the "Harrison" and Nexuotapirus in the "Monroe Creek." The White River holdovers, Palaeolagus and Palaeocastor, last occur together in the "Monroe Creek." Diceratherium (as D. annectens) has a long range in the Arikareean, and the species was described from the Middle John Day.

Albright (1998a) correlated the Cedar Run Local Fauna with the larger Toledo Bend Local Fauna obtained near the Sabine River, Newton County, Texas, just west of the Louisiana border. They share *Daphoenodon notionastes*, possibly *Anchippus* and *Archaeohippus*, *Nexuotapirus*, Diceratherium, Prosynthetoceras orthrionanus, and Prosynthetoceras texanus. Significant additions in the Toledo Bend Local Fauna are Neatocastor, Protospermophilus, Proheteromys (two endemic species), Texomys, Moropus, Dinohyus, "Cynorca," Arretotherium acridens, Nothokemas (Albright 1999b), and Nanotragulus. There are no identified White River relicts. Albright (1999b) pointed out that the occurrence of Daphoenodon, Moropus, Diceratherium, and Nanotragulus limited the fauna to the Arikareean. The presence of Gulf Coast endemic genera Texomys, Anchippus, Nothokemas, and Prosynthetoceras has little biochronologic significance in this context, so the weight of evidence for the age of this assemblage rests with zoogeographically more widespread taxa such as Daphoenodon (although D. notionastes is more primitive than D. superbus and has not been recognized outside of the Gulf Coast); Diceratherium (as D. annectens and D. armatum); Moropus (a species much smaller than M. elatus of the Great Plains late Arikareean, approximating the John Day M. oregonensis; see Coombs et al. 2001), very rare in the early Arikareean of the Great Plains (M. elatus-sized phalanges are known from Muddy Creek, Wyoming; Coombs 1978:9); Nexuotapirus marslandensis, which ranges through the Arikareean into the earliest Hemingfordian (it is only distantly related to prior and contemporary North American tapirs [e.g., *Miotapirus*] and may be an immigrant); *Arretotherium* (compared with A. acridens but not sufficiently distinguished from early Arikareean A. leptodus); and Nanotragulus (possibly close to N. ordinatus, which has a late Arikareean range in the northern Great Plains, succeeding N. loomisi of the early Arikareean). These taxa imply that the Toledo Bend Local Fauna, like that from Cedar Run, could lie in the medial Arikareean position advocated by Albright (1999b).

Florida (Y) Substantial advances have been made in the discovery and description of Arikareean faunas from central Florida, clarification of the age and composition of Barstovian assemblages of northern Florida, and further analysis of the faunal succession in the Bone Valley and correlative faunas of southern Florida.

In a recent review of Arikareean mammal faunas of Florida from the perspective of the Toledo Bend Local Fauna of easternmost Texas, Albright (1998a) assembled a relative Arikareean sequence based on the mammals with reference to the Great Plains. Albright (1999b) reaffirmed this sequence. One of the oldest Florida Arikareean assemblages is the Cow House Slough Local Fauna, from deposits filling the karst developed on the Tampa Limestone Member of the Arcadia Formation. This local fauna was first discussed by Morgan (1993) and later revised by Hayes (2000). It includes Centetodon, Megalagus, Agnotocastor, Arikareeomys, Proheteromys (three species), an entoptychine, Miohippus, "Cynorca," Phenacocoelus, and cf. Nothokemas. As Albright (1998a) points out, the joint association of Centetodon, Megalagus, and Agnotocastor implies an early Arikareean age for these holdover taxa from the White River Chronofauna. To this may be added the species of Proheteromys that represent post-White River taxa and the voderomyine Arikareeomys (Morgan 1993; the "new large eomyid" of Albright 1998a, not listed by Hayes 2000) typified by material from the McCann Canyon Local Fauna of northcentral Nebraska, held by Korth (1992) to be of great "homotaxial similarity to the Monroe Creek Fauna of South Dakota." Isotopic ages using 87Sr/86Sr from mollusks in the fossiliferous fissure containing the Cow House Slough Local Fauna range between 25 and 26 Ma, thus yielding a maximum age for the fauna (Jones et al. 1993).

Hayes (2000) recently described another early Arikareean fauna from the central Florida karst that is more diverse than the Cow House Slough Local Fauna. It is a composite of five sites, closely associated geographically. This assemblage is known as the Brooksville 2 Local Fauna, and like Cow House Slough it contains Centetodon, Megalagus, and Agnotocastor. These White River holdovers are joined by *Parvericius* (or *Amphechinus*); Proheteromys; an entoptychine; Palaeogale; two endemic musteloids; the canids Phlaocyon, Enhydrocyon cf. pahinsintewakpa, and Osbornodon; the horse Miohippus; and the artiodactyls Phenacocoelus, Nothokemas, and Nanotragulus loomisi. The canids, oreodont, and Nanotragulus again point to an early Arikareean age for the Brooksville 2 Local Fauna. Hayes opted for a "medial" Arikareean age for Brooksville 2 and its correlate Cow House Slough but admitted that they lie in an "undefined biochronologic interval" that lacks typification in the Great Plains reference section. Note that the "Brooksville Fauna" of Tedford et al. (1987) is a younger assemblage tentatively correlated with the Buda Local Fauna.

The White Springs Local Fauna (Morgan 1989 and pers. comm., 2002) of northernmost Florida is important in being a near-shore assemblage with a diverse and abundant shark, ray, and dugongid fauna. The associated land mammals include *Megalagus*, cf. *Neatocastor*, *Arikareeomys*, *Protosciurus*, *Heliscomys*, *Leidymys*, *Anchippus*, *Mesoreodon*, cf. *Oxydactylus*, cf. *Gentilicamelus*, and *Nothokemas* cf. *waldropi*. This fauna, like that of Cow House Slough, contains White River relicts (*Megalagus*, *Heliscomys*) but differs significantly in some taxa (*An*- *chippus texanus* and *Neatocastor*; Korth 1996a), whose previous records have been considered later Arikareean. Jones et al. (1993) obtained a ⁸⁷Sr/⁸⁶Sr date of 24.4 Ma on mollusk shells at the White Springs Local Faunal level. Both Albright (1998a, 1999b) and Hayes (2000) show the White Springs Local Fauna as younger than Cow House Slough and Brooksville 2.

In Albright's (1998a, 1999) and Hayes's (2000) estimation, the Franklin Phosphate Pit No. 2 and Buda local faunas are correlatives. Of these the Buda Local Fauna, principally described by Frailey (1979), is the larger assemblage. This fauna has been revised by Albright (1998a), and other taxonomic modifications have been provided by systematic studies. It includes Centetodon, Parvericius, Texomys, Arikareeomys, Proheteromys (two species, including P. cf. magnus as at White Springs and SB-1A), Daphoenodon notionastes, Phlaocyon achoros (Wang et al. 1999), Cynarctoides lemur (Wang et al. 1999), Cormocyon cf. copei (Wang et al. 1999), a nimravid, Moropus cf. oregonensis, Cynorca, Phenacocoelus, Nothokemas, and Nanotragulus loomisi. Many of these taxa are endemic to the Gulf Coast, some representing White River relicts (e.g., Centetodon and the nimravid). Nanotragulus loomisi has a Great Plains range confined to latest White River through Monroe Creek, where it is succeeded by Nanotragulus ordinatus in the Harrison. The Buda Local Fauna is compositionally much like the Toledo Bend and Cedar Run faunas of coastal Texas in the continued presence of White River relicts (Centetodon) and taxa antecedent to later Arikareean forms (Texomys, Daphoenodon, and Moropus). The Franklin Phosphate Pit No. 2 of Simpson (1930) in northern Florida previously mentioned (Tedford et al. 1987) is regarded as equivalent (Albright 1999b).

The fauna of the SB-1A site (also known as the Live Oak site) is derived from conglomeratic sands, resting on the marine early Oligocene Suwanee Limestone of northern Florida. The local fauna lacks marine or aquatic vertebrates but contains taxa similar to those of the Buda Local Fauna, including Protosciurus, Arikareeomys, Proheteromys, Mammacyon cf. obtusidens, Phlaocyon leucosteus (Wang et al. 1999), "Paroligobunis" frazieri, Palaeogale, and Nothokemas waldropi. The rodent fauna is basically like the Florida faunas previously discussed, and the carnivores also suggest an earlier Arikareean age. Phlaocyon occurs in the Great Plains before the Harrison Formation, "Paroligobunis" frazieri is an earlier form preceding the late Arikareean species of Megalictis from the Great Plains, Palaeogale is similar to the Arikareean species of the genus, and Mammacyon obtusidens does not occur in the late Arikareean. Locality SB-1A also has

Daphoenodon notionastes (Hunt, pers. comm., 2001), as at the Buda and Franklin Phosphate Pit No. 2 sites. Thus the SB-1A Local Fauna appears similar in age to the Buda Local Fauna and Gulf Coast correlatives.

MacFadden (1980) described the Martin–Anthony oreodont site and overlying strata containing a few terrestrial mammal remains. The terrestrial elements accompanied dugongs and turtles in an estuarine sequence. Marine invertebrates accompanying the oreodont *Phenacocoelus typus* ("*P. luskensis*" of MacFadden 1980) have been ⁸⁷Sr/⁸⁶Sr dated to 24.6 Ma (Jones et al. 1993), remarkably close to the date for the White Springs Local Fauna. The holotype of this oreodont taxon occurs in the upper part of the type Monroe Creek Formation of Nebraska (Hunt 1985), and the taxon ranges into the Harrison Formation in the northern Great Plains. A similar oreodont is also present in the Buda Local Fauna, here deemed slightly younger than White Springs.

The overlying siliciclastics ("Hawthorne Formation" of MacFadden 1980, now Penny Farms Formation of the Hawthorn Group) contain the Martin–Anthony Local Fauna, whose land mammals include (Albright 1998a) *Mammacyon* (*"Temnocyon,"* Albright 1998a; reidentified by Hunt 1998), *Menoceras arikarense*, and a "small new genus and species" of camelid. The latter unnamed taxon was described by Frailey (1979:151–154) from the Buda Local Fauna and has also been recognized (Albright 1998a) in the White Springs, Franklin Phosphate Pit 2, and Cow House Slough faunas.

The Gulf Coast Arikareean sites have been difficult to place precisely in time mainly because of the lack of correlative faunas in the Great Plains and the zoogeographic and ecologic peculiarities of the John Day sequence, whose radioisotopic calibration indicates that it covers the interval in question. As a first step we have tried to deduce the relative sequence of the Gulf Coast assemblages. Second, we have accepted the 24 Ma strontium age for the White Springs Local Fauna as a calibration point.

If this is credible, the sequence is marked by three features: upward extension of range zones of members of the White River Chronofauna, in dwindling numbers through the reconstructed sequence; presence of several Great Plains Arikareean taxa whose records begin in the late early Arikareean (Ar2) but do not occur in the late Arikareean (Ar3) of the plains; and downward extension of species in genera whose oldest Great Plains record is late Arikareean (Ar3). These include two immigrants, *Menoceras* and *Moropus*; an important member of the Ar3 characterizing fauna, *Daphoenodon*; and such Gulf Coast endemics as *Texomys* and *Prosynthetoceras* better known in younger deposits. Bryant et al. (1992) obtained a 87 Sr/ 86 Sr date on mollusks just below the site producing the Seaboard Local Fauna in the lower Torreya Formation of northern Florida (Olsen 1964; Tedford et al. 1987). The date, 18.4 ± 1.0 Ma, provides the only isotopic indication of the age of the Seaboard Local Fauna and its correlative Thomas Farm Local Fauna. The limits of this date overlap those provided by the same method at the Pollack Farm site in Delaware and suggest equivalence with the Runningwater faunas of the Great Plains.

Important new data are now available for faunas from north Florida that come from the upper or Dogtown Member of the Torreya Formation. The marine Torreya Formation provided a correlation with planktonic foraminiferal zones in our previous work (Tedford et al. 1987:179). This evidence has been reviewed and extended by ⁸⁷Sr/⁸⁶Sr ages and magnetostratigraphy by Bryant et al. (1992) and the fauna revised by Bryant (1991). The Midway and Quincy faunas of the northern Florida fuller's earth mines were treated together by Tedford et al. (1987). The Quincy Local Fauna contains only "Merychippus" gunteri as a land mammal. Bryant (1991) has shown that this taxon has a longer stratigraphic range in the Torreya, so the age of that local fauna is not constrained on that basis. The Midway Fauna (s.s.) has a larger suite of nonmarine mammals that appear to represent a younger fauna than the medial Hemingfordian Thomas Farm Local Fauna of central Florida.

Bryant (1991) was able to lithologically correlate local quarry exposures in northern Gadsden County over several kilometers and thereby relate fossiliferous levels into a coeval fauna, the Willacoochee Creek Fauna. This assemblage contains the following nonmarine mammals: Lanthanotherium, Mylagaulus, ?Protospermophilus, Perognathus, Proheteromys, Copemys, Cynorca, Ticholeptus, Bouromeryx, Rakomeryx, ?Blastomeryx, Anchitherium clarencei, "Merychippus" gunteri, "Merychippus" primus, Acritohippus cf. isonesus, ?Aphelops, and a possible proboscidean (not in situ or from the better-sampled sites). This fauna has several wide-ranging taxa whose biochrons are well known from the midcontinent to the West Coast, supporting an early Barstovian age with range extensions needed only for A. clarencei and "M." primus. If verified as a part of this fauna, the mastodont would constitute the earliest Florida occurrence of proboscideans (early Barstovian).

Strontium isotope age estimates between 14.7 ± 1.5 and 16.6 ± 1.0 Ma were obtained from mollusk shells in the fossil vertebrate-containing strata within the Dogtown Member of the Torreya Formation. A magnetostratigraphic study, including the fossiliferous interval produc-

ing the Willacoochee Creek Fauna, showed that the interval is entirely reversed and probably correlates with the distinctive long reversed portion of chron C5B (16.2–15.3 Ma; Berggren et al. 1995). All these data are compatible with calibrations of the early Barstovian interval elsewhere. The strong relationship of the Willacoochee Creek Fauna with correlatives in the midcontinent is echoed by the coeval Trinity River Local Fauna of the Texas Gulf Coast and represents a feature of the zoogeographic relationships of these and younger Miocene faunas of the Gulf Coast.

Barstovian and Clarendonian assemblages lately have been found in the top of the Arcadia and base of the overlying Peace River Formation of the phosphate mining district of southern Florida (Morgan 1993). These assemblages help to fill a previous gap in the Florida sequence between the Hawthorn Group and "Alachua Clays" of the older literature. All these assemblages have a strong affinity with correlates in midcontinental North America.

The stratigraphically oldest is the Bird Branch Local Fauna, for which only *Copemys* and teeth of *Acritohippus* cf. *isonesus* (Hulbert and MacFadden 1991, figure 9A–B) are known, both compatible with early Barstovian faunas elsewhere. Above this level, in the top of the Arcadia or base of the Peace Valley formations, lies the Sweetwater Branch Local Fauna (the fauna of Unit 1 of Webb and Crissinger 1983), which includes a small mustelid, *"Merychippus" goorisi; Merychippus* cf. *brevidontus*, a "parahippine"; a rhino, cf. *Peraceras hessei;* a camelid; and a dromomerycid, cf. *Bouromeryx* (Hulbert and MacFadden 1991:37–39, figure 9B–I). This assemblage can be correlated with the Trinity River Local Fauna of the Texas coastal plain and with early Barstovian assemblages in the midcontinent.

The lower part of the Peace River Formation yields the Bradley Fauna (the fauna of units 2–3 of Webb and Crissinger 1983) of early late Barstovian age, which contains the horses *Megahippus*, *Protohippus perditus*, *Pliohippus mirabilus*, and *Calippus proplacidus*; the dromomycid *Procranioceras* cf. *skinneri*; *Zygolophodon*; and a gomphothere near *Gomphotherium calvertensis* of the Atlantic coastal plain. The Agricola Fauna of early Clarendonian age (the fauna of unit 5 of Webb and Crissinger 1983) contains the borophagine *Epicyon*; the horses *Hypohippus affinis*, *Protohippus supremus*, *Calippus martini*, *Cormohipparion occidentale*, and *Pseudhipparion curtivalum* (Hulbert 1988a, 1988b); the rhino *Teleoceras*; and the protoceratid *Synthetoceras*, all taxa with geographic ranges that include the Great Plains.

Recent additions to the Palmetto Fauna ("Upper Bone Valley Fauna" in Tedford et al. 1987) have elucidated some

elements of this late late Hemphillian fauna in the Gulf Coastal Plain. Description of *Eocoileus gentryorum*, one of the earliest cervids in North America, clarifies its relationships to other odocoileines and indicates that more than one such genus immigrated to North America (Webb 2000). The presence of *Miopetaurista*, previously known from the late Blancan of Florida, indicates this large flying squirrel as a latest Hemphillian immigrant from Eurasia. The Palmetto Fauna is noted for holding over several lineages that evidently survived in the Gulf Coastal Plain after they had disappeared from the High Plains. Examples include *Cormohipparion emsliei*, *Pseudhipparion simpsoni*, *Kyptoceras amatorum*, the last of the protoceratids, and *Pseudoceras*, the last North American gelocid.

Atlantic Coast (Z) Tedford and Hunter (1984) tried to use the association of terrestrial mammals in near-shore marine deposits as a tool to compare marine–nonmarine correlations of the eastern seaboard. For this purpose they reviewed the available data known at that time, particularly those of the historic sites in the Kirkwood Formation of New Jersey and the Calvert and overlying Choptank formations of Maryland and Virginia. These results were discussed only briefly by Tedford et al. (1987). Since that time important new analyses of the mammalian biostratigraphy of the Calvert and Choptank strata have been advanced, and a very important new site in Delaware has greatly improved our knowledge of the early to middle Miocene of the Atlantic coastal region.

Peccaries are the most common fossil mammals in the Calvert Formation faunas. Wright and Eshelman (1987) reviewed this record and on that basis proposed a more detailed biostratigraphy for the containing rocks. Tedford and Hunter (1984) had combined the mammal remains from the upper (Plum Point Marl Member) of the Calvert Formation (Shattuck 1904, Beds 10, 13–15) and the basal strata of the overlying Choptank Formation as a coeval Chesapeake Bay Fauna. Wright and Eshelman (1987) have shown that there is a biostratigraphic sequence of tayassuid taxa through this interval. Following their lead, we present the following bed-by-bed analysis in ascending order:

Bed 10 (Calvert Formation): *?Cynarctus marylandica* (Wang et al. 1999), and *Cynorca proterva*

- Bed 12: *Cynorca proterva*
- Bed 13 or 14: *Gomphotherium calvertensis* (Gazin and Collins 1950), holotype
- Bed 14: "Prosthennops" xiphodonticus

Bed 14 or 15: ?Aphelops sp.

Bed 17 (Choptank Formation): cf. *Gomphotherium calvertensis*, "*Prosthennops*" *niobrarensis* ("*Hesperhys*" of Gazin and Collins 1950)

The remainder of the Chesapeake Bay Fauna, including taxa identified by C. D. Frailey from collections made since Gazin and Collins (1950), cannot be stratigraphically allocated. These include *Amphicyon, Tapiravus* cf. *validus* (holotype from the Shiloh Local Fauna, Kirkwood Formation of southern New Jersey, probably of early Miocene age; Emry and Eshelman 1998), *Archaeohippus, "Merychippus,"* a dromomerycid, and *?Aepycamelus.* Wright and Eshelman (1987) compared the Calvert and Choptank peccary taxa with the midcontinent biostratigraphy of these forms to indicate that Bed 10 was early Barstovian, Bed 14 early late Barstovian, and Bed 17 late late Barstovian. Thus the earliest evidence of gomphotheres on the east coast lies in the early part of the late Barstovian.

Overlying the Choptank Formation in Maryland is the St. Mary's Formation, whose basal sands, the Little Cove Point Unit (Blackwelder and Ward 1976), produced a jaw of *Cormohipparion* and a glauconite K–Ar date of 12.3 \pm 0.5 Ma (Blackwelder 1981) that limits the underlying Choptank to the late Barstovian.

The Pollack Farm site in Kent County, central Delaware, was discovered in 1991, while the enclosing rocks were being quarried for building materials. The land mammal remains, grouped as the Pollack Farm Local Fauna (Emry and Eshelman 1998), were obtained from spoil piles and in situ so that the fauna can be confidently assigned to the lower shell bed of the deltaic Cheswold Sand unit of the lower Calvert Formation. The terrestrial mammals include Anchitheriomys, "Monosaulax" (cf. Neatocastor), Proheteromys magnus, Plesiosminthus, "?Hemicyon" (cf. Phoberocyon), Amphicyon, Cynelos, Paracynarctus kelloggi (Wang et al. 1999), Metatomarctus canavus (Wang et al. 1999), Archaeohippus cf. blackbergi, Anchitherium, Parahippus leonensis, cf. Tylocephalonyx, Cynorca sociale, and Blastomeryx galushai. This assemblage has a strong resemblance to midcontinent faunas of early Hemingfordian age; the only Gulf Coast taxa are the horses, but that may reflect the lack of knowledge of the taxonomic status of the midcontinent equid fauna of this age. Strontium isotopic age estimates from shells in the lower shell bed range from 17.8 to 18.2 Ma, with a mean of 17.9 \pm 0.5 Ma (Jones et al. 1998). This is slightly younger than the paleomagnetically established local upper limit of the Runningwater Formation of western Nebraska (18.0 Ma; MacFadden and Hunt 1998) but in agreement with the estimated age of the upper Runningwater Formation, which probably extends from 17.5 to 18.0 Ma (Hunt, pers. comm., 2001).

Emry and Eshelman (1998) reevaluated the ages of the Shiloh and Farmingdale faunas of New Jersey in light of new stratigraphic and geochronologic information (see also Benson 1998). Subsurface tracing of the Shiloh Marl from its outcrops to the Pollack Farm site shows that it stratigraphically underlies the Pollack Farm Local Fauna (separated by a disconformity fide Benson 1998), so that the holotype of *Tapiravus validus* (Marsh 1871) is not correlative with the Pollack Farm or Chesapeake Bay assemblages (the latter *contra* Tedford and Hunter 1984). Sugarman et al. (1993) give strontium isotope estimates of 20.0 to 20.3 Ma for the Shiloh Marl, clearly late Arikareean dates (MacFadden and Hunt 1998).

The Farmingdale Fauna from the basal Kirkwood Formation of central New Jersey, placed in the early Hemingfordian by Tedford and Hunter (1984), is more properly dated to the late Arikareean on the joint occurrence of Diceratherium and Menoceras, as pointed out by Emry and Eshelman (1998). The fauna, assembled from sites at and near Farmingdale, Monmouth County, New Jersey, was described by Marsh in the nineteenth century: Diceratherium matutinum (Marsh 1870), Daeodon leidyanum (Marsh 1893), and Hesperhys antiquus (Marsh 1870), to which have been subsequently added (AMNH collection) Menoceras cf. arikarense, Anchitherium, and Prosynthetoceras. Strontium isotopic estimation of age from nearby boreholes penetrating the base of the Kirkwood give values of 19.2–22.6 Ma (Sugarman et al. 1993), in good agreement with dated ash beds and magnetostratigraphy for the type Harrison Formation of western Nebraska (MacFadden and Hunt 1998).

BIOCHRONOLOGY

In the 1987 report the nature and methods of typification of the North American mammal ages were discussed in their historical context and in light of the refinements that were possible at that time. The present review has marshaled more evidence for the faunal succession in various parts of North America, which leads in some instances to better biostratigraphic documentation of the faunal sequence, augmented by improved taxonomic resolution. In addition, a rapidly growing body of geochronologic data is available from ash dating and element comparison accompanied by comprehensive magnetostratigraphies relating fossil mammal occurrences to the radioisotopic and Geomagnetic Polarity Time Scale (GPTS). It is possible to correlate distant biostratigraphies on these physical bases to test biological correlations and to better place events in geologic time.

The accumulated evidence, once again, allows a rough delineation of zoogeographic provinces characterized by contrasting but contemporaneous faunal compositions. This is particularly true of the Hemingfordian through Barstovian interval, where magnetic data from the Great Plains to West Coast allow such precise correlation.

This review has also reinforced the existence and faunal distinction of later Cenozoic chronofaunas and provided data on their assembly, acme, and decline. Webb (1983) has traced the history of the Miocene Chronofauna and, in a more general treatment (Webb and Opdyke 1995), has further delineated the chronology and succession of such events in the Oligocene and Miocene and tried to show that aspects of their history seem to relate to global climatic change. In a related treatment, Woodburne and Swisher (1995) have examined faunal change, particularly the episodes marked by immigration, in terms of sea level history. In this work we refine the chronology and nature of these events in terms of the revisions now possible and show that chronofaunal turnover occupies a span of time during which the previous assemblage is replaced by extinction and the elevated evolution of new autochthones as new allochthonous taxa ("immigrants") are added.

Dawson's (1999) recent analysis of dispersal of Miocene land mammals between Eurasia and North America provides a critique of the taxa chosen in 1987 to define the mammal ages and their subdivisions. We have accepted this timely advice for the most part but depart when we believe the evidence is secure. In the recognition of allochthones we place particular weight on their phyletic isolation from comparable taxa in the contemporary and preceding autochthonous faunas. A penetrating analysis of the relationship of New and Old World Miocene insectivores and rodents by Engesser (1979) rejected most previous claims of allochthonous status where he detected morphologic differences between the presumed vicars. He attributed the similarity of the putative Old and New World vicars to parallel evolution involving similar adaptive trends and conservation of primitive features. These hypotheses deserve testing by more detailed phyletic analysis and serve as a warning regarding facile assumptions of close affinity demanded by the hypothesis of dispersal. A summary of the defining taxa proposed here for each mammal age and their subdivisions is presented in figure 6.3.

Typology still plays a controlling role in determining the temporal span of the NALMAs such that the limits set by Wood et al. (1941) are not significantly compromised. Evidence discussed in 1987 and in this revision certainly suggests striking turnover events more suitable for biochronologic boundaries, but these must be subordinated to the traditional limits of each age to avoid wholesale revision of the content of every NALMA. Following Woodburne and Swisher (1995) we designate subdivisions of each NALMA by numbered intervals preceded by an abbreviation for the mammal age.

ARIKAREEAN

This NALMA was equated with the limits of the Arikaree Group as "redefined by Schultz (1938), but including the Rosebud" (Wood et al. 1941:11). In these terms the Arikaree (and Arikareean) was originally confined to the Gering, Monroe Creek, and Harrison formations of northwestern Nebraska and their postulated equivalent in adjacent South Dakota, the Rosebud Formation of Matthew and Gidley (1904).

In faunal terms the Arikareean included the total faunal content of the Arikaree Group so defined but with "Agate [i.e. Agate Springs Local Fauna] being [the] most typical locality" and the "John Day (in part)" as a "principal correlative" (Wood et al. 1941:11). However, the faunal characterization ("Index fossils" and "First appearances") listed mainly taxa drawn from the Harrison Formation, and the "Last appearances" were taxa characteristic of the assemblages of the Gering, Monroe Creek, and Lower Rosebud strata.

Modification of the limits of the stratal span of the Arikareean has since been proposed. At the base, the age now includes the fauna of the uppermost member of the Brule Formation ("Brown siltstone" unit of Swinehart et al. 1985) of the White River Group, a unit included in the Gering Formation by Vondra et al. (1969), whose lithostratigraphy was the basis of Martin's (1973) pioneering study of the "Gering Fauna." The detailed biostratigraphic and geochronologic study of the Brown Siltstone and overlying Gering and of correlative Sharps Formation strata discussed earlier now provides a more secure basis for a faunal definition and characterization of the early Arikareean.

Faunas representing the earliest phase of the Arikareean (Ar1) combine elements of both the White River Chronofauna and new taxa arising by evolution and immigration that increase faunal diversity. Study of this early phase by Tedford et al. (1996) has modified the definition and characterization of the early Arikareean. The Arikareean is now defined by the earliest appearance of a single immigrant, the zapodid rodent *Plesiosminthus*.



FIGURE 6.3 Chronology used in this chapter. Epoch boundaries and chronologic scale follow Berggren et al. (1995). North American land mammal age (NALMA) boundaries as proposed in this work are denoted by solid lines where well calibrated, dashed where approximately located. Allochthonous genera represent taxa exotic to the North American fauna. They are regarded as immigrants that have their oldest records as indicated. This figure supersedes figure 6.3 of Tedford et al. (1987).

The age is characterized by the earliest appearance in the Great Plains of autochthonous taxa including the beavers *Capacikala* (*C. gradatus*) and *Capatanka* (*C. cankpeopi*); the oreodonts *Sespia* (*S. nitida*) and *?Mesoreodon* (*?M. minor*); the hypertragulid *Nanotragulus* (*N. loomisi*) and within the interval, but not necessarily in its oldest phase, the appearance of the primate *Ekgmowechasala*; the erinaceid *Ocajila*; the talpid *Scalopoides*; the murid *Paciculus* (*P. woodi*); the rodent families Mylagaulidae (Promylagaulinae) and Aplodontidae (*Niglarodon*); the hesperocyonine canid *Enhydrocyon* (*E. pahinsintewakpa*); the entelodont *Dinohyus*; the oreodont *Megoreodon* (*M. grandis*); and the stenomyline camel *Miotylopus*.

Confined to the early early Arikareean (Ar1) are the limited occurrences of the rabbit *Palaeolagus hypsodus*, the beaver *Palaeocastor nebrascensis*, the florentiamyid *Kirkomys* (*K. schlaikjeri*), and the hesperocyonine canids *Cynodesmus* (*C. martini*) and *Shunkahetanka* (*S. geringensis*). Correlative faunas of the John Day Formation are bracketed by the AB Tuff (29.75 \pm 0.02 Ma) and Deep Creek Tuff (27.89 \pm 0.57 Ma). These John Day strata indicate first appearances of the following additional autochthonous genera: the rabbit *Archaeolagus* (*A. ennisianus*); the aplodontids *Allomys, Meniscomys*, and *Alwoodia* (*A. magna*); the entoptychine *Pleurolicus* (*P. sulcifrons*); the oreodont *Oreodontoides* (*O. oregonensis*); and the *Hypertragulus* subgenus *Allomeryx* (*A. planiceps*).

Last occurrences in the early early Arikareean (Ar1) of the Great Plains include such White River genera as Agnotocastor, Palaeocastor, Eumys, Hyaenodon, Eusmilus, Hesperocyon, Cynodesmus, Protapirus, Hyracodon, Elomeryx, Leptochoerus, Perchoerus, Chaenohyus, Hypertragulus, Leptomeryx, Hypisodus, and Agriochoerus. In the John Day Formation Agriochoerus, Leptomeryx, and Hypertragulus persist into younger strata, and in the Gulf Coast Agnotocastor and Palaeocastor also persist.

Additional taxa appear in lower Arikaree strata above the basal Gering and correlative strata in the Great Plains (Tedford et al. 1996). These can be used to define and characterize a second phase in the early Arikareean (Ar2): the late early Arikareean. This phase is defined by the first appearance of allochthonous taxa: the erinaceids *Amphechinus* and *Parvericius* and the brachyericine *Metechinus*, the Ochotonidae (*Gripholagomys*; Green 1972), the aplodontid *Parallomys*, the eomyid *Pseudotheridomys*, and the mustelid *Promartes*. Accompanying these in the Great Plains are the first appearance of such autochthones as the leporid *Archaeolagus* (*A. cf. ennisianus*); the beaver *Fossorcastor* (*F. fossor* and *F. brachyceps*); the promylagaulines *Trilaccogaulus* and *Promylagaulus*; the aplodontid *Alwoodia* (*A. harkseni*); the entoptychines *Entopty*- chus, Pleurolicus, and Gregorymys; the florentiamyids Fanimus and Florentiamys; the amphicyonid Mammocyon; the tapir Nexuotapirus; the peccary Cynorca; the anthracothere Arretotherium; the oreodonts Oreodontoides (O. oregonensis) and Promerycochoerus; and the camel Stenomylus. In the Gulf Coast such taxa as Daphoenodon and Prosynthetoceras have their first appearances in the later part of the Ar2 interval but achieve larger ranges in late Arikareean and Hemingfordian time.

Last occurrences in the late early Arikareean (Ar2) of the Great Plains include forms that do not occur in the Harrison Formation (ca. 23 Ma) after a hiatus in the local record of nearly 3 m.y. These include the remaining White River taxa: the Nimravidae (*Nimravus*), the Proscalopidae (*Proscalops*), the Geolabididae (*Centetodon*), the Palaeolaginae (*Palaeolagus*), the Eutypomyidae (*Eutypomys*), and the Yoderomyinae (*Arikareeomys*), as well as the florentiamyid rodents *Sanctimus* and *Hitonkala*, the cricetine *Geringia*, the promylagauline *Crucimys*, the equid *Mesohippus*, the entelodont *Archaeotherium*, and the leptauchenine oreodonts. In addition, many of the taxa listed as first appearances in the late early Arikareean also do not survive the turnover concealed by the mid-Arikareean hiatus.

In the John Day Formation, the interval from the Deep Creek Tuff (27.89 \pm 0.57 Ma) to the Tin Roof Tuff (25.9 \pm 0.31 Ma) covers the early part of the Great Plains hiatus. Local first appearances during this interval include the entoptychine *Entoptychus*; the oreodonts *Merycoides, Hypsiops (H. brachymelis)*, and *Paroreodon;* and the nothokematine camelid *Gentilicamelus (G. sternbergi)*.

Our reconstruction and calibration of the early Arikareean faunal sequence in the Gulf Coast suggest the continued presence of such White River taxa as *Centetodon*, *Palaeolagus*, and *Palaeocastor* and the presence of such late Arikareean taxa as *Moropus* and *Daphoenodon*, indicating that a phase of turnover to faunas typical of the late Arikareean of the Great Plains was under way by 24 Ma in that region. The Castolon and to a greater extent the Santana Mesa faunas of the Big Bend in Texas are associated with 23 Ma basalts and contain *Merychyus*, early *Ustatochoerus*, *Michenia*, and *Nanotragulus ordinatus*, showing that faunas of late Arikareean (Ar3) were already in place in the continental interior by the earliest Miocene.

We believe that the Florida "medial" Arikareean lies in the Great Plains Arikaree hiatus and therefore carries elements that later typify the late Arikareean at least to 23 Ma, especially the immigrant rhinoceratid *Menoceras* and chalicothere *Moropus*. We use these two taxa to define the earliest late Arikareean (Ar3). Other immigrants have their earliest appearance in the Harrison Formation maximally calibrated to 23 Ma. The following taxa also define the Ar3: the amphicyonid *Ysengrinia*, the ursid *Cephalogale* (Hunt, pers. comm., 2001), and the mustelid *Zodiolestes*.

The late Arikareean as a unit (i.e., Ar3 and Ar4) is characterized by the earliest occurrence of such autochthones as the mylagaulid *Mylagaulodon*; the amphicyonid *Daphoenodon*; the borophagine canid *Desmocyon*; the tapir *Miotapirus*; the horses *Kalobatippus*, *Archaeohippus*, *Desmatippus*, and "*Parahippus*"; the tayassuid *Hesperhys*; the oreodonts *Merycochoerus*, *Ustatochoerus*, and *Merychyus*; the kyptocerine protoceratid *Syndyoceras*; the protolabine camels *Michenia*, *Protolabis*, and *Tanymykter*; and the "oxydactyline" camels *Priscocamelus* and *Oxydactylus*.

The late Arikareean is also characterized by the last occurrence of Gripholagomys; the flat-incisor, burrowing beavers Euhapsis, Pseudopalaeocastor (P. barbouri, incorrectly assigned to a new genus Nannasfiber by Xu 1996), and Fossorcastor (F. fossor, sensu Xu 1996, referred to Palaeocastor by Martin 1987, the Daemonelix burrow maker); most entoptychines and florentiamyid rodents; the canid Cormocyon; the amphicyonids Temnocyon and Mammacyon; the mustelids Zodiolestes and Megalictis; the horse Miohippus; the rhino Diceratherium (may survive into the late Hemingfordian in Panama); the oreodonts Eporeodon, Phenacocoelus, Promerycochoerus, Pseudodesmatochoerus, Desmatochoerus, Hypsiops, Oreodontoides, Paroreodon, Paramerychyus, and Submerycochoerus; the camels Pseudolabis and Miotylopus; the protoceratid Syndyoceras; the hypertragulids Hypertragulus and Nanotragulus; and the leptomerycid Pronodens.

A further subdivision, Ar4, the late late Arikareean (fauna of the Upper Harrison beds, now Anderson Ranch Formation; Hunt 2002), is defined by the first appearance of the immigrant amphicyonid *Cynelos*, the first Moschidae (*Problastomeryx*), the earliest representatives of the Dromomerycidae (*Barbouromeryx*), and Antilocapridae (*Paracosoryx*).

Autochthonous taxa appearing first in the late late Arikareean, Ar4, as shown principally by the fauna of the Upper Harrison and Rosebud (*sensu* Macdonald 1963) beds of the Great Plains include the mylagaulid *Mylagaulodon*, the mustelid *Megalictis*, the equid *Desmatippus*, the oreodonts *Merycochoerus* and *Merychyus arenarum*, the protolabine camels *Tanymykter* and *Protolabis*, the miolabine camel *Miolabis*, and the moschids *Blastomeryx*, *Parablastomeryx*, and *Machaeromeryx*.

The loss of burrowing beavers and representatives of many oreodont clades that rapidly diversified in the early Arikareean, as well as members of other earlier autochthonous lineages, indicates that a major turnover was in progress before the time when younger Arikaree Group rocks began to accumulate in the Great Plains. Limited evidence from the Gulf Coast and Columbia Plateau (John Day) indicates that this change was under way by 24 Ma. This extinction is accompanied by renewed immigration, the true dimensions of which become more evident in the succeeding Hemingfordian, when small mammal faunas also become available. By the close of the Arikareean the remaining autochthonous fauna and the evolving allochthonous clades (Moschidae, Dromomerycidae, and Antilocapridae) formed the core assemblage for the Hemingfordian.

HEMINGFORDIAN

The Hemingfordian of Wood et al. (1941) was "based on the Hemingford Group including the Marsland and, especially, the limited or lower Sheep Creek fauna (Cook and Cook 1933, pp. 38-40), and not on the formation limits as extended upward (Lugn 1939b)." These qualifications demonstrate that the Hemingfordian is not to be equated with the total Hemingford Group of Lugn (1939), but it was still ambiguous with regard to its lower limits because of the confusion regarding Schultz's (1938) original definition of the Marsland Formation. As discussed in more detail in Tedford et al. (1987:185-186), the view we have accepted equates the Marsland Formation as used by Schultz (1938) as a composite made up of two formation rank rock units: the Upper Harrison beds of Peterson (1907, 1909), a name recently replaced by the term Anderson Ranch Formation (Hunt 2002), and the superjacent Runningwater Formation of Cook (1965). Schultz considered Peterson's Upper Harrison beds as roughly equivalent to his "lower Marsland" and Cook's Runningwater Formation as his "upper Marsland." It is clear from the characterizing assemblage of the Hemingfordian given by Wood et al. (1941) that the base of the Hemingfordian was marked by taxa of the Runningwater Formation, not those of the Upper Harrison (containing Agate Springs Quarries, the "typical locality" for the Arikareean; Hunt 1985). These considerations remove the potential typologic overlap between the Arikareean and Hemingfordian.

As noted in Tedford et al. (1987), the typification of the early Hemingfordian (and thus the total NALMA) is based mainly on evidence from the Great Plains, supplemented by Gulf Coast assemblages. Scattered local faunas from the Great Basin and West Coast can be identified as representing the early Hemingfordian. Although they do not contribute much to the biological characterization of the Hemingfordian, they do contribute to its chronology and zoogeography.

An invasion of immigrants defines the beginning of Hemingfordian and hence early Hemingfordian (He1) time. Small mammals become more visible, and the immigrant fauna is more balanced in size range and breadth of adaptation. This event is accompanied by an overall change in sedimentary environment as volcaniclastic aeolian deposits of great lateral extent representing the Arikaree Group give way to coarser epiclastic fluviatile sands and gravels of the Ogallala Group that locally fill deeply incised river valleys containing evidence of more varied ecologies. The Hemingfordian can be defined by the following immigrants: the Soricinae (Antesorex), the Plesiosoricidae (*Plesiosorex*), the ochotonids Oreolagus and ?Desmatolagus, the trogontheriine beaver Euroxenomys, the amphicyonid Amphicyon, the Hemicyonidae (Phoberocyon), the Ursidae (Ursavus earliest certain record), the Procyonidae (Amphictis and Edaphocyon), the Leptarctinae (Craterogale and Leptarctus), the Mustelinae (Miomustela), the Semantorinae (Potamotherium), the Teleoceratinae (Brachypotherium), the Aceratherinae (Floridaceras), and the dromomerycid Aletomeryx.

The early Hemingfordian (He1) is characterized by the earliest appearance of the mylagaulid *Mesogaulus*; the heteromyine *Cupidinimus*; the borophagine canids *Paracynarctus*, *Metatomarctus*, *Euoplocyon*, *Microtomarctus*, and *Prototomarctus* (Wang et al. 1999); the mustelid *Brachypsalis*; the equids *Hypohippus* and "*Merychippus*" ("M." *gunteri*); the peccary *Floridachoerus*; the oreodonts *Merychyus elegans*, *Ticholeptus*, and *Mediochoerus*; the protoceratid *Lambdoceras*; and the camels *Floridatragulus*, *Blickomylus*, and *Australocamelus*.

The early Hemingfordian (He1) contains the limited occurrence of *Amphictis*, *Craterogale*, *Floridaceras*, *Lambdoceras*, *Aletomeryx*, and *Probarbouromeryx* and the latest occurrence of florentiamyine rodents (Korth et al. 1990), *Desmocyon*, *Menoceras*, *Nexuotapirus*, *Kalobatippus*, Entelodontidae, Anthracotheriidae, *Merycochoerus*, *Tanymykter*, and *Stenomylus*.

A striking faunal change takes place between the early and later Hemingfordian, which demonstrates the folly of tying a biochronology to the depositional record. This turnover event is not clearly recorded in any continuously fossiliferous section in North America, perhaps exaggerating the perception of its rate of change. It is particularly well documented in groups that have received phylogenetic study such as canids and equids but seems evident in most well-represented clades and is marked by accelerated cladogenesis and extinction and some immigration. In the borophagine canids (Wang et al. 1999) the event signals the extinction of nearly all Phlaocyonini and primitive Borophagini, accompanied by the origin and fundamental cladogenesis of all later borophagine clades in Cynarctina, Aelurodontina, and Borophagina. The horses (Hulbert and MacFadden 1991) show the early stages of cladogenesis of the Equinae, with both the Equini and Hipparionini in evidence in the late Hemingfordian. Similar events are seen in the Camelidae, Dromomerycidae, and merycodontine Antilocapridae. Chronologically this turnover takes place between the youngest dated early Hemingfordian deposits (about 17.5 Ma for the type area; MacFadden and Hunt 1998; Hunt, pers. comm., 2002) and the oldest dated late Hemingfordian (about 17 Ma for the Barstow sequence; MacFadden et al. 1990), or during a span of about 0.5 m.y.

The late Hemingfordian (He2) is defined by the earliest appearance of the immigrant petauristine squirrel (Petauristodon); the cricetine Copemys (toward the end of the span); the eomyid *Eomys*; the mustelines *Plionic*tis, Dinogale, Sthenictis, and Mionictis; the Felidae (Pseudaelurus); and the rhinos Peraceras, Teleoceras, and Aphelops. It is characterized by the earliest appearance of the rabbit Hypolagus; the beaver Anchitheriomys; the amphicyonid Pliocyon; the Equinae (both Equini and Hipparionini clades, including Merychippus, Protohippus, Parapliohippus, and Acritohippus); the oreodont Brachycrus; the camelids Paramiolabis, Nothotylopus, and Aepycamelus; the dromomerycids Sinclairomeryx, Rakomeryx, Subdromomeryx, Dromomeryx, and Bouromeryx; and the antilocaprids Merriamoceros, Merycodus, Meryceros, and Submeryceros and by the last appearance of Phlaocyon, Metatomarctus, Prototomarctus, Barbouromeryx, Blickomylus, and Oxydactylus.

BARSTOVIAN

Originally the Barstovian had a very local rock and faunal basis ("Barstow Formation, San Bernardino County, California, and specifically on the fossiliferous tuff member in the Barstow syncline and its fauna"; Wood et al. 1941:12), but as discussed previously (Tedford et al. 1987:187–188) this left in limbo a large part of the biostratigraphic section between those containing late Hemingfordian faunas and those designated Barstovian. Tedford et al. (1987) recommended extending the Barstovian to the intervening strata to include the presence of taxa found in the principal correlative faunas (Pawnee Creek, Deep River, Virgin Valley, and Mascall, all reviewed in this and the previous work).

214 Richard H. Tedford, et al.

The Barstovian faunas identified across North America indicate the presence of zoogeographic provinces, especially the northwest, far west, midcontinent, and southeast and, with our extended coverage, into Central America as well. Radioisotopic and paleomagnetic data for faunal sequences scattered across these provinces have linked the Barstovian faunas of the Caliente Formation (California Coast Ranges), Barstow Formation (Northern Great Basin, California), Tesuque Formation (Southern Great Basin, New Mexico), and Pawnee Creek Formation (Northern Great Plains, Colorado) so that their respective biostratigraphies can be compared chronologically with some precision. In addition to some endemicity, diversity changes in space can be documented as previously noted and as briefly explored by Tedford and Barghoorn (1997, figure 10). To a certain extent this partitioning of the mid-Miocene biota of North America presents problems in defining and characterizing the NALMAs and their subdivisions. To this is added the difficulty that there are remarkably few defining taxa noted for this interval.

In addition to these problems, the classic "standard" succession of Miocene faunas from the Great Plains of Nebraska is contained in a rock sequence that is notoriously incomplete, being broken by disconformities inherent in the style of sedimentation in valley-filling epiclastic deposits. There, much of the record is represented by lateral rather than the vertical accretion characteristic of the tectonically active basins of the western part of the continent. Thus the Hemingfordian-Barstovian transition in Nebraska is broken at the contact between the Sheep Creek and Olcott formations, which sharpens the perception of faunal change but does not show its transitional steps. Fortunately the sequences in the Tesuque Formation, New Mexico, and the Barstow Formation, California, contain these spans of time and show local biostratigraphic details.

A general problem in defining these medial Miocene NALMAs is the paucity of immigrant taxa in comparison with those of the early and late Miocene. Reliance on one or two such taxa, often with limited geographic ranges, limits the application of this method of recognition so useful for most NALMAs. This problem is further compounded by the largely anagenetic sequences of autochthonous taxa in this chronofaunal interval so that characterizing faunas are best delineated at the specific rather than at the generic level.

Prominent among the allochthonous taxa suggested to define parts of the Barstovian are the earliest appearances of mammutid and gomphotheriid proboscideans in North America. These events need to be reevaluated ac-

cording to the data summarized earlier. Woodburne and Swisher (1995:347) indicated the presence of the Proboscidea (a tooth fragment, thought to be a mammutid) in the late Hemingfordian Massacre Lake Local Fauna of northwestern Nevada. Recently Reynolds and Woodburne (2001) identified proboscidean trackways in the Barstow Formation of the Calico Mountains, adjacent to the Mud Hills, Mojave Desert, California, that date to about 16.2 Ma, as in northwestern Nevada. These are the earliest known occurrences, but we have noted several other early Barstovian occurrences as well: California Coast Range (North Coalinga Local Fauna) and Sharktooth Hill Local Fauna, Zygolophodon and possibly Gomphotherium, near the Relizian-Luisian boundary, 15.7 Ma; Columbia Plateau (Virgin Valley Fauna and High Rock Lake site, northwestern Nevada, Sucker Creek and Skull Springs faunas of eastern Oregon), Zygolophodon, 15.7-14.7 Ma (note that the Sucker Creek occurrence lies below the Owyhee Basalt, 14.7 Ma contra Tedford et al. 1987); Northern Rocky Mountains (Deep River and Madison Valley faunas), Zygolophodon, 16.2–14.6 Ma by local correlation; and Gulf Coastal Texas and Florida (Burkeville and Willacoochee Creek faunas), undetermined Proboscidea, chron C5Br, 16.2–15.3 Ma. Where the fossil material is well preserved, these early Barstovian remains seem to be largely Zygolophodon sp., or Z. merriami. Thus the record indicates the presence of Proboscidea at the earliest in the late Hemingfordian, and thereafter mammutids are certainly known in the early Barstovian in the northwestern and coastal parts of North America. Confirmed records of gomphotheriids in the continental interior are limited to post-14.8 Ma strata. However, the record of Gomphotherium in Ixtapa, Chiapas, collected from strata located 200 m below a tuff dated as 15-16 Ma, and the North Coalinga specimen would extend the occurrence of such records into the early Barstovian or even late Hemingfordian. At their first occurrence, the Proboscidea are too rare to be used as a defining taxon for the beginning of the late Hemingfordian, and their actual first appearance probably is late in the span, but it may be useful to include Zygolophodon as part of the characterizing fauna of the early Barstovian and to regard the midcontinent appearance of gomphotheriids as an event defining the beginning of the late Barstovian (Ba2) at about 14.5–14.8 Ma.

With all these problems in mind we propose the following revision of the Barstovian. It previously relied on two immigrant taxa for its definition: the hemicyonine *Plithocyon* and the cricetid *Copemys*. Both taxa were found together in the Barstow Formation at the base of the stratal span characterized by the Green Hills Fauna (Steepside Quarry; Woodburne et al. 1990). Subsequent collecting of small mammals from the underlying Rak Division by Lindsay (1995) has carried *Copemys* (and most of the Green Hills rodent fauna) down into the top of the Rak Division and into the base of chron C5Cn2 (16.2 Ma; Berggren et al. 1995), only 164 m below and 0.2 m.y. older than the Steepside Quarry occurrence. This does not substantially change the chronologic position of this defining taxon but does serve as a warning (if one is needed) of the stratigraphic behavior of defining taxa, especially those that are rare or needing special collecting techniques for their detection.

The beginning of Barstovian time, and hence the early Barstovian (Ba1), can be defined by the first appearance of the hemicyonine Plithocyon and the definite occurrence of Zygolophodon. It can be characterized by the first appearance of such autochthones as the mylagaulines Umbogaulus, Pterogaulus, and Ceratogaulus in the Great Plains and Hesperogaulus in the Columbia Plateau (Korth 1999a, 2000); the beaver *Monosaulax* (sensu Korth 1999c); the heteromyid rodents Perognathus, Peridiomys, and Mojavemys; the borophagine canids Cynarctus, Paratomarctus, and in the west Aelurodon, Paratomarctus, Carpocyon, and Protepicyon; the procyonids Probassariscus and Arctonasua; the mustelid Martes; the equids Megahippus, Calippus, and Hipparion; the peccaries Dyseohyus and Prosthennops; the camelids Procamelus and Rakomylus; and the merycodontine antilocaprids Ramoceros and Cosoryx.

The early Barstovian (Ba1) contains the last occurrence of the Promylagaulinae (*Galbreathia*; Korth 1999b), the amphicyonids *Pliocyon* and *Amphicyon*, the Hesperocyoninae (*Osbornodon*), the borophagine canids *Cynarctoides* and *Euoplocyon*, the equids *Desmatippus* and *Parahippus*, the peccary *Cynorca*, the oreodonts *Brachycrus* and *Merychyus*, the camelid *Paramiolabis*, the moschid *Problastomeryx*, the dromomerycids *Subdromomeryx* and *Rakomeryx*, the Stenomylinae (*Rakomylus*), and the antilocaprid *Merriamoceros*. The early Barstovian contains the limited occurrence of *Tomarctus*, *Psalidocyon*, *Tephrocyon*, *Edaphocyon*, *Rakomylus*, *Drepanomeryx*, and *Matthomeryx*.

The beginning of the late Barstovian (Ba2, medial Barstovian *sensu* Voorhies 1990a) is defined by the first appearance of gomphotheriid Proboscidea. Taxonomically identifiable gomphotheriid remains are largely confined to late Barstovian assemblages in North America, and many from California to Maryland, where datable, first occur around 14.8–14.5 Ma. This proboscidean datum is reasonably isochronous in the majority of instances, and we will continue to regard it as the most useful way

to define late Barstovian time, bearing in mind that this definition is also backed up by the characterizing fauna of that span.

Fortunately the Barstovian was based fundamentally on the faunal sequence in an unbroken sedimentary section in the Great Basin, thus avoiding the hiatuses that break the more fossiliferous midcontinent sections that have been so important in determining the faunal diversity of this phase of the Miocene of North America. There is a trade-off here: The Great Basin Barstovian faunas do not display a chronofaunal relationship with those of the Great Plains; rather, they remain at lower diversity and have an endemic character that must reflect important environmental gradients across North America.

There is a gap between the early and late Barstovian faunas of the Great Plains, only partially filled by the faunal sequence in the Pawnee Creek Formation of northeastern Colorado. In Nebraska these phases of the Barstovian are not superposed and are separated from one another by 300 km. The time value of the hiatus between them is difficult to judge, but the late Barstovian sequence in the Valentine Formation of north-central Nebraska must begin shortly before the dated Hurlbut Ash (13.6 Ma) near the base of the unit. This equates on geochronologic grounds with the upper part of the Barstow faunal span in California (about the level of the Hemicyon Tuff, chron C5An, 14.0 Ma). Thus the true biochrons of the taxa first appearing at the base of the Valentine Formation (e.g., the gomphotheriid Proboscidea) may extend into the hiatus, as these proboscideans do elsewhere (14.8 Ma at Barstow, older than 14.6 Ma in New Mexico, 14.4 Ma in Colorado).

Because of the zoogeographic diversity of the Barstovian assemblages involved in defining and characterizing the late Barstovian (Ba2), we indicate with an asterisk the taxa limited to the Great Plains and Gulf Coast provinces. The late Barstovian is defined by the earliest appearance of the Gomphotheriidae, the hedgehogs Lanthanotherium and Untermannerix*, the ochotonids Hesperolagomys and Russellagus*, the limited occurrence of the zapodid Megasminthus*, the mephitine Pliogale, and the amphicyonid Pseudocyon*. The characterizing fauna of Ba2 includes the earliest occurrences of the Leporinae Alilepus and Pronotolagus (Voorhies and Timperley 1997); the mylagauline Mylagaulus (Korth 2000); the beaver Eucastor (E. tortus); the geomyoid Lignimus; the eomyid Leptodontomys; the cricetid Tregomys*; the borophagine canids Cynarctus saxatilis*, Aelurodon (Strobodon)*, and A. ferox*; the ursid Ursavus pawniensis; the amphicyonid Ischyrocyon; the horses Pliohippus (P. mirabilis), Pseudhipparion*, Neohipparion (N. coloradense), and Cormohippar-

216 Richard H. Tedford, et al.

ion; the oreodont Ustatochoerus medius; the moschid Longirostromeryx*; the dromomerycid Procranioceras; and the merycodontine Ramoceros. The late Barstovian contains the last occurrence of the erinaceid Parvericius, the mylagauline Umbogaulus (Korth 2000), the beavers Monosaulax and Anchitheriomys, the ochotonid Oreolagus, the aplodontid Allomys, the zapodid Megasminthus, the Chalicotheriidae (Moropus), the equids Archaeohippus and Anchitherium, the oreodont Ticholeptus, the protoceratid Prosynthetoceras, the Leptomerycidae (Pseudoparablastomeryx), and the dromomerycids Dromomeryx and Bouromeryx.

CLARENDONIAN

The Clarendonian (Wood et al. 1941:12) originally was based on the "Clarendon local fauna (and member?) near Clarendon, Donley County, Panhandle of Texas" and the age limits suggested by the list of principal correlatives, "Burge, Big Spring Canyon, Fish Lake Valley, Ricardo," and also by the correlation chart and glossary entries that constrain the upper limit of the age to the "Minnechaduza local fauna, late Clarendonian or, possibly, early Hemphillian" (Wood et al. 1941:26). Superposed younger faunas from the "Xmas and Kat Quarries, local channel fauna or faunas in the Ash Hollow Formation, later than the Minnechaduza, northeastern Cherry County, Nebraska" (Wood et al. 1941:30), were shown as basal Hemphillian on the correlation chart. Thus in terms of the superposed sequence in north-central Nebraska, the Burge Fauna from the uppermost part of the Valentine Formation delimited the oldest and the Minnechaduza Local Fauna from the lower part of the Ash Hollow Formation was considered the youngest part of the Clarendonian. In his review of the Burge and Minnechaduza faunas, Webb (1969) followed Wood et al. (1941) in including the Burge Fauna in the Clarendonian. He also included the "Leptarctus B" site in his concept of the Minnechaduza Fauna, but in his discussion of the antilocaprine, Plioceros flobairi, from that site, he indicated that "the exact age of material from this quarry is in doubt. Several species indicative of a late Clarendonian age occur, but there are other unusual forms that either indicate a different ecological situation or a younger age. A transitional Clarendonian–Hemphillian age is suggested" (Webb 1969:172-173). Much later, Skinner and Johnson (1984), based on a regional stratigraphic synthesis, separated the rocks above the Cap Rock Member (containing the Minnechaduza Fauna) as the Merritt Dam Member of the Ash Hollow Formation and listed many sites in this unit, including the *Leptarctus* Quarry,

and the Xmas and Kat quarries as containing a post-Minnechaduza fauna. The fauna of these younger deposits has a strong chronofaunal relationship with the Burge and Minnechaduza assemblages. Tedford et al. (1987) included the post–Cap Rock faunas in their concept of the Clarendonian without specific discussion, but their intent was clear from their correlation chart and is followed here.

On the other hand, Tedford et al. (1987:189) excluded the fauna of the Burge Member of the Valentine Formation from their concept of the Clarendonian on the grounds that "the hiatus between the Valentine and Ash Hollow formations is accompanied by perceivable faunal change, and this provides the basis for an objective characterization of the Clarendonian." The Burge Member is separated from adjacent units by disconformities that contain hiatuses that break chronofaunal continuity. In their view the faunal relationships of assemblages from the Burge and older Valentine deposits were more closely related than they were with the Ash Hollow faunas. Also on the matter of definition, always difficult in a span of low immigration, the first appearance of the nimravid Barbourofelis seemed more recognizable (it has a unique skeleton) despite the inherent rarity of carnivores in any fossil assemblage. This genus has been recognized at several sites scattered across the North American midcontinent. On this basis Barbourofelis seemed a plausible defining taxon for the Clarendonian.

Subsequently Voorhies (1990a:142) raised objections to this truncation of the Clarendonian on several grounds. First, the Burge Fauna was originally included in the Clarendonian as a "principal correlative" (Wood et al. 1941). Second, the degree of faunal change between the Burge and Ash Hollow "does not appear to be more remarkable than that which separate the Burge faunas from those collected at lower stratigraphic levels in the Valentine Formation." Third, the presence of Barbourofelis at the base of the Ash Hollow did not seem an intrinsically more useful marker than the presence of the gelocid Pseudoceras at the base of the Burge. Finally, although not strongly advocated, the short Clarendonian of Tedford et al. (1987) is "severely curtailed in stature." Of these arguments the most telling is the typology, which we have otherwise tried to preserve, and the arbitrariness of any change in boundary position within a chronofaunal sequence. The choice of a definitive taxon in this type of faunal sequence usually is subordinate to the characterizing fauna in age determination.

Recent studies of the geochronology of faunal sequences provide means for determining the tempo of faunal change and for estimating the time value of hiatuses that break faunal sequences. In the Mojave Desert region of California, the principal reference sequence for the Barstovian extends upward into deposits lying in chron C5ABn at about 13.4 Ma (in agreement with ash dates at that level). The Ricardo Fauna, "principal correlative" of the Clarendonian, extends downward (as the Burge equivalent Iron Canyon Fauna) into deposits older than 12 Ma and probably 12.5 Ma (magnetostratigraphy and ash dates; Whistler and Burbank 1992; Perkins et al. 1998). The striking turnover implied by this faunal and geochronologic data suggests a major event in western North America contemporaneous with the little-perturbed chronofaunal progression characteristic of the midcontinent. The fauna that emerges from this event in the Great Basin is compositionally like those of the Great Plains Clarendonian. The fact that this break takes place below the Burge-equivalent local faunas at the base of the Ricardo succession is another reason to place the Barstovian-Clarendonian boundary in its typologic position.

We thus return to the typologic boundary for definition of the beginning of Clarendonian time, and for lack of other defining taxa we use the first appearance of the gelocid Pseudoceras for this purpose. It is morphologically distinct in dentition and extends from the northern Great Plains around the Gulf of Mexico and into Honduras but is geographically limited to east of the Rocky Mountains. It is usually rare but has a well-defined biochron-early Clarendonian (Cl1) to late early Hemphillian (Hh2)—and occurs only as a relict in the latest Hemphillian (Hh4) of Florida. The characterizing fauna of the early Clarendonian (Cl1) includes the first appearances of the beavers Eucastor planus and E. dividerus; the gomphotheriids Eubelodon and Megabelodon; the borophagine canids Cynarctus voorhiesi, Aelurodon (Strobodon) stirtoni, and Paratomarctus euthos; the equids Pliohippus pernix, Cormohipparion occidentale, Pseudhipparion retrusum, Protohippus supremus, and Megahippus matthewi; the oreodont Ustatochoerus major (including U. profectus fide Stevens, pers. comm., 2002); and the dromomerycid Cranioceras.

The medial Clarendonian (Cl2) is defined by the reappearance of the Nimravidae (*Barbourofelis whitfordi* and *Barbourofelis osborni*) in North America. It is characterized by the following first appearances of autochthonous clades: the borophagine canids *Borophagus* (*B. littoralis*) in western North America and *Epicyon* (*E. saevus*), *Carpocyon robustus, Aelurodon taxoides*, and *Cynarctus crucidens* in the midcontinent; the equids *Pseudhipparion gratum, Hipparion tehonense, Neohipparion affine*, and *Dinohippus*; the oreodont *Ustatochoerus californicus*; the protoceratid *Synthetoceras*; and the limited occurrence of *Proantilocapra*. A few taxa show last appearances in the medial Clarendonian: the mustelid *Brachypsalis*, the ursid *Hemicyon*, the equids *Merychippus* (s.s.) and *Megahippus*, the rhino *Peraceras*, and the protoceratine *Paratoceras*.

The late Clarendonian (Cl₃) is defined by the first appearance of the shovel-tusk gomphotheriid *Platybelodon*, the ischyrictine mustelid *Hoplictis* (= *Beckia*), and the simocyonine ailurid *Actiocyon*. The characterizing fauna includes the first appearances of the beaver *Hystricops*; the sigmodontine cricetid *Antecalomys*; the marmot *Marmota*; the procyonids *Protoprocyon* and *Paranasua*; the Canini (*Eucyon*); the nimravids *Barbourofelis morrisi* and *Barbourofelis lovei*; the felids *Nimravides thinobates* and *Nimravides galiani*; the equids *Pseudhipparion skinneri*, *Hipparion forcei*, *Neohipparion trampasense*, *Protohippus gidleyi*, and *Calippus cerasinus*; and the antilocaprine *Plioceros*.

The close of the Clarendonian is marked by an extinction event removing a number of taxa characteristic of the medial Miocene. At the same time, new autochthones appear and faunal diversity begins to decline toward the comparatively depauperate assemblages of the late Miocene. The following taxa have their last appearance in the late Clarendonian: the Erinaceidae (Untermannerix and Metechinus); the beaver Eucastor; the sciurids Protospermophilus and Petauristodon; the geomyids Phelosaccomys and Mioheteromys; the eomyid Pseudotheridomys; the cricetine Tregomys; the ochotonids Hesperolagomys and Russellagus; the mustelids Hoplictis and Mionictis; the Amphicyonidae (Ischyrocyon and Pseudocyon); the borophagine canids Aelurodon, Paratomarctus, and Cynarctus; the Anchitheriinae (Hypohippus); the Merycoidodontidae (Ustatochoerus); the miolabine camels Miolabis and Nothotylopus; the Moschidae (Blastomeryx, Parablastomeryx, and Longirostromeryx); the dromomerycid Cranioceras; and the Merycodontinae (Cosoryx).

HEMPHILLIAN

The principal characterization of the Hemphillian shifts to the southern Great Plains, where a sequence was chosen in the "Hemphill Member of the Ogallala, which includes both the Hemphill Local Fauna from the Coffee Ranch Quarry and the Higgins Local Fauna, Hemphill [and Lipscomb] County, Panhandle of Texas" (Wood et al. 1941:12). This was a particularly fortunate choice because superposition of the Hemphill Member on deposits containing Clarendonian faunas is present, as is a fairly detailed biostratigraphic sequence in the Hemphill. Schultz (1990) gives a very useful review of our understanding of this sequence, and with Voorhies's (1990a) discussion of the Nebraska Hemphillian, the biochronol-

218 Richard H. Tedford, et al.

ogy of this interval in the Great Plains has been conveniently reviewed.

The Hemphillian, approximately the late Miocene and a little more than 4 m.y. in duration, is marked by continual loss of autochthonous taxa and by a rising immigration rate marked by the first waifs from South America; diverse rodents, insectivores, and carnivores; and some ungulates from Asia. Most of the remaining elements of the "Miocene" chronofauna are extinct by 6-7 Ma, so the Hemphillian can be conveniently divided by that turnover event, as previously noted (Tedford et al. 1987:191-192). Hemphillian faunas seem more homogeneous in composition across North America than earlier NALMAs, although the Great Basin and West Coast show particularly reduced horse diversity, as in older parts of the Miocene. The Gulf Coast retains some relictual Clarendonian taxa, and the Great Plains (including Mexico and Central America) show the greatest ungulate diversity.

Immigrant taxa whose first appearances in North America have been established in the Great Plains can be used (as in Voorhies 1990a) to distinguish four phases of the Hemphillian, with important turnover events marking the end of the late early (Hh2) and the close of the Hemphillian.

The beginning of Hemphillian time (Hh1) is defined by the first appearance of the Edentata (Megalonychidae, Pliometanastes), the prometheomyine murid Paramicrotoscoptes, the eomyid Kansasimys, the cricetodontine murid Pliotomodon, the desmanine mole Lemoynea, and the nectogaline shrew Crusafontina (including Anouroneomys). First appearances in the autochthonous characterizing fauna include the archaeolagine Hypolagus vetus; the beaver Dipoides; the geomyid Pliosaccomys; the sigmodontine murid Paronychomys; the badger Pliotaxidea; the borophagine canid Borophagus pugnator and its coexistence with Epicyon haydeni; the Vulpini (Vulpes stenognathus) and Canini (Eucyon davisi); the gomphothere Rhynchotherium; the rhino Teleoceras fossiger; the equids Neohipparion leptode, Nannippus, Hippidion, and Pliohippus nobilis; the llamine Alforjas and cameline Megatylopus gigas; and the antilocaprine Osbornoceras.

Late early (or medial; Voorhies 1990a) Hemphillian (Hh2) is defined by the first appearance of the sloth *Thinobadistes* (Mylodontidae), the bear *Indarctos*, the ailurid *Simocyon*, the galictine mustelid *Lutravus*, the otter *Enhydritherium*, the mellivorine *Eomellivora*, the felid *Machairodus*, and the Bovidae (*Neotragocerus*). The characterizing fauna includes the first appearances of the beaver *Dipoides stirtoni*; the murid *Goniodontomys*; the tremarctine bear *Plionarctos*; the borophagine canid *Borophagus secundus*; the felid *Nimravides catocopis*; the shovel-tusked gomphothere Amebelodon; the rhino Aphelops mutilus; the horses Dinohippus leidyanus, Astrohippus ansae, Pliohippus spectans, and Neohipparion eurystyle; the peccaries Prosthennops serus and Platygonus; and the antilocaprines Sphenophalos, Ilingoceros, and Texoceros.

During the late early Hemphillian (Hh2) a number of taxa reached the limit of their chronologic ranges, including some characteristic of the Clarendonian. The list of last occurrences includes the beaver *Hystricops*; the eomyid *Leptodontomys*; the mustelids *Leptarctus* and *Sthenictis*; the felid *Nimravides*; the Nimravidae (*Barbourofelis*); the horses *Protohippus*, *Hipparion*, *Calippus*, and *Pliohippus*; the Protolabinae (*Protolabis* and *Michenia*); the llamine *Aepycamelus*; the cameline *Procamelus*; the dromomerycid *Yumaceras*; and the antilocaprines *Osbornoceros* and *Plioceros*. Most of the early Hemphillian immigrants also do not survive except *Machairodus*, *Neotragocerus*, and the sloths.

The late Hemphillian (Hh3) is defined by several immigrants: the sloth Megalonyx, the pika Ochotona, the arvicoline murid Prosomys, the zapodid Pliozapus, the beaver Castor, the ursid Agriotherium, the wolverine Plesiogulo, and the cat Felis. The characterizing fauna of the early late Hemphillian (Hh3) includes first occurrences of the mole Scalopus (Hesperoscalops); the horned mylagauline Ceratogaulus hatcheri; the large marmot Paenemarmota; the sigmodontine cricetids Calomys and Prosig*modon;* the cricetines *Peromyscus*, Galushamys, Onychomys, and Paraneotoma; the geomyid Pliogeomys; the heteromyid Prodipodomys; the raccoon Procyon; the tremarctine bear Plionarctos edensis; the borophagine canid Borophagus parvus; the equids Dinohippus interpolatus, Nannippus aztecus, Nannippus lenticularis, and Onohippidion (O. galushai); and the dromomerycid Pediomeryx. Taxon extinctions during this interval include the immigrants Platybelodon, Prosomys, Pliozapus, Eomellivora, Lutravus, and Pliogale and the autochthones Amebelodon, Alforjas, Sphenophalos, Ilingoceros, and Texoceros.

Chronologically the latest (or late late) Hemphillian (Hh4) just extends across the Miocene–Pliocene boundary (5.3 Ma) to 4.6–4.9 Ma, as shown by the ash date at Rancho El Ocote, Guanajuato, the magnetostratigraphy at the Yepómera site in Chihuahua, Mexico, and the early Blancan ash date from Nevada (data presented earlier). This final phase of the Hemphillian begins at the chron C3r–C3An boundary at about 5.9 Ma (Berggren et al. 1995). It closes with the extinction of most of the clades characteristic of the late Hemphillian: the families Plesiosoricidae, Mylagaulidae, Rhinocerotidae, Protoceratidae, and Dromomerycidae; the wolverine *Plesiogulo;* the badger *Pliotaxidea* (survives as *Taxidea*); the borophagine canids *Carpocyon* and *Borophagus secundus*; the sabre-cat *Machairodus*; the proboscidean *Gomphotherium*; the equids *Dinohippus* (survives as *Equus*), *Astrohippus*, and *Neohipparion*; and the antilocaprine *Hexameryx*.

The defining taxa of this final phase of the Hemphillian (Hh4) include the flying squirrel Miopetaurista, the arvicoline Propliophenacomys, the weasel Mustela, the mustelids Trigonictis and Sminthosinis, the otter Lutra, the cat Megantereon, and the Odocoileini (Eocoileus; Webb 2000). The characterizing fauna includes the leporine Lepoides; the marmots Marmota (M. vetus) and Paenemarmota sawrockensis; the gopher Thomomys (Plesiothomomys); the cricetines Baiomys and Repomys (R. gustelyi); the canids Borophagus hilli and Borophagus dudleyi; the skunk Buisnictis; the horses Dinohippus mexicanus, Neohipparion cf. eurystyle, and Astrohippus stocki; the tayassuid Mylohyus; the camel Megacamelus; the antilocaprine Subantilocapra; and the last protoceratid, Kyptoceras. Most of the ungulates on this list have biochrons limited to the late late Hemphillian. A number of lineages extended their ranges into the late Hemphillian but limited their geographic ranges to the southern Great Plains, Gulf Coastal Plain, and Mexico, including a small species of Gomphotherium, the Protoceratidae (Kyptoceras), the Gelocidae (Pseudoceras), and the hipparionine equids Cormohipparion emsliei, Nannippusa ztecus, and Pseudhipparion simpsoni, the last reaching as far north as Buis Ranch, Oklahoma, and MacPherson, Kansas.

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The present compilation was put together in much the same way as the previous, with the senior author distilling the combined efforts at his colleagues into a synthesis that represents a largely consensus effort. We have been assisted in important ways by the following colleagues who contributed data and ideas to this work: T. Fremd, R. Hulbert, W. W. Korth, E. B. Lander, E. L. Lundelius, G. S. Morgan, M. S. Stevens, X.-M. Wang, and M. O. Woodburne.

Alejandra Lora was responsible for bringing the text into order, and Edward Heck translated pencil sketches into clear graphics.

APPENDIX

Selected radiometric and fission-track dates used to calibrate the correlation charts (reference numbers on figure 6.2). Dates published before 1979 were recalculated using International Union of Geological Sciences constants following Dalrymple (1979). This list includes most material previously published by Tedford et al. (1987), augmented by relevant dates obtained since that writing.

NO.	DATE (MA, + SD)	UNIT DATED	REMARKS
1	10.3	Moraga Fm.ª	Revised date of basal andesitic basalt flow (see KA 993, 1001) ^b
2	10.2	Siesta Fm. ^b	Plagioclase from tuff, base of unit, KA 829
3	7.9	Bald Peak Volcanics ^b	Basalt, minimum date, KA 1003
4	5.3 ± 0.1	Pinole Tuff ^c	Feldspar from tuff, a few feet above fauna, KA 1005
5	$5.9 \pm 0.6;$ 6.3 ± 0.1	Sycamore Fm. ^{c,d}	Tuff near top of unit
6	5.5 ± 0.2	Pinole Tuff ^c	Tuff at top of Sycamore Fm., imme- diately beneath Hemme Hills LF
7	4.1 ± 1.0; 4.6 ± 0.5	Lawlor Tuff ^c	Tuff in Tassajara Fm.
8	22.1–22.9	Dacite, dacite agglomerate ^e	Intertongues with top of Tecuya Fm., minimum date for faunas, KA 2114–5, 2166, 2175
9	28.20 ± 0.2	Willard Canyon Tuff ^f	Top of fossiliferous interval containing South Mountain Fauna
10	16.5 ± 1.3	Caliente Fm. ^e	Lowest Triple Basalt, KA 2127
11	$14.6 \pm 0.6;$ 14.8 ± 0.8	Caliente Fm. ^e	Uppermost Triple Basalt, KA 2116, 2125
12	13.4 ± 0.14	Dry Canyon Tuff ^g	Ar–Ar on biotite, revises age of "Dated Tuff," unit 10 in Tedford et al. (1987)
13	22.9 ± 0.4	Hector Fm. ^h	K–Ar on biotite from tuff near base Hector Fm., North Cady Mountains; maximum date for overlying faunas
14	20.3 ± 0.7	Saddleback Basalt ⁱ	Boron LF 146 m above top of basalt, B-4
15	21.6	Hector Fm. ^j	Tuff near top of stratigraphic occurrence of Black Butte Mine LF, KA 2223
16	18.5 ± 0.2	Peach Spring Tuff ^k	Interbedded with rocks containing Hackberry Fauna
17	18.5 ± 0.2	Peach Springs Tuff ^h	K–Ar on sanidine from tuff stratigraphically between local faunas, northeastern Cady Mountains
18	17.8	Wildhorse Mesa Tuff ¹	Interbedded with top of unit yielding Hackberry Fauna
19	16.3 ± 0.3	Rak Tuff ^m	K–Ar date on biotite from tuff near base of Rak Division, Barstow For- mation
20	15.8 ± 0.02	Oreodont Tuff ^m	K–Ar date on biotite from tuff, 40 m above base of Green Hills Division, Barstow Fauna
21	14.8 ± 0.06	Dated Tuff ^m	Ar–Ar date on biotite from tuff near base of First Division of Barstow Fm.
22	14.0 ± 0.09	Hemicyon Tuff ^m	Ar–Ar date on biotite from tuff about 80 m above base of First Divi- sion, Barstow Fm.

220 Richard H. Tedford, et al.

NO.	DATE (MA, + SD)	UNIT DATED	REMARKS	N0.	DATE (MA, + SD)	UNIT DATED	REMARKS
23	13.4 ± 0.2	Lapilli Tuff ^m	K–Ar date on biotite from tuff about 30 m below top Barstow Fm.	46	28.7 ± 0.07	Picture Gorge Ignimbrite ^s	Ar–Ar date, John Day Fm.
24	12.6 ± 0.1	Cronese Tuff ^g	Pumice, just above fossil site	47	27.89 ±	Deep Creek	Ar–Ar date, John Day Fm.
25	12.0/ ± 0.04	Tuff V ⁿ	Nevada, identified by element	48	27.18 ± 0.13	Biotite Tuff ^s	Ar–Ar date, John Day Fm.
			analysis; about 100 m above base	49	25.9 ± 0.31	Tin Roof Tuff ^s	Ar–Ar date, John Day Fm.
26	10.94 ±	Cougar Point	of Dove Spring Fm. Ar–Ar date type locality northeastern	50	22.6 ± 0.13	Across the River Tuff ^s	Ar–Ar date, John Day Fm.
	0.03	Tuff XIII ⁿ	Nevada, identified by element analysis; just above upper basalt, Dove Spring Fm.	51	15.77 ± 0.04	Mascall Fm. ^g	Ar–Ar date on plagioclase from tuff 25 feet below base of Unit 5 of Downs (1956) and below fauna
27	8.50 ± 0.13	Unnamed tuff ⁿ	K–Ar date (86CS-R4), 1400 m above base of Dove Spring Fm.	52	15.79 ± 0.07	Unnamed tuff ^g	Ar–Ar date on sanidine, from tuffaceous fossil horizon, Skull
28	17.4 ± 0.3; 17.6 ± 0.3	Fraction Tuff ^o	K–Ar date, sanidine and biotite, respectively, U.S. Geological Survey (M) 11549-1	53	12.4	Juntura Fm. ^t	Springs Fauna; Red Basin Basalt at top of lower member, Jun- tura Fm., above Stinking Water
29	16.6 ± 0.4	Brougher Dacite ^p	K–Ar date, sanidine and biotite, 659–66 ^q	54	0.4 ± 0.6	Drewcey Em u	Flora, KA 1240 Sanidine from Welded Tuff of
30	15.16 ± 0.063	Tonopah Tuff ^g	K–Ar date on plagioclase from just below fossil quarry	94	9.4 ± 0.0	Diewsey Thi.	Devine Canyon, lowest unit in Drewsey Fm., beneath local faunas
31	14.89 ± 0.53	Unnamed ash ^g	K–Ar date on plagioclase; ash overlies Stewart Springs localities	55	7.1 ± 1.09	Drinkwater Basalt ^v	Whole rock date; minimum age for Bartlett Mountain and other local
32	11.74 ± 0.03	Esmeralda Fm. ^g	Ar–Ar date on biotite, tuff from middle of fossiliferous section ^b	56	6.6 ± 0.1;	Rattlesnake	faunas in the Drewsey Fm. Sanidine from ignimbrite member of
33	11.58 ±	Esmeralda	Ar–Ar date on biotite, tuff just		6.8 ± 0.2	Fm. ^q	Rattlesnake Fm., above fauna
34	0.05 11.5	Fm. ⁶ Fm. ^b	K–Ar date on biotite, tuff near base of fossiliferous section, KA 414	57	29.5 ± 2.8	Unnamed ignimbrite ^w	Fission-track from zircon in welded tuff unconformably beneath Cabbage Patch Fm.
35	11.1	Coal Valley Fm. ^b	K–Ar date on biotite, tuff near middle of fossiliferous section	58	28.26 ± 0.05	Chimney Rock Perrierite Ash ^x	Ar–Ar date on sanidine, near base of Gering Fm.
36	9.6	Coal Valley Fm. ^b	K–Ar on biotite from tuff below beds containing Smiths Valley Fauna, KA 485	59	28.11 ± 0.18	Roundhouse Rock Pisolitic Ash ^x	Ar–Ar date on sanidine and plagioclase, near top of Gering Fm.
37	6.76 ± 0.06; 7.20	Unnamed basalt ^q	Whole rock K–Ar dates from basalts unconformably overlying Wassuk	60	22.9 ± 0.08	Agate Ash ^y	K–Ar biotite from tuff near base of Harrison Fm.
	± 0.07		Group, KA 2365 and 2369, respectively	61	19.2 ± 0.5	Eagle Crag Ash ^z	Fission-track on zircon from ash just above Agate Springs LF
38	4.96	Unnamed tuff ^r	Tuff in the base of section yielding Blancan mammals	62	17.4 ± 0.08	Split Rock Ash ^y	K–Ar date on sanidine from an ash (unit 2 of Love 1961:19) in stratal
39	16.58 ±	Steens Basalt ^g	Ar–Ar whole rock date on upper				span of Split Rock Fauna
	0.12		gon; minimum age for genetically related basalt at site of Massacre	63	16.36 ± 0.07; 16.4 + 0.07	Sheep Creek Tuff ^{g,y}	Ar–Ar date on anorthoclase from the third ash in the Sheep Creek Fm. type section above fauna
40	16.47 ± 0.04	Tuff of Big Basin ^g	Lake LF Ar–Ar date on anorthoclase; ash flow immediately above rocks with	64	13.55 ± 0.09	Hurlbut Ash ^g	Ar–Ar date on glass, ash above Norden Bridge LF, Cornell Dam Mbr. Valentine Fm.
41	16.13 ±	Canyon	Massacre Lake LF Ar–Ar on anorthoclase from rhyolite	65	12.18 ± 0.12	Swallow Ash ^g	K–Ar date on glass, ash near local
	0.03	Rhyolite ^g	flow that underlies Virgin Valley Fauna	66	11 55 ± 0.12	Davis Ashs	Fm. K_{-} Ar date on glass, ash near base
42	15.84 ± 0.13	Virgin Valley Pumice ^g	Ar–Ar date on sanidine, lower part of Virgin Valley Fm. below fossil	00	0.12	Lungar J 100	Merritt Dam Mbr., Ash Hollow Fm.
43	15.18 ±	Virgin Valley	sites Ar–Ar date on anorthoclase, overlies	67	$\delta.0 \pm 0.7$	Unnamed ash ^{aa}	rission-track from glass in Ogallala lectotype section of Elias, ^{bb} beneath Feltz Ranch LF
	0.76	Tuff ^g	main fossil horizon	68	6.6 ± 0.3	Ash Hollow	Fission-track from glass near top of
44	14.49 ± 1.14	Fly Tuff ^g	K–Ar date on plagioclase, 8 m above main fossil horizon	50		Fm. ^s	type section, Garden County, Nebraska
45	29.75 ± 0.02	AB Tuff ^s	Ar–Ar date, John Day Fm.	69	5.0 ± 0.2	Santee Ash ^{cc}	Fission-track from glass, ash overlies Santee LF

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Mammalian Biochronology of the Arikareean Through Hemphillian Interval 221

	DATE	UNIT	
N0.	(MA, + SD)	DATED	REMARKS
70	14.36 ± 0.18	Pawnee Creek Fm. ^g	Ar–Ar date on glass, ash near middle of section underlies first local appearance of Proboscidea
71	6.8 ± 0.2; 6.5; 6.8 + 0.03	Coffee Ranch Ash ^{y,dd,ee}	Fission-track date on zircon from ash just above Coffee Ranch Quarry; age revised using magnetostratigraphy, ^{ee} maximum date; Ar–Ar date on sani- dine ^y
72	15.3 ± 0.05; 15.45 ± 0.06	No. 4 White Ash ^{y,ff}	Ar–Ar date on sanidine; ash in upper part of Skull Ridge Mbr., Tesuque Fm., 3 m above White Operation Quarry ^{gg}
73	9.6 ± 0.2	Lobato Basalt ^{hh}	Whole rock K–Ar age from a flow assigned to the Lobato field; mini- mum date for lower part of Chamita Fm.
74	7.7 ± 0.3	Lower Tuffaceous Zone ^{ff}	Ar–Ar on hornblende, Lower Tuffaceous Zone, Chamita Fm., maximum date for fauna
75	6.93 ± 0.05; 6.78 ± 0.03;	Upper Tuffaceous Zone ^{ff}	Ar–Ar on sanidine, samples from lower and upper part of Upper Tuffaceous Zone, Chamita Fm., bracketing fauna in ash
76	13.64 ± 0.09	Cerro Conejo Fm. ⁱⁱ	K–Ar on biotite from ash near top of fossiliferous interval, Ceja del Rio Puerco
77	11.3 ± 0.10	Cerro Conejo Fm. ^{ij}	Ash tentatively identified with Cougar Point Tuff XI, ⁿ Ar–Ar dated at type locality, northeastern Nevada
78	23	Basalt ^{kk}	Whole rock K–Ar date on basalt in base of the Delaho Fm., underlies fauna
79	23.3	Basalt ^{kk}	Whole rock K–Ar date on basalts at base of Closed Canyon Fm., brackets fauna
80	$\begin{array}{c} 19.3 \pm 0.3; \\ 20.3 \pm 0.3 \end{array}$	Etla Tuff ¹¹	K–Ar dates on biotite and plagioclase, respectively
81	$15.3 \pm 0.8;$ 16.0 ± 0.8	Unnamed ^{ll}	K–Ar dates on biotite and plagioclase, respectively; pyroclastics underlying fauna
82	15.02 ± 0.35; 16.02 ± 0.53	Unnamed lower tuff ^l	K–Ar dates on biotite and plagioclase, respectively; tuff overlies fauna
83	15.0 ± 0.8; 16.47 ± 0.71	Yautepec Tuff ^{ll}	K–Ar dates on biotite and plagioclase, respectively; tuff underlies faunal sites
84	12.12 ± 0.19; 12.24 ± 0.19	Unnamed upper tuff ¹¹	K–Ar dates on biotite and plagioclase, respectively; tuff overlies fauna
85	4.6	Unnamed ^{mm}	Fission-track age of tuff, overlying fauna

Fm., Formation; LF, Local Fauna; Mbr., Member.

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^aD. E. Savage, pers. comm., 1973.

^bEvernden et al. 1964.

^cSarna-Wojcicki 1976.

^dBartow et al. 1973.

^fMason and Swisher 1989. ^gSwisher 1992. ^hWoodburne 1998. ⁱArmstrong and Higgins 1973. ^jWoodburne et al. 1974. ^kNielson et al. 1990. ¹Reynolds et al. 1995. ^mMacFadden et al. 1990. ⁿPerkins et al. 1995, 1998. °Silberman and McKee 1972. ^pAlbers and Stewart 1972. ^qParker and Armstrong 1972. rLindsay et al. 2002. ^sSwisher 1992. ^tEvernden and James 1964. ^uGreene 1973. ^vGreene et al. 1972. WC. W. Naeser, pers. comm., 1973. *Tedford et al. 1996. yIzett and Obradovich 2001. ^zHunt et al. 1983:366. ^{aa}Boellstorff 1976. bbStirton 1936. ^{cc}Boellstorff 1978. ^{dd}Naeser et al. 1980. ^{ee}Lindsay et al. 1984. ffMcIntosh and Quade 1995. ggBarghoorn and Tedford 1993. hhTedford and Barghoorn 1993. ⁱⁱTedford and Barghoorn 1999. ^{jj}S. Connell, pers. comm., 2002. ^{kk}Stevens and Stevens 1989; Henry et al. 1998. ¹¹Ferrusquia-Villafranca 1992, 1996. ^{mm}Kowallis et al. 1986.

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The Blancan, Irvingtonian, and Rancholabrean Mammal Ages

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HIS CHAPTER EXAMINES the last three North American land mammal ages of the Cenozoic: the Blancan, Irvingtonian, and Rancholabrean. It also incorporates the arvicoline rodent biochronology that was a separate chapter in the first edition of this volume (Repenning 1987). These mammal ages encompass approximately the last 5 million years and span most of the Pliocene and all of the Pleistocene (the latest Hemphillian is part Pliocene and is covered by Tedford et al., chapter 6, this volume). Vertebrate faunas from these epochs are known from several thousand localities in North America and are distributed over a wider geographic area than those of any other epoch or equivalent interval of time. The short duration of the Pliocene and Pleistocene and the availability of numerous and diverse dating methods (Noller et al. 2000) permit a refined temporal resolution and critical evaluation of faunal change on much shorter time scales than is possible for most of the Cenozoic. In addition, many of the taxa represented in Pliocene and Pleistocene faunas are still extant or have close living relatives (this is particularly true for the latter part of the Pleistocene). This temporal proximity between fossil and living forms creates a unique bridge between neontology and paleontology and provides a valuable perspective on the biological components that add to the complexities of biostratigraphy and biochronology. Although there is extensive evidence of evolutionary change in many Pleistocene mammal lineages, the relative paucity of cladogenic speciation probably is a result of the short time involved. Detailed excavations of fossil deposits that accumulated over sometimes quite short periods of time reveal that complex faunal changes took place over short

time intervals. These deposits thus permit a greater understanding of the interaction between biotic and abiotic factors in shaping mammalian faunal dynamics and provide a broader perspective on the implications of timeaveraging and provinciality for biochronology. These implications are relevant not only for the Pliocene– Pleistocene but also for all the Cenozoic.

The problems involved in the use of vertebrate fossils for latest Tertiary and Quaternary geochronology are similar to those of older time periods. Additional complications are caused by strong environmental zonation that resulted from climatic changes due to repeated pulses of glacial advance and retreat. The boundaries of these environmental zones shifted over short time intervals and were often associated with dramatic faunal changes.

Long, richly fossiliferous sequences with well-dated superpositional control provide the ideal basis for studying faunal succession in the Pliocene and Pleistocene of North America. We are fortunate to have several complementary sections in the West and Midwest that provide an adequate geochronologic framework for the study of late Cenozoic mammalian biostratigraphy. These include deposits in Meade County in Kansas, the western Snake River Plain of Idaho, the San Pedro Valley of Arizona, the Gila River Valley in southeastern Arizona and western New Mexico, the Medicine Hat sequence in Alberta, the Anza-Borrego Desert in the Salton Sea Basin of southern California, the San Timoteo Badlands of California, and the Ringold Formation of southeastern Washington. Geochronologic data from these and other isolated localities make the North American Pliocene and
Pleistocene mammal ages, despite their limitations, among the best dated in the world.

External age control of Pliocene and Pleistocene faunas comes primarily from radioisotopic dating techniques and paleomagnetism. Volcanic ash, pumice, and rhyolite units significant for correlation of these faunas are summarized in table 7.1. The dates of the geomagnetic polarity chrons are subject to revision as improved methods and procedures are developed and as new stratigraphic sections are discovered and studied. To retain some measure of consistency in this volume we follow Berggren et al. (1995) for the dates of geomagnetic polarity event boundaries. In a few cases, radiometric dates of a particular sequence conflict with the global Geomagnetic Polarity Time Scale (GPTS) proposed by Berggren et al. (1995); these cases are discussed individually. When citing prior publications in which time designations for faunas were based on older geomagnetic polarity stratigraphy calibrations, we altered the published designation to conform to that of Berggren et al. (1995); in those cases our ages do not necessarily match those given in the earlier publications.

Four magnetic polarity chrons were initially established for the Pliocene and Pleistocene (Cox et al. 1963); from oldest to youngest these are the Gilbert, Gauss, Matuyama, and Brunhes. These names, and the names of associated subchrons (e.g., Jaramillo, Olduvai), are now firmly established in the literature and are used in this chapter. The numeric designations proposed for chrons from the Miocene through Mesozoic also are standardized (Opdyke and Channell 1996) and are extended through to today (e.g., in that system the Brunhes chron is redesignated chron C1n). For completeness and clarity, we provide the numeric chron and subchron designations in addition to the traditional named chrons.

The correlation of the North American mammal ages with the epochs of the geologic time scale was difficult to establish previously, especially for the Pliocene through Holocene. Resolution of debates over the epochal boundaries and subsequent designation of stratotypes for these boundaries in the last two decades provide new opportunities to evaluate temporal correlation between defined European epochal stratotypes and the North American mammal ages. In this chapter, we provide a brief summary of epochal boundary stratotypes and current interpretations of their ages. Subsequent sections of this chapter address the Blancan, Irvingtonian, and Rancholabrean mammal ages in terms of their history, definition, characterization, and temporal extent and the geographic distribution of relevant faunas for each age. Summary characterizations are shown in table 7.2.

LATE CENOZOIC EPOCHAL BOUNDARIES

THE MIOCENE-PLIOCENE BOUNDARY

The complicated early history of the use of the term Pliocene, from its original definition by Lyell (1833) through the early twentieth century, was reviewed by Wilmarth (1925). In recent usage, the base of the Pliocene was placed at the base of the Zanclean Stage at Capo Rossello, Sicily, marked by an acknowledged unconformity between the Trubi Formation (Trubi marls) and the underlying alluvial/lacustrine Arenazzolo Formation of the Messinian Stage (Cita 1975). This boundary was interpreted to mark the return of marine conditions to the Mediterranean after the Messinian salinity crisis. The lack of good magnetostratigraphy in the proposed type section was pointed out by Rio et al. (1991), who also indicated that the Miocene strata at Capo Rossello are nonmarine (making biostratigraphic correlation to the marine section difficult) and suggested the need for a boundary stratotype outside the Mediterranean to avoid the problem of endemism in the marine faunas. The Capo Rossello section does not satisfy the operational requirements of a global boundary and stratotype section series because of the unconformity at the base of the Trubi Formation at that locality (Hilgen and Langereis 1993). An alternative boundary in the Eraclea Minoa (Sicily) section shows evidence of a transitional interval rather than an unconformity at the base of the Trubi Formation (Hilgen and Langereis 1993). The evaporite cycles in the Trubi Formation are tuned to the astronomical precession cycles and thereby provide a presumably precise determination of the date. There are five precession cycles between the base of the Thvera subchron (chron C3n.4n) and the basal contact of the Zanclean. With an average cycle length of 21,000 years, the base of the Zanclean therefore is approximately 105,000 years older than the base of the Thvera (given as 5.23 Ma by Berggren et al. 1995). The age of the base of the Pliocene therefore would be considered 5.335 Ma using the Berggren et al. (1995) GPTS. This boundary was ratified by the International Commission on Stratigraphy in January 2000 and now is established as the base of the Pliocene series (see Van Couvering et al. 2000 for discussion).

THE PLIOCENE-PLEISTOCENE BOUNDARY

International Stratotype The term *Pleistocene* had a complicated early history (reviewed by Wilmarth 1925), but modern usage corresponds roughly to the definition

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NAME	PUBLISHED AGES	REFERENCES		
Lava Creek B Ash (Pearlette type O)	0.602 ± 0.004 Ma Between 0.66 \pm 0.01 and 0.67 \pm 0.01 Ma	Gansecki et al. 1998 Izett and Honey 1995; Izett et al. 1992		
Hartford Ash	Approximately 0.74 Ma	Boellstorff 1973, 1978		
Bishop Ash	0.7589 ± 0.0018 Ma Approximately 0.70 Ma	Sarna-Wojcicki et al. 2000 Izett et al. 1970		
Tsankawi Pumice Bed (lower bed of the Tshirege Member of the Bandelier Tuff)	1.22 ± 0.018 Ma 1.12 ± 0.03 Ma	Izett and Obradovich 1994 Izett et al. 1981		
Cerro Toledo Rhyolite (upper)	$1.23\pm0.02~\mathrm{Ma}$	Izett et al. 1981		
Cerro Toledo "X" Ash (suspected to be derived from Cerro Toledo Rhyolite)	1.2–1.3 Ma (by tentative correlation)	Izett 1977; G. Schultz 1990b		
Mesa Falls Ash (Pearlette type S, Coleridge Ash, "Sappa ash")	1.293 ± 0.012 Ma 1.27 Ma (average) 1.21 Ma 1.21 ± 0.05 Ma 1.20 ± 0.04 Ma About 1.2 Ma	Gansecki et al. 1998 Izett 1981 Boellstorff 1973 Boellstorff 1976 Naeser et al. 1973 Naeser et al. 1971		
Cerro Toledo "B" Ash (from eruptions associated with Cerro Toledo Rhyolite)	Between 1.2 and 1.4 Ma Probably close to 1.4 Ma (by correlation)	Izett et al. 1981 Izett and Honey 1995		
Cerro Toledo Rhyolite (lower)	$1.47\pm0.04~\mathrm{Ma}$	Izett et al. 1981		
Cerro Toledo Rhyolites (as a whole)	Pulse eruptions between approximately 1.54 and 1.22 Ma	Spell et al. 1996		
Guaje Pumice Bed (lower bed of the Otowi Member of the Bandelier Tuff)	1.608 ± 0.01 Ma 1.613 ± 0.011 Ma 1.40 ± 0.04 Ma	Spell et al. 1996 Izett and Obradovich 1994 Izett et al. 1981		
"Guaje ash" (informal) near Mt. Blanco in Texas (chemical and petrographic resemblance to Guaje Pumice Bed in New Mexico)	1.77 ± 0.44 Ma 1.4 ± 0.2 Ma	Boellstorff 1976 Izett et al. 1972		
Huckleberry Ridge Ash (Pearlette type B, "Borchers ash")	$2.003 \pm 0.014 \text{ Ma}$ $2.10 \pm 0.02 \text{ Ma}$ $2.09 \pm 0.01 \text{ Ma}$ $2.09 \pm 0.01 \text{ Ma}$ 2.01 Ma $1.96 \pm 0.2 \text{ Ma}$	Gansecki et al. 1998 Honey et al. 1998 Izett and Honey 1995 Obradovich and Izett 1991 Izett 1981 Boellstorff 1976		
Blanco Ash	2.8 ± 0.3 Ma	Boellstorff 1976		
Peters Gulch Ash	3.75 ± 0.36 Ma	Izett 1981		
Lawlor Tuff	4.1 ± 0.2 Ma	Sarna-Wojcicki et al. 1991		
Healdsburg tephra	4.69 Ma or 4.64 ± 0.03 Ma	Lindsay et al. 2002		
"Tracer pumice bed," Nevada	$4.96\pm0.02~\mathrm{Ma}$	Lindsay et al. 2002		
Pinole Tuff	5.2 ± 0.1 Ma	Evernden et al. 1964		

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TABLE 7.1 Late Cenozoic Volcanic Units Useful in Correlating North American Mammal Faunas

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The names used in this chapter are provided with alternative names in parentheses. Ages and references for the dates are provided.

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TABLE 7.2 Characteristic Taxa of the Blancan, Irvingtonian, and Rancholabrean Mammal Ages

A, begins in mammal age but also persists after it; B, begins before mammal age but persists into it; C, confined to mammal age; 5T, species with five closed triangles on lower first molar. Asterisk (*) indicates taxa that first appear in the latest Blancan faunas that are elsewhere often considered to be early Irvingtonian.

Ψ

	BLANCAN	IRVINGTONIAN	RANCHOLABREAN
Megalonyx leptostomus	С		
Glossotherium chapadmalense	С		
Aluralagus	С		
Pewelagus dawsonae	С		
Pratilepus kansasensis	С		
Dipoides rexroadensis	С		
Sigmodon curtisi	С		
Sigmodon minor	С		
Mictomys vetus	С		
Ogmodontomys	С		
Ophiomys	С		
Pliopotamys	С		
Ondatra idahoensis	С		
Pliolemmus	С		
Borophagus diversidens	С		
Canis lepophagus	C		
Chasmaporthetes	С		
Ursus abstrusus	С		
Platveonus bicalcaratus	С		
Platveonus pearcei	C		
Nannippus peninsulatus	C		
Aliletrus	В		
Hypolagus	В		
Nekrolagus	В		
Paenemarmota	В		
Prodipodomys	В		
Satherium	В		
Borophagus hilli	В		
Trigonictis	B		
Megantereon	B		
Rhynchotherium	В		
Nothrotheriops*	A	В	В
Paramylodon harlani*	Δ	B	B
Cluptotherium	Δ	B	B
Holmesina	Δ	B	B
Blarina	Δ	B	B
Sulvilague	A	B	B
Uptrimero Latrice*	Δ	R	B
Allophaiomus pliocasnisus*	A	D	U
Microtus (T)*	л л	D	в
Mictomus kansasansis/maltoni*	л л	U D	U
Naofiher*	A	D	В
Oudatra annoctous*	A	D	D
	A	D	D
Enerucomys	A	B	۵ D
Synuptomys [*]	A	В	B
	A	В	ß
Lutra canadensis"	A	В	В
nomotnerium	A	В	
Miracinonyx inexpectatus	А	В	

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236 Christopher J. Bell and Ernest L. Lundelius Jr. (co-chairmen), et al.

TABLE 7.2 (continued)

	BLANCAN	IRVINGTONIAN	RANCHOLABREAN
Smilodon gracilis	А	В	
Canis edwardii*	А	В	
Platygonus vetus*	А	В	
Stegomastodon	А	В	
Mammut americanum	А	В	В
Microtus llanensis		С	
Microtus meadensis		С	
Microtus paroperarius		С	
Canis armbrusteri		С	
Tetrameryx irvingtonensis		С	
Didelphis		А	В
Brachylagus idahoensis		А	В
Sylvilagus palustris		А	В
Clethrionomys		А	В
Lemmiscus curtatus		А	В
Ondatra zibethicus		А	В
Marmota flaviventris		А	В
Marmota monax		А	В
Cynomys gunnisoni		А	В
Cynomys ludovicianus		А	В
Panthera onca		А	В
Smilodon populator		А	В
Mustela erminea		А	В
Brachyprotoma		А	В
Conepatus		А	В
Canis latrans		А	В
Canis lupus		А	В
Arctodus simus		А	В
Euceratherium		А	В
Oreamnos		А	В
Mammuthus		А	В
Megalonyx jeffersonii			С
Platygonus compressus			С
Canis dirus			С
Panthera atrox			С
Miracinonyx trumani			С
Aplodontia rufa			А
Ovis canadensis			А
Bison			А
Rangifer tarandus			А
Felis concolor			А
Vulpes velox			А
Homo sapiens			A

 (\square)

proposed by Forbes (1846:386), who equated the Pleistocene with the glacial deposits of England. The concept of worldwide Pleistocene glaciation followed soon thereafter, and the recognition of multiple glaciations on a worldwide scale was seen as a means to establish temporal divisions within the Pleistocene. A more precise and traditional placement for the base of the Pleistocene was given in 1948 by the 18th International Geological Congress. By their edict, the Lower Pleistocene Series included the marine Calabrian Stage of Gignoux (1910, 1916), with its recognized terrestrial equivalent, the Villafranchian Stage, as its basal member. The Pliocene–Pleistocene Commission of that congress noted that this boundary coincided with evidence of climatic cooling in the Italian Neogene succession. Some significant changes in the planktonic foraminiferal record ultimately were driven by climatic change, and Berggren and Van Couvering (1974) correlated these changes with the GPTS. Their efforts provided an important means of simultaneously including paleontological, paleomagnetic, and climate change data in a discussion of the boundary.

Disagreement over the relative importance of climatic events in the determination of the Pliocene–Pleistocene boundary stimulated an extensive debate over the placement of the boundary. Recent arguments presented by Morrison (1991) pertaining to the boundary were based in part on a desire to identify the boundary with a significant climatic event. However, a strict reliance on climatic criteria for establishing boundaries is not advisable because of the time-transgressive nature and wide geographic variance of climatic conditions.

The placement of the Pliocene–Pleistocene boundary at Vrica, Italy, at the base of the claystone conformably overlying sapropelic marker bed "e" was adopted by the International Geological Correlation Project 41 and the International Union for Quaternary Research (INQUA) Sub-Commission 1-d at the 27th International Geological Congress at Moscow in 1984. The boundary is situated just above the top of the Olduvai normal polarity subchron (chron 2n; now dated at 1.77 Ma; Cande and Kent 1995; Berggren et al. 1995). The age of the boundary therefore is slightly younger than 1.77 Ma. An age of 1.8 Ma, derived by rounding off the upper age of the Olduvai event to one decimal place, was given by Pasini and Colalongo (1997). This date is close to several microplankton events and seems to coincide with the entrance of the mollusk Arctica islandica into the Mediterranean (the historical basis for recognizing the base of the Pleistocene in Italy). This boundary was ratified and adopted as a Global Stratotype Section and Point (GSSP) by the International Union of Geological Sciences in 1985 (Bassett 1985). Because at present it is not possible to resolve time intervals as short as 30,000 years in 2-m.y.-old sediments, an age of 1.8 Ma can be accepted as an approximation for the age of the Pliocene-Pleistocene boundary, but we emphasize that the actual age is slightly younger than 1.77 Ma. A more detailed history of the dispute over the placement of the Pliocene-Pleistocene boundary was provided by Berggren and Van Couvering (1974) and Van Couvering (1997).

North American Boundary Recognition Recognition of the Pliocene–Pleistocene boundary in North America ultimately must be based on the boundary as defined in

a marine section in Italy. Early efforts to recognize the Pliocene–Pleistocene boundary in North America were based on the traditional concept that this boundary was marked by the initiation of widespread glaciation. Consequently, North American stratigraphers turned their attention to the extensive glacial deposits in the northern plains and midwestern states, where the most complete glacial sequence is preserved.

Temporal relationships among Pleistocene terrestrial deposits in North America traditionally were based on the recognition of four major glacial pulses, designated (from oldest to youngest) the Nebraskan, Kansan, Illinoian, and Wisconsinan. Interglacial units between these major glacial pulses were called (from oldest to youngest) Aftonian, Yarmouthian, and Sangamonian. Study of deep sea stratigraphic cores, application of new radiometric dating techniques, and detailed stratigraphic reconstructions in the Great Plains reveal that this traditional classification is oversimplified; as many as 20 discrete glacial pulses over the last 2 million years are now recognized (e.g., Richmond and Fullerton 1986).

Fission-track dates of volcanic ash deposits in stratigraphic association with classic glacial till sequences demonstrate that continental glaciation in the New World predates 2.2 Ma (Boellstorff 1978). Especially significant in this respect is Nebraska Geological Survey core 5-A-75, recovered from a well near Afton, Iowa (Boellstorff 1978). This core revealed at least two tills underlying the classic Nebraskan till exposed in the region. The lowermost till in this core is overlain by a "Pearlettetype" ash dated to 2.2 Ma by Hallberg and Boellstorff (1978). Thus the "Nebraskan" till certainly does not represent the earliest North American continental glaciation, and the differentiation of at least seven tills in the type "Nebraskan-Kansan" sequence demonstrates that these terms are meaningless where they were defined originally (Boellstorff 1978). Ashes dated at approximately 0.60-0.67 Ma ("Type O" or "Lava Creek B" of Izett et al. 1981; Izett and Wilcox 1982; "Pearlette restricted" of Boellstorff 1973) and 0.74 Ma ("Hartford Ash" of Boellstorff 1973, 1978) lie stratigraphically above classic Nebraskan till and below classic Kansan till (Hallberg 1980). The Cudahy Fauna in Kansas also lies immediately below the 0.60-0.67 Ma Lava Creek B Ash. Although this fauna is approximately the age of classic "Aftonian" sediments, it traditionally was considered to be "late Kansan" in age (Hibbard 1970; Paulson 1961).

The age and stratigraphic relations of these ashes clearly indicate that traditional glacial age designations of High Plains faunas are misaligned with respect to the till sequences and that the terms *Nebraskan*, *Aftonian*, and *Kansan* have lost meaning as chronologic units (see also Richmond and Fullerton 1986). Similar problems are associated with the use of *Yarmouthian*, *Illinoian*, and *Sangamonian*. It is questionable whether climatic criteria that lack independent chronologic calibration are a sound basis for any chronostratigraphic or geochronologic unit. Thus, use of this nomenclature with Pleistocene faunas should be abandoned. A possible exception to this general statement is the Wisconsinan glacial interval, which is unique among the traditional terms because it is reliably and accurately dated by radiocarbon dating and is still in wide use.

Correlations for the base of the Pleistocene in North America must be established on evidence independent of local climate and ultimately must be correlated with the stratotype base in Italy. Although paleontological data relevant to the establishment of the boundary stratotype are derived from marine organisms, land mammal faunas do contribute significantly to correlations. European terrestrial mammalian faunas were successfully correlated with the classic Italian marine sequences as early as the late 1960s (Hürzeler 1967; Savage and Curtis 1970; Azzaroli and Ambrosetti 1970; Azzaroli and Berzi 1970). Terrestrial mammalian faunas in North America and Italy can be correlated, at least loosely, with roughly contemporaneous mammalian faunas elsewhere in Europe and Asia. In addition to faunal correlations, direct radiometric dates and paleomagnetic stratigraphy are used to correlate mammalian faunas within and between North America and Europe (Repenning and Fejfar 1977; Repenning et al. 1990; Azzaroli et al. 1997; Fejfar et al. 1998). Welldated faunas in turn form the foundation for correlating North American faunas that lack independent age control.

PLEISTOCENE-HOLOCENE BOUNDARY

Lyell (1833) defined the Recent based on the appearance of humans, but the term *Holocene* was first used by Gervais (1869:32), who gave no definition other than that it follows the "diluvial or Pleistocene deposits." Modern authors equate Lyell's Recent with Gervais's Holocene, but there is no agreement on the placement of a boundary between the Pleistocene and Holocene. Holocene sediments are entirely within the Brunhes chron (chron C1n), and although there is polar wander and minor fluctuations in geomagnetic paleointensity during this interval, these data are not yet appropriate for deriving potential boundary markers (Opdyke and Channell 1996; Stoner et al. 1998, 2002). Four alternatives for the placement of the boundary were noted by the 6th INQUA subcommittee for the Holocene (de Jong 1965): the beginning of the Bølling (13 ka), the beginning of the Allerød (11.8 ka), between the Younger Dryas and Preboreal (between zones III and IV of the pollen chronologic sequence, or at approximately 10 ka), and at the disappearance of large, extinct mammals in Europe (we followed Mangerud et al. 1974 for approximate boundary ages of Bølling and Allerød). The terms Bølling, Allerød, Younger Dryas, and Preboreal are derived from the pollen and plant sequence in Scandinavia (see Flint 1971 and Mangerud et al. 1974 for summaries). The beginning of the Allerød marks the beginning of deposition of autochthonous continental organic remains after the recession of the last ice sheet in northwestern Europe (a biotic event tied to a climatic event in a localized area) and was proposed by Neustadt (1967) as an appropriate boundary. The term Younger Dryas is widely used outside Scandinavia for a cool interval corresponding in age to the Younger Dryas in the type area (Rodbell 2000). Its recognition is not on the basis of mammalian faunas but on pollen or geochemical data. The applicability of these terms in North America and elsewhere outside of Scandinavia is questionable (Bennett et al. 2000; but see Mayle and Cwynar 1995). A similar European nomenclature (the Blytt–Sernander sequence) was reported to be applicable to the Holocene worldwide (Bryson et al. 1970), and it is used in North America, especially in archaeological literature (e.g., Semken and Falk 1987).

Based on data from the deep sea record, Morrison (1991) suggested that the boundary should be placed between oxygen isotope stages 2 and 1. This transition usually is radiocarbon dated to between 11 and 12 ka, but on a worldwide basis this boundary is time transgressive between 9 and 13 ka. There is currently no agreed-upon stratotype for the Pleistocene–Holocene boundary. Operationally, most North American workers appear to be using either an arbitrary age of 10 ka or the disappearance of large-bodied extinct mammals to mark the boundary. The latter event is widely recognized to be time-transgressive between about 23 and 9.5 ka (Grayson 1989, 1991).

Interest in a nontraditional and arbitrary boundary, expressed in terms of thousands of years, has been in the literature for decades (de Jong 1965). The Holocene Commission of INQUA in 1973 confirmed the Paris decision of 1969 to place the base of the Holocene at 10,000 years B.P. and recommended that the international boundary stratotype be located in southern Sweden (Fairbridge 1974). Hopkins (1975) pointed out that eight contributors to the *Quaternary of the United States* volume (Wright and Frey 1965) placed the boundary in seven positions over a span of 6000 years and that a date within every millennium from 18,000 to 4000 has been proposed. He suggested adoption of an arbitrary boundary at 10 ka as a compromise "because it is a nice round number" (Hopkins 1975:10). That compromise was adopted as a provisional date by Richmond and Fullerton (1986) with the notation that it is a chronometric boundary without a stratigraphic basis. That proposal does not meet the requirement of the International Stratigraphic Code that a chronostratigraphic boundary of this rank be based on an internationally accepted stratotype, but we accept it here as a working definition that is in keeping with general operational practice.

FAUNAL CORRELATIONS

The problem of faunal contemporaneity and the duration of dispersal events and transitions can best be resolved by dating methods that are independent of the faunas themselves. Figure 7.1 places the major Blancan, Irvingtonian, and Rancholabrean mammal faunas of North America into a chronologic framework based on faunal correlations, volcanic ash beds, radiometric dates, and correlations with the GPTS. We recognize that many other faunas are known from other locations on the continent (e.g., Alaska, the Yukon, Mexico, Greenland), but because most of them lack reliable stratigraphic, radiometric, or paleomagnetic data on which to base their ages and because of the probability of diachrony across wide geographic and ecological boundaries, many were omitted from figure 7.1. Recent summaries of the Pliocene and Pleistocene mammalian faunas from other parts of North America can be found in the following sources: Greenland (Bennike 1997), Alaska (Guthrie and Matthews 1971; Repenning et al. 1987; Repenning and Brouwers 1992), Canada (Churcher 1984a; Harington 1978, 1989, 1990a, 1990b; Harington and Clulow 1973; Morlan 1984, 1996; Stalker 1996), Mexico (Ferrusquía-Villafranca 1978; Carranza-Castañeda and Ferrusquía-Villafranca 1978; Miller 1980; Lindsay 1984; Carranza-Castañeda and Miller 1996, 1998, 2000; Miller and Carranza-Castañeda 1984, 1998a, 1998b; Kowallis et al. 1998). Some of the faunas shown in figure 7.1 are tentatively placed because of inadequate dating or faunal correlation but are included because they are of historical significance or are persistently referenced in the literature. A range chart for selected taxa discussed in this chapter is provided in figure 7.2.

TAXONOMIC CONSIDERATIONS

Like all healthy sciences, mammalian biostratigraphy and biochronology develop with continued efforts in the field and laboratory. Although all biostratigraphers deal with fossils preserved in the rock record, alternative perspectives on the systematic relationships of taxa and their evolutionary histories can lead to alternative, sometimes confusing taxonomic treatments of the same specimens. New philosophical and methodological approaches to the recognition and naming of fossil taxa are now available (Rowe 1987; Rowe and Gauthier 1992; de Queiroz 1992) and are in wide use, but these methods are rarely applied in research on Pliocene and Pleistocene mammals.

The differing perspectives on the evolutionary history and taxonomy of the voles, lemmings, and muskrats, collectively called microtines or arvicolines, are of special significance for this chapter because of their historical importance in North American Pliocene and Pleistocene biochronology. Controversy over the taxonomy and systematic relationships of arvicoline rodents complicates attempts to summarize their evolutionary history in North America and to establish unambiguous geochronologic boundaries based on various members of the group. Unfortunately, these complications sometimes overshadow the potential importance of these rodents in biostratigraphic correlations and biochronologic interpretations of Pliocene and Pleistocene North American faunas.

The higher-level taxonomy (e.g., family, subfamily, tribe, genus) of the group is especially complicated. Most neontologists now classify these animals in the family Muridae, subfamily Arvicolinae (following Carleton and Musser 1984; Musser and Carleton 1993), and some paleontologists adopted this classification in their work (McKenna and Bell 1997). Earlier systems placed these rodents either in the family Muridae, subfamily Microtinae (Hinton 1926; Hall 1981); family Cricetidae, subfamily Microtinae (Simpson 1945; Gromov and Polyakov 1992; Corbet 1978); or family Cricetidae, with several subfamilies (Repenning et al. 1990). Some paleontologists often classify the group in the family Arvicolidae (Chaline 1987; Fejfar and Heinrich 1990; R. Martin et al. 2000). Korth (1994) recognized a family Microtidae but classified it in the family Cricetidae. The informal terms microtine and



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FIGURE 7.1 Correlation of selected Pliocene and Pleistocene faunas discussed in the text. Positions and radiometric ages of key ash beds are indicated by "xxxx." Faunas with known paleomagnetic orientations are indicated by triangles to the right of faunal name, upright for normal polarity and inverted for reversed polarity. The dates of the geomagnetic polarity boundaries follow Berggren et al. (1995). LMA, land mammal age; RLB, Rancholabrean. Geomagnetic polarity subchrons: C, Cochiti; CM, Cobb Mountain; J, Jaramillo; K, Kaena; M, Mammoth; N, Nunivak; O, Olduvai; R, Reunion; S, Sidufjall; T, Thvera. Key ash and lava beds: Ba, Blanco Ash; CT-B, Cerro Toledo B Ash; CT-X, Cerro Toledo X Ash; DGL, Deer Gulch Lava; Ga, Guaje Ash; HR, Huckleberry Ridge Ash; HA, Hall Ash; HT, Hartford Ash; LC-B, Lava Creek B Ash; PG, Peters Gulch Ash.



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FIGURE 7.1 (continued)



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FIGURE 7.1 (continued)







FIGURE 7.2 Temporal ranges of selected North American Pliocene and Pleistocene mammals. Many ranges are based on faunas with external age control; possible older or younger occurrences in faunas that are poorly constrained temporally are discussed in the text. Dashed lines indicate a high degree of uncertainty. E, earliest known occurrence; Hemp, Hemphillian; L, latest known occurrence; LMA, land mammal age; RLB, taxon became extinct near the end of the Rancholabrean, between approximately 24 ka and 9.5 ka; 5T, 5 closed triangles on lower first molar. Megantereon, E Hemp, L Rexroad 3; Paenemarmota, E Hemp, L Blanco; Borophagus hilli, E Hemp, L Hagerman; Prodipodomys, E Hemp, L Borchers; Hypolagus, E Hemp, L Froman Ferry; Nannippus peninsulatus, E La Goleta, L Macasphalt; Ogmodontomys sawrockensis, from three approximately contemporaneous localities (Upper Alturas, Maxum, and Saw Rock Canyon); Ursus, E above ash in Pine Nut Mountains, L Recent; Ophiomys, E White Bluffs, L Froman Ferry; Platygonus pearcei, E White Bluffs, L Hagerman; Dipoides rexroadensis, E White Bluffs, L Sand Draw; Ogmodontomys poaphagus, E Verde, L Sand Draw; Pliopotamys, E Kettleman Hills, L Sand Draw; Procastoroides, E Hagerman, L Grand View (Jack Ass Butte); Borophagus diversidens, E Rancho Viejo, L Vallecito Creek-Fish Creek sequence (at approximately 2.1 Ma); Megalonyx leptostomus, E Hagerman, L De Soto Shell Pit; Glyptotherium, E Rancho Viejo, L RLB; Stegomastodon, E Rexroad 3, L Martin Ranch; Platygonus bicalcaratus, E Rexroad 3, L Inglis 1C; Pliolemmus, E Bender, L Sanders or Cita Canyon (all known records lack external age control); Sylvilagus, E Vallecito Creek-Fish Creek sequence (ca. 3.15 Ma), L Recent; Miracinonyx inexpectatus, E Cita Canyon, L Conard Fissure, Port Kennedy Cave, or Hamilton Cave; Glossotherium chapadmalense, E 111 Ranch, L Macasphalt; Mictomys vetus, E 111 Ranch, L Froman Ferry; Ondatra idahoensis, E Seneca or White Rock, L Froman Ferry; Smilodon gracilis, E Santa Fe River 1A, L McLeod or Port Kennedy Cave; Nothrotheriops, E Vallecito Creek-Fish Creek sequence, L RLB; Mictomys kansasensis/meltoni, E Nash, L Cudahy; Allophaiomys pliocaenicus, E Nash or Hansen Bluff Core, L Porcupine

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FIGURE 7.2 (continued) Cave Pit; Lepus, E Borchers, L Recent; Platygonus vetus, E Inglis 1A, L Cumberland Cave; Paramylodon harlani, E Inglis 1A, L RLB; Phenacomys, E Froman Ferry, L Recent; Synaptomys, E Haile 16A, L Recent; Ondatra annectens, E Kentuck or Java, L Cudahy; Microtus sp. (5T), E Vallecito Creek–Fish Creek sequence, L Recent; Megalonyx wheatleyi, E Haile 16A, L Cudahy; Mammuthus, E Bruneau Idaho, L RLB; Euceratherium, E Vallecito Creek–Fish Creek sequence, L RLB; Microtus meadensis, E Hansen Bluff or Porcupine Cave Pit, L Salamander Cave; Lemmiscus curtatus, E Sam Cave or base of Porcupine Cave Pit, L Recent; Microtus paroperarius, E Hamilton Cave, L Salamander Cave; Clethrionomys, E Sam Cave, L Recent; Smilodon populator, E Conard Fissure, L RLB; Ondatra zibethicus, E Kanopolis or Rezabek, L Recent; Bison, E American Falls, L Recent; Megalonyx jeffersonii, E multiple Rancholabrean sites (questionable record from Holloman not plotted here), L RLB; Platygonus compressus, E Papago Springs Cave, L RLB.

arvicoline persist in the mammalogical and paleontological literature, in some cases reflecting an author's formal taxonomic preference or conceptualization of higherlevel systematics, in other cases representing only a convenient vernacular. In this chapter we follow Musser and Carleton (1993) in the higher-level taxonomy and use *arvicoline* for informal designations. Variable generic classifications of the Arvicolinae introduce additional nomenclatural complications for a review such as ours. Many nomenclatural controversies result from the fact that many paleontologists want their taxonomic allocations to reflect their conceptualization of the systematic relationships of the various taxa, yet there is no agreement on the systematic relationships within the

246 Christopher J. Bell and Ernest L. Lundelius Jr. (co-chairmen), et al.

THIS CHAPTER	ALTERNATIVE NAMES	
Allophaiomys pliocaenicus	Microtus pliocaenicus	
Cosomys primus	Mimomys (Cosomys) primus	
Lasiopodomys deceitensis	Microtus deceitensis	
Lemmiscus curtatus	Lagurus curtatus	
Loupomys monahani	Mimomys monahani	
Microtus aratai	Pitymys aratai	
Microtus guildayi	Allophaiomys, Pedomys, or Pitymys guildayi	
Microtus llanensis	Pedomys llanensis	
Microtus meadensis	Pitymys meadensis, Terricola meadensis	
Mictomys kansasensis	Synaptomys kansasensis	
Mictomys meltoni	Synaptomys meltoni	
Mimomys virginianus	Mimomys (Cromeromys) virginianus	
Mimomys dakotaensis	Mimomys (Cromeromys) dakotaensis	
Ogmodontomys poaphagus	Mimomys (Ogmodontomys) poaphagus	
Ogmodontomys sawrockensis	Mimomys (Cosomys) sawrockensis	
Ondatra annectens	Ondatra zibethicus/annectens (chronomorph)	
Ondatra idahoensis	Ondatra zibethicus/idahoensis (chronomorph)	
Ondatra zibethicus (in part)	Ondatra nebracensis, Ondatra nebrascensis, Ondatra zibethicus/zibethi	
	(chronomorph)	
Ophiomys	Mimomys (Ophiomys)	
Pliopotamys meadensis	Ondatra zibethicus/meadensis (chronomorph)	
Propliophenacomys parkeri	Pliophenacomys parkeri, ?Cseria parkeri	

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TABLE 7.3 T	'axonomic S [,]	ynonymies f	for Arvico	line Roc	lents
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group as a whole or of species within certain groups. Perhaps the most controversial generic classifications concern species variously placed in the genera Cosomys, Mimomys, Ogmodontomys, and Ophiomys (representing predominantly Blancan radiations) and those placed in Allophaiomys, Arvicola, Lasiopodomys, Microtus, Pedomys, Phaiomys, Pitymys, and Terricola (representing predominantly Irvingtonian and Rancholabrean radiations). A recent molecular analysis of the extant members of the latter group resulted in the recognition of a monophyletic clade of endemic North American species that includes the species placed in the "pitymyine" genera Pedomys and Pitymys and those placed in the genus Microtus (Conroy and Cook 2000). "Pitymyines" were found to be paraphyletic (supporting previous statements to that effect by Moore and Janecek 1990 and Repenning 1992). In light of these multiple studies indicating an independent derivation of "pitymyine" species, we place these species in the genus Microtus. To provide a guide to the literature, we list common alternative nomenclature in table 7.3 and indicate alternative generic assignments parenthetically in the text where confusion is most likely to occur.

A similar problem, perhaps even more intractable, surrounds the nomenclature and relationships of Pliocene and Pleistocene horses. Recent taxonomic and systematic treatments (Winans 1989; Azzaroli and Voorhies 1993; Downs and Miller 1994; Azzaroli 1995; Repenning et al. 1995) differ significantly in conclusions and recommendations. We made no effort to resolve these issues, particularly those surrounding the propriety of using *Plesippus* or *Equus* for the nominal species *francescana, idahoensis,* and *simplicidens* (see also Albright 1999). For these latter taxa, we retain the most common (or most recent) usage in our discussion of faunas but indicate the taxonomic uncertainty with the use of quotation marks around the name.

The fossil equids assigned to *Nannippus phlegon* are more properly referred to *Nannippus peninsulatus*. *Equus phlegon* was transferred to *Nannippus* by Hibbard (1937) and Stirton (1940). The type specimen of *Hippotherium peninsulatum* was subsequently determined to be indistinguishable from *N. phlegon* (MacFadden 1984). *Nannippus peninsulatus* is used throughout our text for this species.

The details of the taxonomic problems with North American mylodont sloths were reviewed by McDonald (1995), who recommended using *Paramylodon harlani* for the Irvingtonian and Rancholabrean form and *Glossotherium chapadmalense* for Blancan forms. Because the recognized temporal ranges of land mammal ages are dynamic, such a division would necessitate taxonomic changes on the basis of shifting temporal boundaries. In light of the presumed (but not yet fully demonstrated) ancestor-descendant relationship of the two forms (McDonald 1995), it may be preferable to synonymize the taxa or delimit the lineage based on morphologic rather than chronologic criteria. As used by McDonald, *P. harlani* and *G. chapadmalense* differ greatly in size. We use the size criterion here in order to preserve the effective taxonomy of McDonald, but because the mammal age boundaries proposed here differ from those used by McDonald, *P. harlani* is known not only from the Irvingtonian and Rancholabrean but also from the latest Blancan.

TEMPORAL DIVISIONS OF THE MAMMAL AGES

Temporal divisions of the Blancan and Irvingtonian mammal ages were first proposed in the 1970s and can be categorized generally based on two operational approaches. Figure 7.3 summarizes the different approaches and their current relationships to one another. The first approach used broad-scale changes in mammalian faunas as the basis for temporal division. This was the foundation for the recognition (Kurtén 1971; C. Schultz et al. 1977, 1978) of two major divisions of the Blancan (Rexroadian and Senecan) and two of the Irvingtonian (Sappan and Sheridanian).

The second approach was based on evolutionary changes and dispersal history within a single lineage of mammals, the arvicoline rodents (voles, lemmings, muskrats). Following the initial explorations of the biostratigraphic utility of arvicoline rodents for faunal correlation (Hibbard 1944, 1949a, 1959; Hibbard and Zakrzewski 1967), they were soon recognized to be among the most useful biostratigraphic tools in many terrestrial settings. They are abundant, reproduce at a phenomenal rate, and appear to evolve rapidly. Several lineages demonstrate a number of significant evolutionary trends in the dentition, including the increase in hypsodonty and height of dentine tracts, the reduction, fusion, or loss of roots, the addition of cement in the reentrant angles, and an increase in crown complexity and length of the lower first molar (Hinton 1926; L. Martin 1979; Repenning 1987; Fejfar and Repenning 1992). These rodents are not well represented in deposits in the southern part of North America, thus limiting their applicability to biochronologies in lower latitudes. Longitudinal effects have been proposed also, but some may be a result of inadequate sampling and all need further critical evaluation.

Two alternative frameworks for dividing the Blancan and Irvingtonian based extensively on arvicoline rodents

were proposed almost simultaneously (Repenning 1978; L. Martin 1979). An outline of the structure for each is provided here, but the details are discussed under the relevant mammal ages.

L. Martin (1979) established a series of arvicoline rodent zones for the late Cenozoic faunas of the United States based primarily on faunas from the Great Plains. He proposed seven zones for the late Cenozoic based on first and last appearances of taxa and stages of progressive evolution within lineages. Zones were numbered consecutively from oldest to youngest. Zone I was considered to be Hemphillian, zones II and III were within the Blancan, zones IV through VI spanned the Irvingtonian, and zone VII represented an undifferentiated Rancholabrean and Holocene. Early attempts to include faunas from outside the Great Plains in these zones and preliminary attempts to correlate the proposed zones with the Eurasian sequence were explored by L. Martin (1979), but the zones were and are used almost exclusively in the Great Plains. The proposed zones and their boundaries have not been critically reevaluated in recent years, but the taxa used to define boundaries in Martin's proposal were nearly identical to those used in Repenning's model; therefore changes over the last two decades in our understanding of the evolutionary history and temporal range of these taxa apply equally to both models (figure 7.3).

A more elaborate arvicoline biochronology was outlined by Repenning and Fejfar (1977) and subsequently expanded in an extended abstract by Repenning (1978). Continued development and modification in subsequent years (Repenning 1980, 1984, 1987, 1992; Repenning et al. 1990, 1995; Fejfar and Repenning 1992; Bell and Repenning 1999; Bell 2000) resulted in a current biochronology that differs in many key aspects from that originally proposed. From its inception, this scheme relied extensively on external age control from radioisotopic dating, paleomagnetic correlations, and climatic correlations. Repenning proposed five divisions of the Blancan, Blancan I through Blancan V, numbered consecutively from oldest to youngest. The early papers (through 1987) outlining this scheme recognized two temporal divisions of the Irvingtonian and two of the Rancholabrean, again numbered I and II from oldest to youngest within each mammal age. Rancholabrean I included faunas that were acknowledged to be pre-Bison in age. Following the recommendation by Lundelius et al. (1987) that Bison be used as the defining taxon for the Rancholabrean, Rancholabrean I was abandoned by Repenning et al. (1990); faunas previously placed in Rancholabrean I were accommodated by a new division, Irvingtonian III, thus leaving an undifferentiated Rancholabrean.



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FIGURE 7.3 Summary chart showing temporal boundaries of the late Hemphillian, Blancan, Irvingtonian, and Rancholabrean, relative to defined epochal boundaries and the geomagnetic polarity time scale of Berggren et al. (1995). The subages proposed by C. Schultz et al. (1978), the arvicoline rodent zones of L. Martin (1979), and the arvicoline divisions proposed by Repenning (1987; Repenning et al. 1990) are shown. Dashed lines represent uncertain boundary placements or undefined temporal divisions. Temporal divisions in parentheses are not recognized in this chapter (see text).

The Blancan, Irvingtonian, and Rancholabrean Mammal Ages 249

GEOGRAPHIC RESTRICTION

There are problems with defining mammal ages that are intended to be used over entire continents and to have isochronous boundaries. Dispersal is by nature a timetransgressive phenomenon, and when the temporal duration of dispersal of defining taxa can be resolved, mammal age boundaries may become time-transgressive (see also Walsh 1998). The diachronous boundaries that result may, in some cases, be a more accurate reflection of our understanding of faunal dynamics (see discussion in Fejfar and Repenning 1992; Repenning 1992; Repenning et al. 1995), but they also present additional complications that remain largely unexplored. The issues and questions surrounding mammalian faunal provinciality in the Pliocene and Pleistocene are discussed in greater length in this chapter, but one persistent problem we encountered in our efforts to prepare this chapter must be clarified at the outset.

Sufficient evidence is available to indicate that the higher latitudes in North America warrant an independent biochronology for the Pliocene and Pleistocene. In recognition of that fact, and in an effort to stimulate development of such a chronology, we formally recommend that use of the terms Blancan, Irvingtonian, and Rancholabrean be restricted geographically to the portions of the continent south of 55°N latitude. This boundary is arbitrary and must be evaluated critically, but it is drawn along a "data-free zone" where no relevant mammal faunas are known between those of southern Canada and the United States and those of Alaska and the Yukon Territory. This geographic restriction is consistent with our understanding of faunal change at higher latitudes and conforms with existing operational practice of members of this committee and many of our colleagues.

In the case of the Blancan, Irvingtonian, and Rancholabrean, we suggest that Alaska be regarded as part of the Beringian faunal region (*sensu* Fejfar and Repenning 1992). Faunas located north of 55°N latitude may be considered temporal equivalents of their counterparts to the south but clearly need independent biochronologies.

BLANCAN

HISTORICAL CONTEXT

The term *Blancan* was first proposed by Wood et al. (1941), based on the fauna at Mt. Blanco and the adjoining draws, near the "old rock house" north of Crawfish

Draw, Crosby County, Texas. The Blanco Fauna was at different times regarded as Pliocene (Osborn and Matthew 1909; Osborn 1910; Matthew 1924; Simpson 1933) and early Pleistocene (Meade 1945; Hibbard 1958). It is now considered to be largely Pliocene in age, but latest Blancan faunas (those dating to between 1.77 and 1.35 Ma) are Pleistocene.

HISTORICAL CHARACTERIZATION

In the following paragraphs, we review the historical characterization of the Blancan. The definition and characterization as currently understood appear under the next heading.

In the original characterization of the Blancan, Wood et al. (1941) listed *Borophagus*, *Ceratomeryx*, *Ischyrosmilus*, and *Plesippus* (now sometimes identified as *Equus*) as "index taxa" for the Blancan (the taxa known only from the Blancan as of 1940). The following additional taxa were noted by Wood et al. (1941) to appear for the first time during the Blancan (but were not limited to it): glyptodonts, *Megalonyx*, *Paramylodon*, hystricomorphs, *Canis*, *Felis*, *Camelops*, *Tanupolama*, *Platygonus*, *Cervus*, and *Odocoileus*. In their article, the last appearance of *Anancus*, *Lutravus*, *Megatylopus*, *Nannippus*, and ?*Neohipparion* was during the Blancan.

Several of the taxa involved in the characterization provided by Wood et al. were reevaluated in subsequent years, and changes in their taxonomy and known stratigraphic range resulted in changes in the characterization of the Blancan. For example, the small Blancan mylodont sloth (*"Paramylodon"* of Wood et al. 1941) is now recognized as *Glossotherium* (McDonald 1995), *Tanupolama* is now recognized as *Hemiauchenia* (Webb 1974b), and *Megalonyx* (Hirschfeld and Webb 1968) and *Platygonus* (Voorhies 1990) are now known from the Hemphillian.

Further discussion of the historical treatment of the Blancan was provided by Lundelius et al. (1987). In that report, the Blancan was not formally defined (*sensu* Woodburne 1977) but was characterized by the presence of Nannippus peninsulatus, "Equus (Dolichohippus) simplicidens," Stegomastodon, Borophagus diversidens, Trigonictis, Nekrolagus, Procastoroides, cotton rats in the Sigmodon medius–Sigmodon minor lineage (all here considered S. minor), and arvicolines with rooted teeth (e.g., Ophiomys and Nebraskomys). The Blancan was distinguished from the Hemphillian by the absence of Machairodus, Agriotherium, Plesiogulo, Osteoborus, Osbornoceras, Prosthennops, Pliohippus, Astrohippus, Dinohippus, Neohipparion, and the rhinoceroses Teleoceras and Aphelops. After that publication Dinohippus sp. was reported from low in the Blancan portion of the Palm Springs Formation of southern California (Downs and Miller 1994), a rhinoceros was reported by Madden and Dalquest (1990) from the Blancan Beck Ranch Fauna of Texas, and *Teleoceras* was reported from the Pipe Creek Sinkhole in Indiana (Farlow et al. 2001), a fauna that also includes *Ogmodontomys* (and is therefore Blancan by our definition). *Teleoceras* was also listed without comment from the Saw Rock Canyon Fauna in Kansas by Prothero and Manning (1987), Prothero et al. (1989), and Prothero (1998); we are not aware of any published description or other records of that occurrence, but the Saw Rock Canyon Fauna contains *Ogmodontomys* and is therefore Blancan.

CURRENT DEFINITION AND CHARACTERIZATION

The Blancan is currently defined by the first appearance in North America south of 55°N latitude of arvicoline rodents in the genera Mimomys, Ogmodontomys, and Ophiomys. Ogmodontomys sawrockensis and Ophiomys mcknighti were used by Repenning (1987) and Repenning et al. (1990) to define the Blancan (reported under the names Mimomys (Cosomys) sawrockensis and Mimomys (Ophiomys) mcknighti). The earliest appearance of these two species was reported to be at approximately 4.8 Ma in the Upper Alturas Fauna in California (Repenning 1987). An alternative species, Mimomys panacaensis, was proposed by Lindsay et al. (2002). The enamel microstructure of this species is similar to that of Eurasian Mimomys and differs from the North American lineages Cosomys, Ogmodontomys, and Ophiomys (Mou 1998). This species was recovered from the Panaca Fauna in Nevada, where its earliest appearance is at approximately 4.98 Ma.

The characterization of the Blancan includes taxa that are limited to the Blancan, those that appear in earlier mammal ages but are common in Blancan faunas, and those that make their first appearance in the Blancan but persist into younger mammal ages. These are listed separately here, followed by comments justifying our treatment of some of the taxa and relevant faunas.

Taxa limited to the Blancan include Megalonyx leptostomus, Glossotherium chapadmalense, Sylvilagus webbi, Aluralagus, Pewelagus dawsonae, Pratilepus kansasensis, Dipoides rexroadensis, Procastoroides, Guildayomys, Hibbardomys, Nebraskomys, Pliophenacomys, Sigmodon curtisi, Sigmodon minor, Mictomys vetus, Ogmodontomys, Ophiomys, Pliopotamys, Ondatra idahoensis, Pliolemmus, Borophagus diversidens, Canis lepophagus, Ursus abstrusus, Platygonus bicalcaratus, Platygonus pearcei, and Nannippus peninsulatus. Taxa that make their first appearance in earlier mammal ages but persist into the Blancan include *Alilepus*, *Hypolagus*, *Nekrolagus*, *Paenemarmota*, *Prodipodomys*, *Satherium*, *Borophagus hilli*, *Trigonictis*, *Megantereon*, and *Rhynchotherium*.

Taxa that first appear in the Blancan but persist into the Irvingtonian or younger include *Glyptotherium*, *Blarina*, *Sylvilagus*, *Miracinonyx inexpectatus*, *Smilodon gracilis*, and *Stegomastodon*. Taxa that first appear in latest Blancan faunas (those that are elsewhere often considered to be early Irvingtonian) include *Nothrotheriops*, *Paramylodon harlani*, *Holmesina*, *Lepus*, *Allophaiomys pliocaenicus*, *Microtus* with five closed triangles on the lower first molar, *Mictomys kansasensis/meltoni*, *Neofiber*, *Ondatra annectens*, *Phenacomys*, *Synaptomys*, *Sciurus*, *Canis edwardii*, *Chasmaporthetes*, *Lutra canadensis*, *Homotherium*, *Platygonus vetus*, and *Mammut americanum*.

A Hemphillian record of *Nekrolagus* from Florida was mentioned by White (1991b), but the list of referred specimens in that article does not include any Hemphillian fossils or any specimen from Florida. The single specimen catalogued as *Nekrolagus* in the Florida Museum of Natural History is referable to *Alilepus* based on dental morphology (D. R. Ruez, pers. obs., 2001).

Stegomastodon survived into the Irvingtonian, and it is found with *Mammuthus* in several faunas, but the few localities with external age control suggest that the time of overlap was brief. Co-occurrences were reported from the Gilliland Fauna of Texas (Hibbard and Dalquest 1966); the Martin Ranch Fauna at the base of the Tule Formation in Briscoe County, Texas (G. Schultz 1990b; Dalquest and Schultz 1992), at the same stratigraphic level as a volcanic ash dated at 1.2–1.3 Ma (Izett 1977, 1981; Izett et al. 1981); possibly Holloman, Oklahoma (Hay and Cook 1930; Meade 1953; but see Madden 1983); Tortugas Mountain, New Mexico (Lucas et al. 1998); Fullerton, Nebraska (Madden 1986); near Taylor, Arizona (Madden 1986); and Faunule C in Mesilla Basin, New Mexico (Vanderhill 1986).

Our restriction of *Pliophenacomys* to the Blancan is based in part on the transfer of *Pliophenacomys parkeri* to *Propliophenacomys* by L. Martin (1994); *Pliophenacomys osborni* was reported from the Wellsch Valley faunas (Stalker and Churcher 1982; Repenning 1987) and was shown schematically to be associated with *Borophagus diversidens, Mammuthus*, and *Microtus paroperarius* on the Stalker and Churcher wall chart. Until the Wellsch Valley faunas are published in their entirety with adequate stratigraphic data, we discount these occurrences in our evaluation of temporal ranges of taxa. We are aware of only one Irvingtonian occurrence of *Chasmaporthetes*. It is found with *Mammuthus* in the El Golfo Fauna in Mexico (Shaw 1981; Lindsay 1984).

HEMPHILLIAN-BLANCAN BOUNDARY DETERMINATION

In recent years, additional work on latest Hemphillian and earliest Blancan faunas yielded new information on the age of the Hemphillian–Blancan boundary. The beginning of the Blancan now appears to fall between approximately 4.6 and 5.2 Ma. This age range is based on nine vertebrate localities with radiometric dates or paleomagnetic data, discussed individually later in this chapter. If these age estimates for the boundary are correct, then the transition from Hemphillian faunas to Blancan ones took place somewhat later than the 5.335 Ma Miocene–Pliocene boundary as defined in the Mediterranean marine section (Van Couvering et al. 2000).

The Pinole and Santee faunas are the youngest radiometrically dated Hemphillian faunas. The Pinole Fauna in California was recovered from an ash with a K-Ar date of 5.2 ± 0.1 Ma (Evernden et al. 1964; Sarna-Wojcicki 1976). The Pinole Fauna contains Machairodus, Plesiogulo, Osteoborus, Dinohippus, Sphenophalos, and Megalonyx and therefore is considered to be late Hemphillian in age (Stirton 1939, 1951; Tedford et al. 1987). The Santee Fauna in Nebraska (Boellstorff 1978; Voorhies 1990) is overlain by an ash dated 5.0 ± 0.2 Ma by fission-track methods on glass shards (Voorhies 1977). The Santee Fauna contains Hesperoscalops mcgrewi, Dipoides sp., mylagaulids, megalonychids, a rhinoceros, an early cervid, and Protopliophenacomys parkeri (="Propliophenacomys" of L. Martin 1975 and "?Cseria parkeri" of Voorhies 1990; see Korth 1994 and L. Martin 1994) and is considered to be late Hemphillian (Voorhies 1977, 1990; L. Martin 1975).

The Palmetto Fauna from the Upper Bone Valley Formation of central Florida includes *Felis rexroadensis*, *Megantereon hesperus*, *Mylohyus elmorei*, *Hexobelomeryx*, *Nannippus minor*, *Neohipparion phosphorum*, and *Calippus* sp. It is considered to be latest Hemphillian (Wright and Webb 1984). The earliest North American appearance of an antlered deer, *Eocoileus gentryorum*, was also reported from this fauna (Webb 2000). The Upper Bone Valley Formation intertongues with the marine Tamiami Formation. The phosphatic sands and gravels of the Upper Bone Valley Formation represent a high-energy backfilling episode, correlated on the basis of the marine fauna of the Tamiami Formation with an immediately post-Messinian (Zanclean) sea level rise in the early Pliocene (Webb et al. 1978). This interpretation makes the Upper Bone Valley Formation correlative with chron C₃n at approximately 5.0 Ma.

The oldest stratigraphic horizon containing the arvicoline rodent *Ogmodontomys sawrockensis* in the Upper Alturas Fauna of California is 21 m beneath a basalt flow dated 4.7 \pm 0.5 Ma (Repenning 1987). This occurrence led Repenning (1987) to place the Hemphillian–Blancan boundary at 4.8 Ma.

The San Timoteo Badlands in southern California contain a stratigraphic section that spans the Hemphillian-Blancan boundary (Albright 1999). The basal unit of the section contains Repomys gustelyi reported to be in chron C3An.2n, dating about 6.3 Ma. The Mt. Eden Fauna from near the top of the Mt. Eden Formation contains Megacamelus merriami, Teleoceras, Agriotherium gregoryi, Dinohippus osborni, and Pediomeryx hemphillensis (Webb 1983; Albright 1999), and was interpreted to be Hemphillian; it was correlated to chron C3r and assigned a tentative age of approximately 5.6 Ma (Albright 1999). The earliest taxon indicative of a Blancan age, Thomomys, occurs well up in the San Timoteo Formation in chron C2Ar at about 3.8 Ma (the only Hemphillian records of Thomomys of which we are aware are from the Santee and Devils Nest Airstrip faunas; Voorhies 1990). Other characteristic Blancan taxa occur at various positions above this. Thus, although superposed faunas are present, detailed resolution of the boundary is not possible. In this section the Hemphillian-Blancan boundary lies somewhere between 5.6 and 3.8 Ma.

Fission-track and 40 Ar/ 39 Ar dates from sediments containing both Blancan and Hemphillian faunas in Guanajuato, Jalisco, and Hidalgo, Mexico, were reported by Kowallis et al. (1998). The fission-track dates from Blancan sediments range from 3.9 ± 0.3 to 4.6 ± 0.3 Ma, whereas the fission-track dates associated with the Hemphillian faunas range from 4.8 ± 0.2 to 4.4 ± 0.3 Ma. The 40 Ar/ 39 Ar dates for the Blancan range from 3.36 ± 0.04 to 4.74 ± 0.14 Ma. The one 40 Ar/ 39 Ar date for the Hemphillian is 4.89 ± 0.16 Ma. These dates place the Hemphillian–Blancan boundary in Mexico between 4.74 ± 0.14 and 4.89 ± 0.16 Ma.

In Chihuahua, Mexico, the late Hemphillian Yepómera Fauna is overlain by the early Blancan Concha Fauna (Lindsay et al. 1984; Lindsay and Jacobs 1985). These faunas are separated by approximately 25 m of section in the same reversed magnetozone, interpreted to be chron C3n.2r dated between 4.62 and 4.80 Ma (Berggren et al. 1995) between the Sidufjall (chron C3n.3n) and Nunivak (chron C3n.2n). No discernible breaks in the sequence were recorded (Lindsay and Jacobs 1985). The late Hemphillian Yepómera Fauna contains Machairodus, Megantereon, Pseudaelurus, Agriotherium, Taxidea, canids, Paenemarmota, Spermophilus, Notolagus, Prosthennops, Hexobelomeryx, Megatylopus, Astrohippus stocki, Dinohippus mexicanus, Nannippus, Neohipparion, Teleoceras, and a proboscidean (Ferrusquía-Villafranca 1978; Lindsay et al. 1984; Lindsay and Jacobs 1985). The Concha Fauna is approximately 25 m higher in the section and contains the arvicoline rodent Pliophenacomys wilsoni and the gopher Geomys minor; Lindsay and Jacobs (1985) considered it to be early Blancan. The Concha Fauna also contains a horse that Lindsay and Jacobs (1985) referred to ?Equus sp. The boundary in this section presumably falls somewhere between 4.62 and 4.80 Ma. This placement is younger than boundary determinations in other sections.

Recent work by Lindsay et al. (2002) demonstrated the presence of superposed Blancan and Hemphillian faunas in eastern Nevada. The Panaca Formation previously produced a Hemphillian fauna with Pliohippus, ?Teleoceras, and Hemiauchenia (Stock 1921), but Lindsay et al. did not find Hemphillian fossils from the Panaca Formation. Blancan small mammals were recovered from a reversed magnetozone they assigned to chron C3n.3r (the reversed interval between the Sidufjall and Thvera). The fauna includes Hypolagus edensis, Hypolagus tedfordi, Hypolagus cf. H. ringoldensis, Pewelagus dawsonae, Lepoides lepoides, Nekrolagus progressus, Pliogeomys parvus, Perognathus mclaughlini, Prodipodomys minor, Prodipodomys tiheni, Repomys panacaensis, Repomys n. sp., and Mimomys panacaensis (Lindsay et al. 2002). The Hemphillian fauna from the Panaca beds (of Stock 1921) was attributed to a normal magnetozone exposed in the area where Stock made his collections. On this basis they place the Hemphillian-Blancan boundary at about the top of the Thvera (chron C3n.4n) dated to approximately 4.98 Ma (Berggren et al. 1995).

In western Nevada, a 280-m-thick section on the western slope of the Pine Nut Mountains, near Carson City, produced six magnetozones correlated by an included pumice zone dated isotopically at 4.96 ± 0.02 Ma. Ursus abstrusus was recovered from a reversed magnetozone (chron C3n.3r) above the pumice zone (Kelly 1994; Lindsay et al. 2002; this is the earliest dated occurrence of Ursus). A rhinoceros was later recovered (Kelly 1997) 100 m below the pumice zone (and the Ursus specimen) in a reversed magnetozone assigned by Lindsay et al. (2002) to chron C3r. These occurrences support the placement of the Hemphillian–Blancan boundary in Nevada in chron C3n.3r, between 4.89 and 4.98 Ma (Berggren et al. 1995).

TEMPORAL EXTENT

Current age estimates of early Blancan faunas indicate that the beginning of the Blancan dates to between 4.6 and 5.2 Ma. The upper limit of the Blancan is marked by the lower limit of the Irvingtonian, here defined by the earliest appearance of *Mammuthus* south of 55°N latitude. As currently understood, the earliest known specimens of *Mammuthus* appear at approximately 1.35 Ma. Most of the Blancan is therefore within the Pliocene Epoch (5.335–1.77 Ma), but the youngest Blancan faunas are earliest Pleistocene in age (according to the established epochal boundaries discussed earlier).

TEMPORAL DIVISIONS OF THE BLANCAN

Several efforts have been made in the last 30 years to achieve finer temporal resolution in the Blancan. Most of them rely on first and last appearances of certain mammalian taxa in specified stratified sequences or isolated localities. These appearances reflect immigration and extinction events and progressive species evolution within particular lineages. Such efforts may be hampered by problems of provinciality; latitudinal, regional, elevational, and ecological factors lead to faunal provincialism that together with lack of radiometric and paleomagnetic control can make correlation of faunas difficult. Despite such difficulties, some progress has been made in dividing the Blancan, although to date no single method or proposal is universally adopted or considered universally applicable.

One of the earliest attempts to recognize temporal divisions in the Blancan was carried out by Claude Hibbard and his students in the Great Plains. Extensive use of screenwashing techniques (Hibbard 1949c) resulted in the recovery of tremendous numbers of fossils of small mammals, providing a new data set with which to analyze and compare fossil faunas. Through careful analysis of faunal composition, reference to stratigraphic marker beds (as then understood), and tentative correlation to the classic glacial-interglacial sequence, Hibbard and his colleagues proposed an ordered sequence of faunas (Hibbard et al. 1965; see also Zakrzewski 1975b). Although this ordered sequence implicitly recognized change in mammalian faunas through time, Hibbard never proposed formal, named temporal divisions. Nevertheless, his pioneering efforts in this regard laid a solid foundation for subsequent temporal correlations and divisions of Blancan and later times. Not surprisingly, the Great Plains sequence continues to play an important role in biochronologic studies in the late Cenozoic.

Rexroadian and Senecan Other early proposals for dividing the Blancan centered on the initial recognition of two major temporal divisions: an early Blancan and a late Blancan. One such proposal was based on the immigration of South American mammals after the development of the Panamanian isthmus and the great American faunal interchange. Faunas predating the interchange (at approximately 2.5 to 2.7 Ma; Marshall et al. 1979; Webb and Rancy 1996) were proposed to be early Blancan faunas; those after the interchange were late Blancan (Kurtén and Anderson 1980).

An alternative proposal was based on the diverse and well-known Rexroad faunas in Kansas. These were recognizably distinct from other faunas in the region, and Kurtén (1971) proposed recognition of a separate mammal age, the Rexroadian, that would be based on these faunas. This proposal was rejected by C. Schultz et al. (1977, 1978), but the Rexroadian was retained as a unit in their proposed twofold division of Blancan faunas in the Great Plains. The older unit, the Rexroadian of Kurtén (1971), was expanded from the original concept to include the Sand Draw, Broadwater, Lisco, Blanco, and Hagerman, as well as the Rexroad faunas. The Rexroadian was characterized by what was then thought to be the first appearance in North America of Megantereon (now known from the late Hemphillian of Florida; Berta and Galiano 1983), Chasmaporthetes, Ursus, Trigonictis (now known from the Hemphillian; Voorhies 1990), Satherium, Stegomastodon, Mammut, Glyptotherium, true cervids, and, in part, by certain arvicoline rodents lacking cement in their reentrant angles (e.g., Nebraskomys, Pliopotamys, Ophiomys, and Pliolemmus) and giant beavers that lack distinct ridges on their incisor enamel (Procastoroides sweeti).

The upper part of the Blancan, for which C. Schultz et al. (1977, 1978) proposed the name Senecan, includes the Grand View, White Rock, Dixon, and Seneca faunas and part of the Mullen assemblage described by L. Martin (1972). Senecan faunas are characterized by the first appearance of Synaptomys (Plioctomys), Mictomys (Metaxyomys), Ondatra, Loupomys monahani (= Mimomys monahani of L. Martin 1972; see Koenigswald and Martin 1984), and Procastoroides idahoensis, which has ridged incisors. Based on faunas considered to be Senecan, the Rexroadian-Senecan boundary appears to fall near the Gauss-Matuyama (chron C2An-chron C2r) boundary. The Blanco Fauna, included by C. Schultz et al. (1978) in the Rexroadian, may be more properly considered Senecan. Although it lacks the taxa used to characterize the Senecan (Dalquest 1975), it lies in reversely magnetized sediments interpreted by Lindsay et al. (1975) as representing the early Matuyama chron (chron C2r.2r). The Guaje ash bed, which overlies the Blanco Formation and fauna, is dated to between 1.77 ± 0.44 Ma (Boellstorff 1976) and 1.4 ± 0.2 Ma (Izett et al. 1972).

The terms *Rexroadian* and *Senecan* were based on faunas from the Great Plains sequence and the Snake River Plain. They are most commonly applied to faunas in the Great Plains, and their potential application in other regions remains largely unexplored but seems to be limited.

Divisions Based on Arvicoline Rodents The most successful attempts to temporally divide the Blancan were based on the taxonomic composition and stage of evolution of arvicoline rodents. Arvicoline zones II and III were the two temporal divisions of the Blancan proposed by L. Martin (1979). Zone II was marked by the first appearance of muskrats (Pliopotamys) and arvicoline rodents with rootless teeth (Pliolemmus). The following species were included in this zone: Ogmodontomys poaphagus, Nebraskomys rexroadensis, Nebraskomys mcgrewi, Cosomys primus, Ophiomys taylori, Ophiomys meadensis, Pliophenacomys finneyi, Pliophenacomys primaevus, Pliopotamys minor, Pliopotamys meadensis, and Pliolemmus antiquus. Martin included the Fox Canyon, Rexroad, Broadwater, and Sand Draw faunas in this zone. Zone III was marked by the first records of bog lemmings and the last records of Mimomys, Ophiomys, Ogmodontomys, and Pliolemmus in North America. Martin listed the Grand View, White Rock, Dixon, Seneca, and Mullen b faunas as falling in this zone.

An alternative arvicoline rodent biochronology was presented and refined by Charles Repenning in a series of articles between 1977 and 2001. In its most recent iterations, Repenning's scheme presents a fivefold temporal division of the Blancan. Divisions are numbered consecutively from oldest to youngest and are named Blancan I through Blancan V. Two of the divisions (Blancan II and Blancan IV) currently are not defined (sensu Woodburne 1977) but are characterized by perceived evolutionary changes within species groups. We provisionally accept three of Repenning's temporal divisions in this chapter (Blancan I, Blancan III, and Blancan V), but in an effort to avoid terminological confusion, we do not propose alternative names. Similarly, we do not adopt the numbered dispersal event terminology proposed by Repenning (1987), and used in his subsequent reports. The ungainly problems and nomenclatorial confusion that can result from additional (purported or real) dispersal events limit the utility of that convention (see, for example, the terminological adjustments proposed by Repenning et al. 1995:16 to accommodate a purported record of the Eurasian muskrat Dolomys in California, the identification of which was subsequently changed to *Pliopotamys* [Repenning 1998:49]).

The recognition of the defined temporal divisions in Repenning's chronologic framework is based on purported immigration events into North America across the Bering Land Bridge, but not all presumed immigrants have a fossil record in Beringia that predates their appearance in the United States. Multiple-taxon definitions were and are used for Repenning's arvicoline divisions. Potential intercontinental dispersal corridors and intracontinental dispersal pathways were discussed most recently by Repenning (1998). The reported temporal extent, definition, and characterization of the Blancan divisions are provided later in this chapter and are based on the most current published versions of Repenning's scheme (Repenning et al. 1990, 1995; Repenning 1998, 2001; Bell 2000). For the sake of completeness, we present Repenning's framework in its full form, but our consensus is that the Blancan II and IV should not be recognized at this time.

The temporal spans presented here for the divisions are somewhat different from those given by Repenning (1987), Repenning et al. (1990), and Bell (2000). These differences result from different conventions in the use of age calibrations of the Geomagnetic Polarity Time Scale; for the purposes of standardization in this volume we follow Berggren et al. (1995) for the dates of geomagnetic polarity boundaries.

BLANCAN I (APPROXIMATELY 4.9-4.62 MA)

The base of this division is defined by the immigration of Ophiomys and Ogmodontomys (both given as subgenera of Mimomys by Repenning 1987; Repenning et al. 1990). Ophiomys mcknighti is reported from several localities in the western United States, and it is found with Ogmodontomys sawrockensis [= Mimomys (Cosomys) sawrockensis of Repenning 1987 and Repenning et al. 1990] in the Upper Alturas Fauna of California, dated to approximately 4.8 Ma (21 m below a basalt flow dated at 4.7 ± 0.5 Ma; Repenning 1987); O. sawrockensis is also found in the Maxum Fauna of California and the Saw Rock Canyon Fauna in Kansas (May 1981; Repenning 1987; Hibbard 1957), but external age control is unavailable at those localities. Mimomys panacaensis is another early Blancan arvicoline rodent that appears, on the basis of enamel microstructure, to be more closely related to Eurasian Mimomys species than to the North American lineages Ophiomys, Ogmodontomys, and Cosomys (Mou 1997, 1998). It is known from the Panaca Fauna in Nevada

and was assigned an age of 4.98 Ma (Lindsay et al. 2002). It provides an additional taxon by which the Blancan I can be defined.

In the earlier papers of Repenning, *Nebraskomys* also was used to define this interval. The only potential Blancan I specimen (from the Verde Fauna in Arizona) of this rare arvicoline is not referable to that taxon (it cannot be identified reliably to any genus; Czaplewski 1990; Winkler and Grady 1990; see also the discussion in Bell 2000).

Pliophenacomys appears in North America for the first time during the Blancan I; its earliest appearance is in the Concha Fauna in Mexico (Lindsay and Jacobs 1985). The identification of *Pliophenacomys* from the Verde Fauna in Arizona (Repenning 1987) is in error; the material in question was reidentified as *Ogmodontomys poaphagus* by Czaplewski (1990). The Verde Fauna is situated approximately 56 m above a basalt dated at 5.6 Ma and is placed at the base of the Nunivak subchron (chron C3n.2n; Bressler and Butler 1978; Czaplewski 1990), now recalibrated to about 4.62 Ma (Berggren et al. 1995). This fauna thus sits at the boundary of the Blancan I and II as recognized by Repenning et al. (1990).

BLANCAN II (APPROXIMATELY 4.62-4.1 MA)

The Blancan II is currently undefined. Its recognition was based on perceived evolutionary transitions in Ophiomys in the Pacific Northwest and in Pliophenacomys and Ogmodontomys in faunas east of the Rocky Mountains (Repenning 1987). An expanded justification for the Blancan II was provided by Repenning et al. (1990), whose support for this interval was based in part on a desire to "maintain equivalent biochronologic units" between Europe and North America (Repenning et al. 1990:386, 398). To this end, the age of the earliest record of *Germanomys* in Asia was used to draw an arbitrary boundary for the Blancan II in North America (Repenning et al. 1990:397-398), although no North American immigration event can be definitively identified. The Germanomys record used by Repenning et al. (1990) was from Yushe Basin in China, where its first stratigraphic appearance is just below the Nunivak normal magnetic polarity chron (chron C3n.2n). An age of 4.2 Ma was given by Repenning et al. (1990), but recalibration of the GPTS and the Yushe Basin faunas yields a new age of 4.62 Ma for the base of the Nunivak (Berggren et al. 1995; Flynn 1997). We preserve the intent of Repenning et al. (1990) by using the Germanomys record from Yushe Basin to denote the beginning of the Blancan II but note that the arbitrary temporal boundary would now be placed at 4.62 Ma.

The Blancan II is further characterized by a vole with a morphology on the lower first molar that is intermediate between *Ophiomys mcknighti* and *Ophiomys taylori* (known from the Blancan III) and by *Ogmodontomys poaphagus* and *Pliophenacomys finneyi*.

BLANCAN III (APPROXIMATELY 4.1-3.0 MA)

The first appearance of the muskrat lineage defines the beginning of the Blancan III (Repenning 1987; Repenning et al. 1990). The earliest known North American muskrat is a single specimen from the Etchegoin Formation in the Kettleman Hills in California (Repenning et al. 1995). This specimen was originally identified as the Eurasian muskrat *Dolomys* (Repenning et al. 1995) but was subsequently reidentified as *Pliopotamys* (Repenning 1998:49). This specimen is stratigraphically below a volcanic tuff identified as the Lawlor Tuff, which is dated elsewhere at 4.1 ± 0.2 Ma (Sarna-Wojcicki et al. 1991).

Other early records of *Pliopotamys* include *Pliopotamys minor* from near the base of the section in the Hagerman Fossil Beds National Monument in Idaho (Zakrzewski 1969), which may be as old as 4.0 Ma (G. McDonald et al. 1996). It is also known from the Taunton Fauna in Washington (Repenning 1987), which may be approximately correlative with Hagerman (Gustafson 1985) or slightly older (Repenning 1987). *Pliopotamys meadensis* is found in the Great Plains in the Deer Park (Kansas; Hibbard 1956) and Sand Draw (Nebraska; Hibbard 1972) faunas, but reliable external age control for these localities is lacking.

The Blancan III is characterized by *Ophiomys magilli*, *Ophiomys taylori*, *Ogmodontomys poaphagus*, *Cosomys primus*, *Nebraskomys*, and *Pliophenacomys primaevus*. The earliest occurrence of *Pliolemmus antiquus* probably is also from Blancan III, but external age control is lacking for most of the localities from which this species is known. Its earliest occurrence probably is in the Bender locality in Kansas, possibly as old as 3.2 Ma (Hibbard 1972:106; R. Martin et al. 2000). Its youngest occurrence is in either the Sanders or Cita Canyon fauna.

The identification of *Nebraskomys* from the Verde Fauna (Repenning 1987) is in error (Czaplewski 1990; Winkler and Grady 1990). Its earliest appearance seems to be in the Rexroad 3 locality in Kansas, where it occurs in normally magnetized sediments (Lindsay et al. 1975) that R. Martin et al. (2000) tentatively correlated with chron C2An.3n (early Gauss). That normal polarity interval is now dated to between 3.58 and 3.33 Ma (Berggren et al. 1995).

BLANCAN IV (APPROXIMATELY 3.0-2.5 MA)

The Blancan IV is undefined. The lower temporal boundaries proposed by Repenning (1987; at 3.2 ± 0.2 Ma) and Repenning et al. (1990; at 3.0 Ma) were drawn arbitrarily. The 1990 age of 3.0 Ma was chosen to achieve balance in correlation between Europe and North America and to accommodate the entire Hagerman fossil sequence within the Blancan III.

The Blancan IV is characterized by an *Ophiomys* with a lower first molar morphology intermediate between that of *O. taylori* and *O. parvus* (Repenning 1987; Repenning et al. 1990). *Ophiomys magilli* in the Great Plains apparently is replaced by *O. meadensis. Pliolemmus* is still found in faunas in the Great Plains, and *Ogmodontomys* and *Pliophenacomys* persist.

BLANCAN V (APPROXIMATELY 2.5-1.9 OR 1.72 MA)

The beginning of the Blancan V is defined by the immigration from Eurasia of the bog lemmings. To the west of the Rocky Mountains the bog lemming of the Blancan V faunas is Mictomys vetus, which appears in several faunas in Idaho at approximately 2.5 Ma (Repenning et al. 1995). Additional and approximately contemporaneous records are from 111 Ranch in Arizona (Galusha et al. 1984; Tomida 1987) and from Cita Canyon in Texas, where a different lemming (Plioctomys rinkeri) is found. The age estimation for these localities is based on paleomagnetic data; all of these faunas are near the Gauss-Matuyama boundary (the boundary between chrons 2An.1n and 2r.2r), the age of which was given as 2.58 Ma by Berggren et al. (1995). An age of 2.56 Ma for the base of Blancan V was reported by Repenning et al. (1995), based in part on climatic correlations (see Repenning and Brouwers 1992). Plioctomys also is found at approximately 2.4 Ma in the Fish Creek Fauna in Alaska (Repenning et al. 1987).

In latest Blancan V, *Mictomys* appeared in the Great Plains (as *M. landesi*), and *Plioctomys* became extinct. Based on traditional taxonomic treatments of muskrat taxa, the extant genus *Ondatra* appeared during Blancan V. A recent proposal that all North American muskrats, including *Pliopotamys*, be synonymized with the extant *Ondatra zibethicus* and that traditional species be recognized as "chronomorphs" (R. Martin 1996) results in a somewhat cumbersome terminology. Martin's proposal illustrates the problem of defining species boundaries in lineages with rich fossil records, but it has not been adopted elsewhere, and we retain traditional terminology here. Blancan V is characterized by *Ondatra idahoensis*, *Ophiomys parvus*, *Pliophenacomys osborni*, *Mictomys vetus*, and *Mictomys landesi*. The end of Blancan V is marked by the beginning of Irvingtonian I. In the most recent versions of Repenning's chronology, Irvingtonian I is diachronous and is defined in different regions based on different taxa.

We accept Blancan I, III, and V, as just discussed, and consider Blancan II to be essentially a continuation (and further characterization) of Blancan I. Similarly, Blancan IV is a continuation and further characterization of Blancan III. For our purposes, the recognized divisions, as defined by Repenning, span the following intervals: Blancan I (approximately 4.9–4.1 Ma), Blancan III (approximately 4.1–2.5 Ma), and Blancan V (approximately 2.5–1.9 or 1.72 Ma).

GEOGRAPHIC DISTRIBUTION

Blancan faunas occur primarily in the United States west of the Mississippi River, but important faunas are also found in Mexico and Florida, and temporal equivalents are known from Alaska (figure 7.4). Since the appearance of the earlier edition of this volume, we have learned a great deal about Blancan faunas in Mexico and the United States. The most complete sequences of Blancan faunas are in the Snake River Plain in Idaho, the Anza-Borrego Desert in southern California, the San Pedro Valley in southern Arizona, and in the Great Plains, especially Kansas. Where available, the dates of most of these sequences were established by a combination of radiometric and paleomagnetic methods (Johnson et al. 1975; Lindsay et al. 1975; Opdyke et al. 1977; Neville et al. 1979; Lindsay et al. 1984; Lundelius et al. 1987; Repenning 1992; Repenning et al. 1995; G. McDonald et al. 1996; Cassiliano 1999; R. Martin et al. 2000). First and last known stratigraphic appearances of many taxa were noted within the more complete sequences, and these sequences traditionally served as standards for the dating of other Blancan faunas. A summary of the key faunas from the major physiographic regions of North America and the recent literature pertaining to their correlation is presented in this section.

Pacific Northwest Sediments of the Ringold Formation in south-central Washington preserved a series of vertebrate faunas recovered from numerous localities that span the late Hemphillian (River Road Fauna with *Teleoceras;* Gustafson 1977, 1978) through early Blancan (White Bluffs and Blufftop faunas; Gustafson 1978, 1985; Repenning 1987; Repenning et al. 1995) and middle Blancan (Taunton Fauna; Tedford and Gustafson 1977; J. Morgan and Morgan 1995). These faunas, together with those from the northern Snake River Plain, provide the best stratigraphic information available for the Pacific Northwest.

The White Bluffs Fauna includes *Hypolagus, Nekrolagus, Dipoides rexroadensis, Ophiomys mcknighti, Megalonyx rohrmanni, Borophagus hilli* (identification by Wang et al. 1999), *Trigonictis cookii, Platygonus pearcei, Megatylopus,* and *Hemiauchenia.* The age of this fauna is not well established. Paleomagnetic data for the Ringold Formation were presented by Packer (1979) and were used by Repenning to tentatively place the White Bluffs Fauna just above the Sidufjall subchron (chron C3n.3n). The fauna includes what are probably the earliest North American occurrences of *Ophiomys, Dipoides rexroadensis,* and *Platygonus pearcei.*

The Blufftop Fauna contains *Sorex powersi, Paracryptotis rex*, and *Ophiomys mcknighti-taylori* (Gustafson 1985; Repenning et al. 1995). This fauna was recovered from reversely magnetized sediments near a magnetic polarity transition that Gustafson (1985) interpreted to be the Gauss–Gilbert boundary (with an acknowledgment that it could be an older event). An older-age interpretation was favored by Repenning (1987), who placed the fauna just below the Cochiti subchron (chron C3n.1n; Repenning's Haymaker's Orchard locality is part of the Blufftop Fauna).

The Taunton Fauna includes Megalonyx leptostomus, Hypolagus gidleyi, Hypolagus edensis, Hypolagus furlongi, Alilepus vagus, Procastoroides, Paraneotoma, Ophiomys taylori, Pliopotamys minor, Satherium piscinaria, Borophagus diversidens, Canis lepophagus, Trigonictis cookii, Parailurus, Capromeryx, and "Equus (Dolichohippus) simplicidens" (Tedford and Gustafson 1977; Gustafson 1985; White 1987, 1991b; J. Morgan and Morgan 1995; Repenning et al. 1995). The Taunton Fauna was originally reported to be approximately correlative with Hagerman faunas in Idaho (Gustafson 1985). Subsequent placement in chron C2Ar (Repenning 1987) was considered too old by Repenning et al. (1995), who suggested a younger age, approximately correlative with Sand Point, which would place the Taunton Fauna in the Kaena subchron (chron C2An.1r) at approximately 3.05 Ma.

Snake River Plain A series of faunas along the Snake River range in age from early Blancan (e.g., Hagerman) to latest Blancan (e.g., Froman Ferry) and occur over a distance of more than 160 km (100 miles) within the Glenn's Ferry Formation. The Glenn's Ferry Formation exposed at the Hagerman Fossil Beds National Monument (Hibbard 1969; Zakrzewski 1969; Bjork 1970; G. McDonald et al. 1996) spans a stratigraphic interval of approximately 183 m. Lava flows and ash units in the section yielded K–Ar dates ranging from 3.2 to 3.57 Ma and



FIGURE 7.4 Blancan localities and their temporal equivalents discussed in the text. The bold line represents 55°N latitude. Independent biochronologies should be established for the region north of this line, and the term Blancan should not be applied to faunas there. Localities with external chronologic control indicating an age between approximately 5.0 Ma and 1.35 Ma are considered to be temporal equivalents of Blancan faunas elsewhere in North America. Triangles = latest Blancan faunas (elsewhere often considered to be Irvingtonian; see text for discussion); squares = sequences or regions including Blancan and latest Blancan faunas. 1, Cape Deceit, AK; 2, Fish Creek, AK; 3, White Bluffs, Blufftop, and Taunton faunas, WA; 4, Froman Ferry Faunal sequence, ID; 5, Grand View faunas (sensu Repenning et al. 1995), ID; 6, Hagerman, ID; 7, Upper Alturas, CA; 8, Maxum, CA; 9, Buckeye Creek, NV; 10, Fish Springs Flat and Topaz Lake, NV; 11, Panaca and Muddy Valley, NV; 12, Coso Mountains, CA; 13, San Timoteo Badlands (in part), CA; 14, Elsinore Fault Zone (in part) and Temecula Arkose, CA; 15, Anza-Borrego Desert (in part), CA; 16, Verde, AZ; 17, 111 Ranch and Safford and Duncan basins, AZ; 18, San Pedro Valley sequence, AZ; 19, Yepómera (Hemphillian) and Concha, Chihuahua, Mexico; 20, Red Light and Hudspeth, TX; 21, Hueco Bolson, TX; 22, Mesilla Basin, NM; 23, Camp Rice Formation, NM; 24, Mangas Basin (Buckhorn fauna), NM; 25. Santa Domingo and Albuquerque Basins, NM; 26, Donnelly Ranch, CO; 27, Wellsch Valley (in part), Saskatchewan, Canada; 28, Java, SD; 29, Sand Draw, NB; 30, Seneca, NB; 31, Sappa, NB; 32, White Rock, KS; 33, Meade Basin faunas (in part), KS; 34, Saw Rock Canyon, KS; 35, Cita Canyon, TX; 36, Blanco, TX; 37, Beck Ranch, TX; 38, Santa Fe River 1, FL; 39, Haile 15A and Haile 7C, FL; 40, Kissimmee River, FL; 41, De Soto Shell Pit, FL; 42, Macasphalt Shell Pit, FL; 43, Inglis 1A and Inglis 1C, FL; 44, La Goleta (in part), Michoacan, Mexico; 45, Rancho El Ocote and Rancho Viejo, Guanajuato, Mexico; 46, Cedazo (in part), Aguascalientes, Mexico; 47, Las Tunas, Baja California Sur, Mexico.

a zircon fission-track date of 3.75 ± 0.36 Ma (Evernden et al. 1964; Izett 1981). The most current interpretation is that the entire sedimentary sequence at Hagerman dates to between 4.0 and 3.2 Ma (G. McDonald et al. 1996). Paleomagnetic studies by Neville et al. (1979) indicate that the Hagerman sequence corresponds to the upper part of the Gilbert reversed chron (chron C2Ar) and the lower part of the Gauss normal chron (chron C2An.3n). The Sand Point Fauna (Hibbard 1959), 48 km west of Hagerman, is preserved in reversely magnetized sediments that lie stratigraphically above normally magnetized sediments; Repenning (1987) tentatively placed it in chron C2An.2r (Mammoth subchron) but did not rule out the possibility that it could be in chron C2An.1r (the Kaena subchron). White and Morgan (1995:373) appear to have considered Sand Point to be in chron C2An.2r. The Grand View Fauna (Hibbard 1959; Shotwell 1970), from localities 120 to 160 km west of Hagerman, spans the upper part of the Gauss normal chron (chron C2An.1n) and the lower part of the Matuyama reversed chron (chron C2r.2r) (Conrad 1980). No fewer than 10 faunas were included in an expanded "Grand View Faunal Sequence" by Repenning et al. (1995:59; including Jackass Butte, Birch Creek [see also Hearst 1998, 1999], Chattin Hill, Black Butte, Castle Butte, Ninefoot Rapids, Oreana area, Poison Creek, Unnamed Butte, and Wild Horse Butte). Additional faunas from the region (e.g., Flatiron Butte, Tyson Ranch, Three Mile East) provide additional information on faunal succession and diversity through the Blancan (Conrad 1980; Repenning et al. 1995; Sankey 1996, 2002). The Jackass Butte Fauna includes the youngest known occurrence of Procastoroides.

The Hagerman faunal sequence includes the oldest published faunas in the Glenn's Ferry Formation. It includes Paracryptotis gidleyi, Hypolagus limnetus, Hypolagus vetus, Pratilepus vagus, Trigonictis macrodon, Trigonictis cookii, Ursus abstrusus, Mustela rexroadensis, Satherium piscinaria, Pliopotamys minor, Ophiomys taylori, Cosomys primus, Castor californicus, and "Equus simplicidens" ("Plesippus shoshonensis" of Repenning et al. 1995). The sequence also includes the youngest known occurrences of Borophagus hilli and Platygonus pearcei and the earliest known occurrences of Megalonyx leptostomus, Procastoroides, and Canis lepophagus. Chronologic control is provided by a series of radiometric dates on lava flows and ashes. An ash correlated to the Horse Quarry was dated at Ma $3.2 \pm ?$ (Evernden et al. 1964). Lower in the sequence, the Deer Gulch lava flow yielded an age of 3.48 ± 0.27 Ma (Evernden et al. 1964). The Peters Gulch Ash is the lowest dated ash in the sequence, and Izett (1981) reported a fission-track age of 3.75 ± 0.36 Ma. The base of the sequence may be as old as 4.0 Ma (G. McDonald et al. 1996).

The Froman Ferry faunal sequence (Repenning et al. 1995) is the youngest faunal sequence in the Glenn's Ferry Formation. A small mammalian fauna was recovered from reversely magnetized sediments that are capped by the Pickles Butte basalt with an 40 Ar/ 39 Ar date of 1.58 ± 0.085 Ma (Repenning et al. 1995). Although an unconformity of unknown magnitude separates the basalt from the underlying fossiliferous marsh deposits, the fact that the entire marsh section shows reversed orientation indicates that the top of the Olduvai (chron C2n) is not present and that the section cannot be older than the end of the Olduvai (given as 1.65 Ma in age by Repenning et al. 1995 and as 1.77 Ma in Berggren et al. 1995). The temporal span of the section is between 1.77 and 1.58 Ma. Phenacomys gryci makes its first appearance in the section at approximately 744 m (2440 feet) above the base of the section and was used by Repenning et al. (1995) to define the base of the Irvingtonian I arvicoline division in Idaho. Use of the paleomagnetic calibration of Berggren et al. (1995) yields a date of 1.72 Ma for the first appearance of Phenacomys. Mictomys vetus, Ophiomys parvus, Ondatra idahoensis, Hypolagus gidleyi, Gigantocamelus spatula, "Plesippus," and Stegomastodon mirificus, traditionally considered to be Blancan taxa, are also in the fauna, and at least some of them, including Stegomastodon, are found in the upper part of the section overlapping the occurrence of *Phenacomys gryci*. The entire sequence is here considered to be Blancan. Stegomastodon also is found in stratigraphic association with Mam*muthus* (the taxon used here to define the Irvingtonian) in several faunas in the Great Plains and the desert Southwest. The Froman Ferry faunal sequence contains the youngest dated occurrences of Hypolagus, Ophiomys, Mictomys vetus, and Ondatra idahoensis. It includes the earliest dated occurrence of Phenacomys.

California In the Imperial and Palm Springs formations at Anza-Borrego Desert State Park, California, the fossiliferous section spans 4300 m from below the base of the Cochiti subchron (chron C3n.1n) to the Jaramillo subchron (chron C1r.1n) (Cassiliano 1999).The traditional interpretation (e.g., Downs and White 1968) that the sedimentary sequence in the Vallecito–Fish Creek section contained a series of superposed faunas (the Layer Cake, Arroyo Seco, and Vallecito Creek) was recently challenged by Cassiliano (1999), who suggested that these faunal terms be abandoned. In place of the traditional terms, he proposed 10 local range zones. Approximate ages for these range zones are taken from Cassiliano, but his use of lowest stratigraphic datum (LSD) and highest stratigraphic datum (HSD) terminology is equivalent to the more precise LSD_k and HSD_k of Walsh (1998; referring to the lowest and highest known stratigraphic occurrence in the specified section). The latter terminology is adopted here. The significant stratigraphic occurrences noted by Cassiliano include Sigmodon LSD_k, from a reversed chron below the Cochiti (chron C3n.1n), at approximately 4.32 Ma; the *Equus* sp. LSD_{μ} , from a normal chron in the lower Gauss (chron C2An.3n), approximately 3.46 Ma (these specimens cannot be identified to subgenus or species); *Dinohippus* HSD_k , from the top of the Kaena (chron C2An.1r), approximately 3.04 Ma (placing this taxon in the late early Blancan, the youngest occurrence in North America); Erethizon stirtoni LSD₁, from the top of a normal chron above the Kaena, approximately 2.58 Ma (this is the earliest South American immigrant to reach the Anza-Borrego area); Navahoceros LSD₁, early in the reversed chron (C2r.1r) below the Olduvai at approximately 2.11 Ma; Equus (Equus) LSD_k, early in the reversed chron (chron C2r.1r) below the Olduvai, approximately 2.09 Ma (this may be the earliest appearance in North America); Lepus LSD_k, base of the Olduvai (chron C2n) at approximately 1.95 Ma; Pewelagus HSD_k, in the middle of chron C2n (Olduvai), at approximately 1.92 Ma (or slightly younger, using the calibration of Berggren et al. 1995); Smilodon LSD₁, top of Olduvai, 1.77 Ma; and Euceratherium LSD_k, late in the Matuyama, at approximately 1.13 Ma.

We attempt no final determination of the utility of the traditional faunal terms or of the newly proposed range zones, pending a thorough analysis of the stratigraphic distribution of taxa in the sequence. The faunal lists provided by Remeika et al. (1995) and Cassiliano (1999) and those in the database at the Anza-Borrego Desert State Park (G. Jefferson, pers. comm., May 2000) are not concordant, so the resolution of this question must wait.

The sequence contains the earliest temporally constrained North American occurrences of *Nothrotheriops, Sylvilagus, Microtus* with five closed triangles on the lower first molar, and *Euceratherium* (*Euceratherium* from the Topaz Lake Fauna in Nevada may be older). It also includes the youngest occurrence of *Borophagus diversidens*.

External (nonbiostratigraphic) age control in the Anza-Borrego sequence includes a fission-track date (on zircons from a volcanic tuff) of 2.3 ± 0.4 Ma (Johnson et al. 1983). This date helped to anchor the magnetic polarity stratigraphy in the section and confirmed the original polarity determination at the 3.6-km level as representing the Gauss–Matuyama boundary (chron C2An–2r boundary; Opdyke et al. 1977; Johnson et al. 1983). A subsequent challenge to the original interpretation of the higher portion of the magnetic sequence at Anza-Borrego (Repenning 1992) was based on the presence, high in the section, of the vole *Microtus* (= *Terricola*) *meadensis*. Repenning (1992:72) argued that the youngest appearance of this species indicated that the normal polarity recorded in the Vallecito Creek–Fish Creek sequence represented the Brunhes and not the Jaramillo, as originally interpreted by Johnson et al. (1983). Resolution of this question will require additional field work and a careful magnetic sampling in the higher portion of the section, but the single specimen used by Repenning (1992) to argue for the alternative interpretation is associated with contradictory locality data and may not be from the Vallecito–Fish Creek sequence in the park (L. K. Murray and C. J. Bell, pers. obs., 1999).

A small fauna from the Coso Mountains of southern California includes *Hypolagus, Cosomys primus, Borophagus diversidens* (originally identified as *Borophagus solus*; see Wang et al. 1999), *Platygonus* sp., and "*Plesippus francescana*" (Wilson 1932; J. Schultz 1937). K–Ar dates on a series of basalt flows and rhyolites in the Coso Formation indicate that the fauna dates to at least 3 Ma (Bacon et al. 1979).

Two other sequences in southern California also yielded significant collections of Blancan mammals in the last decade. Hemphillian and Blancan faunas from the San Timoteo Badlands (discussed in part earlier) were reported by Albright (1999), who recognized three main stratigraphic sections (Eden Hot Springs-Jack Rabbit Trail, Riverside County Landfill-El Casco, and San Timoteo Canyon-Live Oak Canyon). The Hemphillian Mt. Eden Fauna is late Hemphillian and contains Teleoceras, Dinohippus, Pediomeryx hemphillensis, and Agriotherium; Albright placed it in chron C3r. The section above this lies entirely in the Blancan with Thomomys appearing in chron C2Ar, Sigmodon minor in chron C2An.3n, and Neotoma in chron C2An.1r. At the top of the section Ophiomys, "Plesippus idahoensis," and Erethizon are in chron 2r.2r. The Riverside County Landfill-El Casco section contains Blancan deposits extending from the upper part of the Gilbert (chron C2Ar) and includes Neotoma (Paraneotoma) fossilis, Prodipodomys, Thomomys, and Sigmodon minor from chron C2An.1n and possibly from C2An.2n. The El Casco Fauna in the San Timoteo Badlands of southern California was assigned to the Irvingtonian by Albright (1999). The fauna includes "Plesippus francescana" (the youngest known record of "Plesippus") and lacks Mammuthus (which appears higher in the San Timoteo Badlands sequence; Albright 1999). Microtus, an advanced form of Ondatra idahoensis, Mictomys kansasensis, Neotoma, Canis edwardii, and Erethizon ?cascoensis are also present and provide faunal evidence for assignment to the Irvingtonian as it is traditionally recognized in California. This part of the section is reversely magnetized and was assigned by Albright to chron C1r.2r. Albright suggested that the position of the fauna within this interval indicates an age of 1.3–1.4 Ma. The reported age of the El Casco Fauna is temporally consistent with an assignment to either the latest Blancan or the earliest Irvingtonian as they are recognized here. We treat the fauna as latest Blancan, primarily to exclude "*Plesippus*" from Irvingtonian faunas.

Vertebrate faunas recovered from the Temecula Arkose and an unnamed sandstone unit in the vicinity of Murrieta (Riverside County) include a diverse assemblage of small mammals that record faunal change in the Elsinore Fault Zone from early through late Blancan. These faunas and their correlation were discussed at length by Golz et al. (1977), Reynolds et al. (1991), and Pajak et al. (1996).

Great Basin Little is known of Blancan mammals from the Great Basin. In western Nevada two areas produced superposed Blancan faunas (Kelly 1994). Sediments in the Carson Valley–Pine Nut Mountains (recently given the name *Sunrise Pass Formation* by Trexler et al. 2000) area produced one Hemphillian and two Blancan faunas in superposition. The older Blancan Buckeye Creek Fauna contains *Platygonus* cf. *P. pearcei, Alilepus vagus, Hypolagus gidleyi, Megalonyx leptostomus, Ursus abstrusus, "Equus simplicidens," Hemiauchenia* cf. *H. blancoensis,* and *Odocoileus. U. abstrusus* is limited to the early Blancan, and *H. gidleyi* and *A. vagus* are most common in the early Blancan (Kelly 1994).

The younger Fish Springs Flat Fauna (Kelly 1994) contains Hypolagus furlongi, Satherium ingens, "Equus simplicidens," Equus giganteus, Gigantocamelus spatula, Thomomys carsonensis, Mammut americanum, and Spermophilus howelli. A late Blancan age assessment is based on the joint occurrence of Hypolagus furlongi, Spermophilus howelli, Satherium ingens, and "Equus simplicidens."

Two superposed faunas from an unnamed formation in the Wellington Hills–Antelope Valley area of Douglas County, Nevada, were reported by Kelly (1997). The Blancan Wellington Hills Fauna is depauperate but includes *"Equus idahoensis"* and *Spermophilus wellingtonensis*. The Topaz Lake Fauna includes *Ondatra* cf. *O. idahoensis, "Equus idahoensis," Equus* cf. *E. giganteus, Hemiauchenia,* and *Euceratherium collinum* (Kelly 1997). Kelly (1997) interpreted the Topaz Lake Fauna to be early Irvingtonian based on the presence of *Euceratherium*. This may be the oldest record of *Euceratherium;* the oldest record associated with external age control is in the Vallecito Creek–Fish Creek sequence at approximately 1.1 Ma (Cassiliano 1999). The association with a primitive muskrat is unique (the youngest record of *O. idahoensis* associated with external age control is from Froman Ferry, Idaho, at approximately 1.72 Ma [Repenning et al. 1995]).

Late Cenozoic vertebrates were reported from eastern Nevada by Stock (1921), who called the deposits in Meadow Valley the Panaca beds and those in Muddy Valley the Muddy Valley beds. He considered the Panaca beds to be "early Pliocene" (now considered to be Hemphillian and late Miocene) on the basis of the recovered horse, camel, and rhinoceros remains and the Muddy Valley beds to be slightly older. An age determination, ranging from Barstovian to Clarendonian (Muddy Valley Fauna) and Clarendonian to Hemphillian (Panaca), was suggested by MacDonald and Pelletier (1958). The Meadow Valley Fauna from the Panaca Formation (Reynolds and Lindsay 1999; Mou 1997; Lindsay et al. 2002) contains a number of Blancan taxa such as Sorex meltoni, Hypolagus edensis, Hypolagus tedfordi, Hypolagus cf. H. ringoldensis, Pewelagus dawsoni, Nekrolagus progressus, Pliogeomys parvus, Repomys panacaensis, Mimomys panacaensis, Borophagus diversidens, Taxidea sp., ?Martinogale, Bassariscus casei, Felis sp., ?Cuvieronius, Dinohippus, "Equus cf. E. simplicidens," Equus (Hemionus) sp., Platygonus sp., Megatylopus sp., Hemiauchenia, and an unidentified Caprini species. The earlier reported presence of Ophiomys mcknighti, Ophiomys magilli, and Ondatra or Pliopotamys (Repenning 1987; Reynolds and Lindsay 1999) in this fauna was in error (see Lindsay et al. 2002). The Dinohippus specimen and a rhinoceros (?Teleoceras) are limited geographically and stratigraphically in Meadow Valley; it appears that they came from low in the section and indicate that the lowest exposures of the Panaca beds in Meadow Valley are of Hemphillian age, whereas most of the exposures yield only Blancan fossils. Paleomagnetic and radiometric data from the sequences in both eastern and western Nevada were obtained and used by Lindsay et al. (2002) to date the Hemphillian-Blancan boundary. This boundary was discussed more fully earlier in the section on the Hemphillian-Blancan transition.

The White Narrows Fauna south of Panaca may also represent the earliest Blancan (Reynolds and Lindsay 1999). Definitive species-level identifications for most taxa are not available, but the fauna includes *Sorex*, *Peromyscus valensis*, and *Dipodomys gidleyi*. *Sorex* is known only from Blancan and younger faunas (McKenna and Bell 1997), *D. gidleyi* only from the Blancan, and *P. valensis* only from the Hemphillian. The best available age assessment for the White Narrows Fauna is that it represents the early Blancan (Reynolds and Lindsay 1999; Mead and Bell 2001).

Southwestern United States In the San Pedro Valley in southern Arizona, the St. David Formation is nearly 120 m (400 feet) thick and extends from the upper part of the Gilbert reversed chron (chron C2Ar) to the lower part of the Brunhes normal chron (chron C1n) (Johnson et al. 1975; Lindsay et al. 1975). Within these sediments a series of faunas range in age from the early Blancan Benson Fauna within the Gauss normal chron to the latest Blancan Curtis Ranch Fauna at the Olduvai normal subchron (Gidley 1922, 1926; Gazin 1942; Lindsay et al. 1975). Radiometric control in the paleomagnetic sequence is provided by a zircon fission-track date of 3.1 ± 0.7 Ma on an ash bed immediately below the Post Ranch (type Benson) faunal horizon and by identification of the Huckleberry Ridge (formerly Pearlette B) Ash in the California Wash section by G. Izett (1981); the age of this ash is somewhere between 2.0 and 2.1 Ma (Izett and Honey 1995; Gansecki et al. 1998). A proposed boundary between the Blancan and Irvingtonian was arbitrarily drawn between about 1.8 and 2.0 Ma at the lowest known local stratigraphic occurrence of Lepus in the Curtis Ranch Fauna (Lindsay et al. 1975). The Curtis Ranch Fauna occurs in sediments that straddle the base of the Olduvai subchron at about 1.95 Ma and includes Ondatra idahoensis, the earliest local record of Dipodomys, and a late record of Stegomastodon. Specimens from the fauna originally assigned to Lepus were subsequently reidentified as Sylvilagus (White 1991b:78). Extrapolating from paleomagnetic data presented by Johnson et al. (1975; with modified calibrations for polarity transitions from Berggren et al. 1995), Ondatra idahoensis and Glyptotherium arizonae appear in the local sequence (California Wash Fauna) between about 2.2 and 2.1 Ma, whereas Nannippus disappears at approximately 2.6 Ma (Johnson et al. 1975). The Curtis Ranch Fauna was traditionally considered to be early Irvingtonian but is here considered to be latest Blancan; neither Lepus nor Mammuthus is recorded from the Curtis Ranch Fauna.

Pliocene fossiliferous sediments on the flanks of Dry Mountain on the 111 Ranch were studied by Lance (1960), who recognized two faunas, the Flat Tire and Tusker claims, later modified by P. Wood (1960, 1962) to Flat Tire and Tusker faunas. The lower Flat Tire Fauna was considered to be Blancan on the basis of the presence of *Nannippus*, whereas the upper Tusker was assigned an Irvingtonian age because of the absence of *Nannippus*. Later studies in the San Pedro Valley to the southwest showed the presence of a fauna that lacked *Nannippus* superposed over a fauna with Nannippus, but both faunas were best considered Blancan (Johnson et al. 1975). On the basis of these faunas and the resemblance of the Tusker rodents to the Benson and Curtis Ranch sites of the San Pedro Valley, the Tusker assemblage was assigned to the Blancan (Galusha et al. 1984). No justification for two distinct faunas was found, and the names Flat Tire and Tusker were abandoned. The entire sequence now should be called simply the 111 Ranch Fauna. One hundred meters of section span the later Gauss and the early (pre-Olduvai) part of the Matuyama (Galusha et al. 1984; see also Seff 1960; P. Wood 1960). An ash bed yielded pyrogenic zircons with fission-track dates of 2.33 ± 0.24 Ma (Dickson and Izett 1981; date given as 2.32 ± 0.15 Ma by Galusha et al. 1984). The fauna consists of at least 41 mammal taxa that are not evenly distributed through the section. The highest occurrence of Nannippus is just below the Gauss-Matuyama boundary. The first local occurrences of Glossotherium, Glyptotherium, Neochoerus, and the arvicoline rodents Ondatra idahoensis, Pliophenacomys, and Mictomys vetus are also located in the uppermost Gauss and identify a short time interval that is useful for correlation in the southwest. This record is among the earliest of Mictomys, used to define the base of the Blancan V of Repenning (1987; Repenning et al. 1990).

A new fauna, the Artesia Road Fauna, in the nearby Whitlock Mountains and San Simon Valley was included in an expanded "111 Ranch beds" by McCord et al. (2002). This fauna produced the first records of *Castor* and *Tapirus* from the 111 Ranch area. A new occurrence of cervid was also reported (as "*Bretzia* or *Odocoileus*"). The relationships of this fauna with the traditional 111 Ranch are not well established.

Four stratigraphic sequences with extensive faunas from the Safford and Duncan basins in Arizona were reported by Tomida (1987). The Duncan Fauna produced at least 25 taxa, including 14 small mammals. The rodents include Geomys (Nerterogeomys) cf. G. persimilis, Perognathus gidleyi, Peromyscus hagermanensis, Reithrodontomys rexroadensis, Baiomys minimus, Calomys (Bensonomys) sp., Sigmodon minor (originally identified as Sigmodon medius, but see Harrison 1978; R. Martin 1986), Neotoma (Paraneotoma) fossilis, Pliopotamys, and Ophiomys cf. O. taylori. Large mammals include Nannippus peninsulatus, Equus (Dolichohippus), Equus (Asinus), and camelids. The presence of Nannippus suggests an age no younger than the Gauss-Matuyama boundary. The lower part of the Duncan section has normal polarity, the upper has reversed polarity; the section was correlated with the base of the Mammoth subchron (chron C2An.2r)

by Tomida (1987). The Country Club Fauna contains only a few taxa of small mammals. The section shows a reversed-normal-reversed paleomagnetic pattern and was interpreted to extend from the Mammoth through the Kaena subchron (2An.1r) in the Gauss chron (Tomida 1987). The joint presence of Sigmodon, Neotoma quadriplicata, and Equus precludes an age older than the Gauss chron. The Bear Springs section produced too little material to determine its age other than Blancan. The presence of Nannippus, Geomys, and Sigmodon suggests placement in the Gauss or early Matuyama chrons (the youngest occurrence of Nannippus is in the Macasphalt Shell Pit Fauna in Florida at approximately 2.1 Ma). The thick sequence of normally magnetized sediments at Bear Springs could represent either the long normal chron (chron C2An.3n) below the Mammoth or the long normal chron (chron C2An.1n) above the Kaena.

A number of fossil vertebrate sites on the Pearson Mesa in the Duncan Basin were reported by Tedford (1981), Tomida (1987), and Morgan and Lucas (2000a). Fortythree different sites produced vertebrate fossils on Pearson Mesa (Morgan and Lucas 2000a). Fossils were collected from 60 m of section, but the lower 15 m contains Nannippus peninsulatus, "Equus simplicidens," Equus cf. E. cumminsii (see Cope 1893:67 for correct spelling of the species), Platygonus bicalcaratus, Glossotherium cf. G. chapadmalense, and Hemiauchenia cf. H. blancoensis, all suggesting a Blancan age. Geomys cf. G. persimilis, Stegomastodon mirificus, Nannippus peninsulatus, and Equus sp. from Pearson Mesa were reported by Tomida (1987). All of Tomida's paleomagnetic sites are of normal polarity, which he interpreted to fall in the long normal interval (C2An.1n; 2.581-3.040 Ma) in the Gauss chron between the Kaena subchron and the Matuyama chron. The faunal assemblage and paleomagnetic data indicate a middle Blancan age.

The Verde Fauna, from Yavapai County in central Arizona (Czaplewski 1987, 1990), contains *Ogmodontomys poaphagus, Geomys* (*Nerterogeomys*) *minor, Calomys* (*Bensonomys*) *arizonae*, and *Sigmodon minor. Copemys*, a taxon typically found in Hemphillian and earlier faunas, is present in low abundance in the Verde Fauna and was interpreted by Czaplewski (1990) to be a temporal extension of this taxon into the Blancan. The identification of the rare arvicoline *Nebraskomys* in the Verde Fauna (Repenning 1987) was subsequently shown to be erroneous (Winkler and Grady 1990; Czaplewski 1990); the specimen in question cannot be identified reliably to any arvicoline genus. The Verde Fauna is situated approximately 56 m above a basalt dated at 5.6 Ma and is placed at the base of the Nunivak subchron (chron 3n.2n) (Bressler and Butler 1978; Czaplewski 1990) at about 4.62 Ma (Berggren et al. 1995). The fauna includes the earliest occurrence of *Ogmodontomys poaphagus*.

Many of the Blancan faunas of New Mexico were reviewed by Tedford (1981). Subsequent work by Morgan and Lucas (1999, 2000a, 2000b) and Morgan et al. (1997, 1998) added new localities and new material. Blancan faunas are located in two areas of New Mexico: sedimentary basins along the Rio Grande Valley and structural basins in southwestern New Mexico. The Santo Domingo Basin north of Albuquerque, considered by Morgan and Lucas (2000b) to be a northward extension of the Albuquerque Basin, produced a fauna including Equus scotti and an equid similar to Equus calobatus (Tedford 1981); a late Blancan age was suggested based on the similarity of the horses to those of the Tule Formation of Texas (here considered to be Irvingtonian). The subsequent discovery of Nannippus by Morgan and Lucas (2000b) confirmed Tedford's placement of the fauna in the Blancan. Tedford noted that these deposits are interbedded with the Santa Ana Mesa Basalt dated ~2.4 Ma (Bachman and Mehnert 1978). The deposits are overlain by the lower bed of the Otowi Member of the Bandelier Tuff dated to approximately 1.61 Ma (Izett and Obradovich 1994; Spell et al. 1996; Morgan and Lucas 2000b). This assemblage apparently is late Blancan.

Ten Blancan localities were recently recognized in the Albuquerque Basin (Morgan and Lucas 1999, 2000b). None are clearly early Blancan, but the diversity is low. One fauna, the Belen, contains Scalopus (Hesperoscalopus), Geomys (Nerterogeomys) cf. G. paenebursarius, Equus cf. E. calobatus, and Stegomastodon mirificus. An age range of 2.5-3.7 Ma was suggested by Morgan and Lucas (2000b). The Pajarito locality (= Laguna site of Tedford 1981) produced dentaries of Geomys (Nerterogeomys) that are similar in size to those of the Belen site. An 4° Ar/ 3^{9} Ar date of 3.12 ± 0.10 Ma on a pumice clast (Maldonado et al. 1999) from the Pajarito locality led Morgan and Lucas (2000b) to suggest that G. (N.) paenebursarius also occurs in the middle Blancan, but the clast establishes only a maximum age for the unit. The Tijeras Arroyo area has Blancan and Irvingtonian in superpositional relationship (Logan et al. 1984; Lucas et al. 1993; Morgan and Lucas 1999, 2000b). The lower part of the section has Hypolagus cf. H. gidleyi and Equus cf. E. cumminsii and was assigned a middle to late Blancan age (2.2-3.5 Ma) by Morgan and Lucas (2000b).

Two areas in southwestern New Mexico recently produced Blancan faunas. In the Mangas Basin, the Buckhorn Fauna was recovered from 14 sites (Morgan et al. 1997). It contains *Nannippus*, *Ogmodontomys* cf. *O. poa*- phagus, Repomys cf. R. panacaensis, and "Equus (Dolichohippus) simplicidens," but Neotropical taxa are not present. The presence of "E. simplicidens" seems to preclude a very early Blancan age, and Neotropical taxa would be expected if the fauna were of late Blancan age. The rodents suggest a late–early to early–mid-Blancan age, but definitive species identifications are lacking.

The Camp Rice Formation in Doña Ana County, New Mexico, produced the Tonuci Mountain Fauna (Morgan et al. 1998). The fauna includes *Canis lepophagus, Borophagus, Nannippus* cf. *N. peninsulatus, "Equus simplicidens," Equus scotti, Platygonus* cf. *P. bicalcaratus, Hemiauchenia blancoensis,* and *Cuvieronius*. Biostratigraphic correlation and paleomagnetic data constrain the age to between 3.6 and 3.0 Ma (Morgan et al. 1998).

The Mesilla Basin in south-central New Mexico contains a sedimentary sequence that spans the Blancan-Irvingtonian boundary. Vanderhill (1986) divided the sequence into three biostratigraphic zones. The lowest zone ("Faunule A" of Vanderhill) contains the Blancan taxa Nannippus peninsulatus, Hemiauchenia blancoensis, and Glyptotherium. The presence of Glyptotherium suggests at least a late Blancan age (the earliest appearance of Glyptotherium probably is in the 111 Ranch sequence; Galusha et al. 1984). Paleomagnetic data place this zone in the late Gauss, between the Kaena event (chron C2An.1r) and the Gauss-Matuyama (chron C2An-2r boundary). Faunule B in the Mesilla Basin is derived from sediments that span the base of the Matuyama to the Olduvai event. It lies above the highest occurrence of Nannippus and below the lowest occurrence of Mammuthus and contains a mixture of taxa traditionally used to characterize both the Blancan and Irvingtonian. Characteristic Blancan forms include Gigantocamelus and Blancocamelus. Characteristic Irvingtonian forms are Paramylodon harlani and Smilodon. The uncertain stratigraphic position of some specimens collected before Vanderhill's field work make it impossible at this time to determine the position of the Blancan-Irvingtonian boundary in the Mesilla Basin, but Mammuthus was recovered from chron C1r.2r (between the Cobb Mountain and Olduvai events) within faunule C. Faunule C in Mesilla Basin was derived from sediments that span the time from just after the Olduvai event to the early part of the Brunhes, but most of the specimens were reported to come from sediments that predate the Jaramillo event. (Faunule C is discussed later in this chapter under "Irvingtonian.")

The Hueco Bolson, a topographic basin southwest of the Hueco Mountains in the western part of Trans-Pecos Texas, contains sediments that produced a Blancan fauna that extends through the Fort Hancock and Camp Rice formations (Strain 1966). Although the two formations are separated by an unconformity, the material from both units was combined as the Hudspeth Fauna. Small animals were recovered from the Fort Hancock Formation and large mammals from the Camp Rice Formation. The combined fauna contains *Nannippus peninsulatus*, *"Equus idahoensis*," *"Equus simplicidens," Gigantocamelus, Glyptotherium, Megalonyx*, and *Sigmodon hudspethensis*. Paleomagnetic data for this sequence were obtained by Vanderhill (1986). Most of the Fort Hancock and the lower part of the Camp Rice formations fall in a normal interval that Vanderhill identified as the late Gauss chron (presumably chron C2An.1n). The age is constrained by the presence of the Huckleberry Ridge Ash (between 2.0 and 2.1 Ma; see table 7.1) high in the section.

The sediments of the Red Light Bolson, which lies between the Eagle and Indio mountains on the northeast and the Quitman Mountains on the southwest, in the southernmost part of Hudspeth County, Texas, produced two faunas (Akersten 1972). The Aguila Fauna was recovered from the upper part of the Bramblett Formation and the Red Light Fauna from the overlying Love Formation. The former is represented by a single fish, unidentified birds, and an indeterminate rodent and is not biostratigraphically useful. The Red Light Fauna contains a diverse Blancan fauna including Megalonyx, "Paramylodon" sp., Glyptotherium texanum, Borophagus, Nannippus peninsulatus, Hemiauchenia blancoensis (originally listed as Tanupolama, but see Webb 1974b), and Platygonus bicalcaratus. The presence of Glyptotherium suggests that it is late Blancan. Elsewhere in western North America Nannippus peninsulatus disappears from faunas by approximately 2.5 Ma. In Florida, N. peninsulatus persists until approximately 2.1 Ma (Macasphalt Shell Pit). There are at present no radiometric or paleomagnetic data bearing on the age of this fauna.

Mexico Blancan faunas are known from a number of localities in Mexico, and a few contribute information on the Hemphillian–Blancan boundary. The boundary between Hemphillian and Blancan faunas in Chihuahua was documented by Lindsay et al. (1984) and Lindsay and Jacobs (1985; summarized earlier).

In central Mexico, a number of localities produced faunas of Blancan age. The La Goleta locality (Arellano and Azcón 1949; Repenning 1962; Miller and Carranza-Castañeda 1984) in Michoacan has a fauna that contains *Rhynchotherium falconeri, Paenemarmota barbouri, Nannippus* cf. *N. montezuma, Nannippus peninsulatus, Pliohippus, Equus (Dolichohippus)*, a hyaenid, a tapir, a peccary, a camel, and an antilocaprid. A tentative referral to the Hemphillian was proposed by Repenning (1962) on the basis of *Pliohippus*, but he acknowledged a written communication from R. Tedford that suggested the fauna was Blancan on the basis of the hyaenid and horses. Miller and Carranza-Castañeda (1984) suggested that both Hemphillian and Blancan components may be present. The fauna probably includes the earliest record of *N. peninsulatus*. The uppermost beds of the La Goleta locality include remains of *Mammuthus* and *Equus* (*Equus*), indicating that an Irvingtonian or Rancholabrean deposit caps the sequence.

The Rancho Viejo Fauna in Guanajuato contains *Glyp*totherium, *Glossotherium garbanii*, *Hypolagus mexicanus*, *Pratilepus ?kansasensis*, *Paranotolagus complicatus*, *Paenemarmota*, *Neochoerus cordobai*, *Neochoerus holmesi*, *Borophagus diversidens*, *Nannippus peninsulatus*, and *Equus (Dolichohippus)* sp. (Carranza-C. and Miller 1980; Miller and Carranza-Castañeda 1984; Carranza-Castañeda and Miller 1988). A Blancan age was proposed by Miller and Carranza-Castañeda (1984). A fission-track date of 3.6 Ma was derived from an ash stratigraphically 1 m below the *Borophagus* specimen (Kowallis et al. 1986; Miller and Carranza-Castañeda 1998b). This is the oldest well-dated record of *Glyptotherium* and *Borophagus diversidens* (Wang et al. 1999).

The Rancho El Ocote Fauna in Guanajuato is primarily Hemphillian (Carranza-Castañeda and Ferrusquía-Villafranca 1978; Dalquest and Mooser 1980; Miller and Carranza-Castañeda 1984; Montellano 1989; Carranza-Castañeda and Walton 1992; Carranza-Castañeda and Miller 2000), but there is a Blancan component to the fauna with Rhynchotherium, cf. Glossotherium, and Nannippus peninsulatus (Miller and Carranza-Castañeda 1984; Carranza-Castañeda and Miller 2000). Equus (Dolichohippus) was reported from the Rancho El Ocote by Miller and Carranza-Castañeda (1984) but was excluded from the faunal list provided by Carranza-Castañeda and Miller (2000:43). Early attempts to obtain zircon fission-track ages for the fauna were unsuccessful because of mixing or contamination of the dated materials (Kowallis et al. 1986), but more recent efforts using both fission-track and 40Ar/39Ar successfully differentiated the components and yielded ages for the fauna of between 4.6 \pm 0.3 and 4.70 \pm 0.07 Ma (Kowallis et al. 1998).

One well-studied fauna from Baja California Sur, the Las Tunas (Miller 1980), contains *Hypolagus vetus* (see White 1987), *Borophagus hilli* (originally identified as "*Borophagus ?diversidens*;" identification changed by Wang et al. 1999), *Rhynchotherium* cf. *R. falconeri*, and "*Equus* cf. *E. simplicidens*." No external age control is available, but a tentative assignment to the early Blancan was proposed.

In the state of Aguascalientes, a sequence of three stratigraphic units produced the Cedazo faunas, which probably represent a series of faunas ranging from Blancan through Rancholabrean (Mooser Barendun 1958; Mooser and Dalquest 1975a, 1975b; Montellano-Ballesteros 1992). The age of the faunas is difficult to assess; much of the collection was reported to be in private hands (see Mooser and Dalquest 1975b), and the stratigraphic relationships of the reported species were not published "for the sake of brevity" (Mooser and Dalquest 1975b:784). A more recent attempt to place the faunas in stratigraphic context resulted in the tentative recognition of three discrete units and faunas. The lower unit contains Holmesina, cf. Aluralagus, Pappogeomys, Equus conversidens, and Platygonus sp. and was assigned an Irvingtonian age by Montellano-Ballesteros (1992) on the basis of the tentative identification of cf. Aluralagus and on the morphologic similarity of the Holmesina material to that recovered from Inglis 1A, Florida. We consider the lower unit to be latest Blancan. Complete faunal lists for the other units can be found in Mooser and Dalquest (1975a, 1975b) and Montellano-Ballesteros (1992), but age relationships of the taxa are poorly understood. At least one part of the sequence contains Bison and is therefore Rancholabrean. It is not clear whether a discrete Irvingtonian fauna is present.

Great Plains In the Great Plains, especially in southwestern Kansas and the Texas panhandle, the faunal sequence must be compiled from shorter local sections using mainly paleomagnetic and biostratigraphic criteria because few radiometric dates are available. Careful biostratigraphic studies enabled C. W. Hibbard and his coworkers to compile an impressive succession of Blancan faunas in southwestern Kansas. A large number of Blancan faunas are known from this region, but few are discussed here; ongoing work in the region by R. Martin and colleagues (2000) is building on the foundation laid by Hibbard and expanding our understanding of the taxonomic composition and age relationships of the mammalian faunas. With the adoption of Mammuthus as the defining taxon for the Irvingtonian, many faunas previously considered to be Irvingtonian are here considered to be latest Blancan.

The Saw Rock Canyon Fauna in Seward County, Kansas (Hibbard 1949b, 1953, 1964, 1967), lacks paleomagnetic data but is considered one of the earliest faunas in the Rexroad Formation and is near the Hemphillian– Blancan boundary. The approximate age placement of the Saw Rock Canyon Fauna (at 4.3 Ma) given by Lundelius et al. (1987, figure 3) may be too young according to R. Martin et al. (2000), who gave an age estimate of approximately 5.0 Ma. The mammalian fauna is dominated by small-bodied species and includes several rodent species that are more primitive than species recovered from the early Blancan Fox Canyon and Rexroad faunas (Hibbard 1949b, 1953, 1964, 1967; Zakrzewski 1967; R. Martin et al. 2000). The Saw Rock Canyon Fauna contains a beaver (Dipoides wilsoni), a gopher with rooted teeth (possibly *Pliogeomys*), a primitive arvicoline Ogmodontomys sawrockensis, and Borophagus hilli (originally identified as a species of Osteoborus; identification changed by Wang et al. 1999), but no horses. An evolutionary transition from O. sawrockensis to Ogmodontomys poaphagus was suggested by Zakrzewski (1967) based on material from Saw Rock Canyon.

Several other Great Plains faunas contain characteristic early Blancan taxa. The Fox Canyon Fauna (Meade County, Kansas; Hibbard 1950; Hibbard and Zakrzewski 1972) occurs in reversely magnetized sediments (Lindsay et al. 1975) and is one of the oldest Blancan faunas in the Great Plains area. A recent age range estimate between 4.8 and 4.3 Ma was given by R. Martin et al. (2000). Small mammals are abundant, but large mammals are rare. The fauna contains taxa typical of Blancan and younger faunas (e.g., Pliophenacomys finneyi, Geomys, and Odocoileus) as well as Paenemarmota, a sciurid also known from the Hemphillian. The earlier report of Hypolagus vetus in the Fox Canyon Fauna (Lundelius et al. 1987) was based on a personal communication from John White but cannot be confirmed at this time; it is not listed or discussed from Fox Canyon by White (1987, 1991b) or R. Martin et al. (2000). Recent collecting efforts in Kansas produced new faunas (e.g., Argonaut, Red Fox, Fallen Angel) that may be older than Fox Canyon but younger than Saw Rock Canyon (R. Martin et al. 2000).

The Rexroad 3 Fauna is another diverse early Blancan fauna but is considered to be younger than the Fox Canyon Fauna based on the presence of *Nannippus peninsulatus, Stegomastodon, Canis lepophagus, Trigonictis,* and *Borophagus diversidens* in the Rexroad 3 (R. Martin et al. 2000). The fauna was recovered from normally magnetized sediments tentatively correlated by Martin et al. (2000) with chron C2An.3n (early Gauss), now dated to between 3.58 and 3.33 Ma (Berggren et al. 1995). It includes the youngest known occurrence of *Megantereon* and the earliest known occurrences of *Nebraskomys, Platygonus bicalcaratus,* and *Stegomastodon.*

The White Rock Fauna in Republic County, Kansas, was described by Eshelman (1975). External age control is

lacking, but the fauna includes Megalonyx leptostomus, Hypolagus cf. H. furlongi, Procastoroides sp., Peromyscus cragini, Sigmodon minor, Nebraskomys mcgrewi, Ophiomys meadensis, Ogmodontomys sp., Pliophenacomys, and one of the earliest records of Ondatra idahoensis. All of these taxa are limited to the Blancan.

The Borchers Fauna figures prominently in chronology of the Great Plains sequence because it lies immediately over the Huckleberry Ridge Ash, dated between $2.003 \pm$ 0.014 (Gansecki et al. 1998) and 2.10 \pm 0.02 Ma (Honey et al. 1998). The Borchers Fauna is depauperate but contains Lepus, Geomys, Neotoma taylori, Sigmodon minor, Ondatra idahoensis, Mictomys landesi, Prodipodomys, Dipodomys hibbardi, Perognathus gidleyi, Canis lepophagus, Urocyon, Camelops, and Stegomastodon (Hibbard 1942; R. Martin et al. 2000). It lacks Allophaiomys, which is sometimes used to define the beginning of the Irvingtonian in the Great Plains (Repenning 1992; Repenning et al. 1995; R. Martin et al. 2000). The Borchers Fauna was previously suggested to be indicative of a warm, mild climate (Zakrzewski 1988). The reported occurrence of Lepus in the fauna (Hibbard 1941; R. Martin et al. 2000) must be verified. If it is correct, it represents the earliest record of Lepus in North America; preliminary notice and an illustration of the occlusal surface of the teeth of the only reported specimen were provided by Hibbard (1941:216-217, plate 2, figure 9). No additional discussion of the material or its identification was provided by R. Martin et al. (2000). We tentatively accept the Borchers record as the oldest dated occurrence of Lepus. The fauna also includes the youngest dated occurrence of Prodipodomys. Additional potentially young records of Prodipodomys include the Java Fauna, South Dakota (which lacks external age control), and an occurrence stratigraphically above the Bishop Ash in California Oaks (Reynolds et al. 1991). Subsequent clarification of the California Oaks faunas, California (Pajak et al. 1996), revealed that three of the four putative records of Prodipodomys were questionably identified or came from mixed faunas; the fourth record is not in stratigraphic association with the Bishop Ash and lacks any age control.

There are four faunas stratigraphically above the Borchers; these were ordered from oldest to youngest by R. Martin et al. (2000) as the Nash Fauna, Aries A (= "Aries" of Izett and Honey 1995), Rick Forester, and Aries B. We consider all of these faunas to be latest Blancan. The Nash Fauna (Meade County, Kansas; Bayne 1976) was recovered from a channel fill deposit in the Crooked Creek Formation (Eshelman and Hibbard 1981). The Aries A locality is the original quarry mentioned by Izett and Honey (1995; see R. Martin et al. 2000). The Aries B locality is stratigraphically just above Aries A and just below the Cerro Toledo B Ash (named, but not dated, by Izett 1981; thought to be associated with the eruption of the Cerro Toledo Rhyolite between 1.2 and 1.4 Ma [table 7.1]; Izett and Honey 1995; see R. Martin et al. 2000 for relative stratigraphic placement of the faunas). These localities are situated between the Huckleberry Ridge Ash $(2.11 \pm 0.01 \text{ Ma})$ and Cerro Toledo B Ash. Nash, Aries A, and Rick Forester all contain Allophaiomys pliocaenicus [= Pitymys ("Allophaiomys") of Zakrzewski 1988 and Microtus pliocaenicus of R. Martin et al. 2000], which is missing from the Borchers Fauna. According to Zakrzewski (1988), the presence of Mictomys kansasensis and Allophaiomys suggests the beginning of climatic cooling in this area. If the relative stratigraphic (and temporal) placement of these faunas by R. Martin et al. (2000) is correct, the Nash Fauna would record the earliest known appearance of Allophaiomys and Mictomys kansasensis.

The Sand Draw mammalian fauna in Nebraska was described by Hibbard (1972). It includes *Prodipodomys centralis, Dipoides rexroadensis, Procastoroides, Sigmodon minor* (originally identified as Sigmodon medius, but see Harrison 1978; R. Martin 1986), Nebraskomys mcgrewi, Ogmodontomys poaphagus, Ophiomys magilli, Ophiomys fricki, Pliopotamys meadensis, Pliophenacomys, Pliolemmus, Canis lepophagus, Borophagus diversidens, Trigonictis cookii, Stegomastodon, Gigantocamelus spatula, Nannippus peninsulatus, and "Equus simplicidens." External age control is lacking, but the Sand Draw Fauna often is cited in studies attempting to correlate Great Plains faunas. It includes what may be the youngest records of *Dipoides rexroadensis, Ogmodontomys poaphagus*, and *Pliopotamys*.

The Seneca Fauna in southern Nebraska is not published in its entirety, but the small mammals include *Planisorex dixonensis, Procastoroides idahoensis, Zapus sandersi, Ondatra idahoensis, Ophiomys parvus, Pliophenacomys osborni,* and *Mictomys* cf. *M. vetus* (L. Martin and Schultz 1985). External age control is lacking, but faunal correlations suggest placement in the late Blancan, sometime after 2.56 Ma and before about 2.0 Ma. The fauna may record the earliest occurrence of O. ida*hoensis* (another possible early occurrence is in the White Rock Fauna; Eshelman 1975).

The Sappa Fauna (Harlan County, Nebraska) was collected from sediments approximately 2 m below the Mesa Falls Ash, dated to between 1.2 and 1.3 Ma (Naeser et al. 1971, 1973; L. Martin and Schultz 1985; Gansecki et al. 1998). A preliminary report on the fauna was published by C. Schultz and Martin (1970), with a more expansive discussion, especially of the small mammals, provided by L. Martin and Schultz (1985). Their faunal list includes *Stegomastodon, Geomys* cf. *G. tobinensis, Ondatra* cf. *O. annectens, Allophaiomys,* and *Mictomys kansasensis.* This fauna may be early Irvingtonian but is here considered latest Blancan.

The Blanco Fauna, which originally formed the basis of the Blancan, is derived from deposits in the vicinity of Mount Blanco near the eastern edge of the Llano Estacado in Crosby County, Texas. Comprehensive studies of this fauna began with Gidley (1903a, 1903b). This work was followed by studies by Matthew (1925), Meade (1945), and Dalquest (1975). The last study significantly increased our knowledge of the small-bodied species in the fauna. The fauna includes Glyptotherium texanum, Megalonyx leptostomus, Hypolagus sp., Prodipodomys centralis, Paenemarmota (the youngest known record in North America), Sigmodon minor (originally identified as Sigmodon medius, but see Harrison 1978; R. Martin 1986), Canis lepophagus, Borophagus diversidens, Rhynchotherium praecursor, Nannippus peninsulatus, and Platygonus bicalcaratus. Early estimates of the age of the Blanco Fauna were variously given as Pliocene (Gidley 1903a; Matthew 1925; Osborn 1936) and early Pleistocene (Meade 1945; Evans and Meade 1945; Hibbard 1958). The age was better constrained by dates of two ash beds in the Mount Blanco Section. A volcanic ash bed (informally named the "Guaje ash bed" by Izett et al. 1972) is located in the overlying Blackwater Draw Formation, 9 m above the fossiliferous level of the Blanco Formation (G. Schultz 1990a). This ash bed was correlated with the Guaje pumice bed in the Jemez Mountains, New Mexico, on the basis of petrographic comparisons (Izett et al. 1972). Two fission-track dates on glass shards were reported for this ash: 1.4 ± 0.2 Ma (Izett et al. 1972; Izett 1981) and 1.77 ± 0.44 Ma (Boellstorff 1976). A second ash, the Blanco Ash, located approximately 7.5 m below the Guaje ash bed and thus stratigraphically closer to the fossiliferous Blanco beds, yielded a fission-track age (based on glass shards) of 2.8 \pm 0.3 Ma (Boellstorff 1976). No normally magnetized sediments were found in the Mount Blanco Section by Lindsay et al. (1975), but if the date of the Blanco Ash is correct, it would fall within a normal polarity interval, chron C2An.1n. On our correlation chart (figure 7.1) we plot the ash within a reversed-polarity interval (chron C2r.2r) based on the paleomagnetic analysis of Lindsay et al. (1975), but we also provide its published fission-track age.

The Cita Canyon faunas were derived from exposures at the head of Cita Canyon in Randall County, Texas. The first report of the fauna was by Johnston (1938). A subsequent analysis revealed characteristic Blancan taxa such as *Megalonyx* cf. *M. leptostomus*, *Glyptotherium* cf. *G. tex*- anum, Hypolagus cf. H. regalis, Borophagus, Canis lepophagus, Chasmaporthetes johnstoni, Platygonus bicalcaratus, "Equus simplicidens," and Nannippus peninsulatus (Johnston and Savage 1955; more extensive faunal lists were provided by G. Schultz 1977 and Kurtén and Anderson 1980). Two mammal-bearing stratigraphic units are separated by a sand that produced no mammalian fossils. Although stegomastodonts and glyptodonts are limited to the upper unit (Savage 1955), the faunas from the two units were listed together because many taxa are common to both. The lower fossiliferous sequence is normally magnetized and was referred to chron C2An.1n (the upper part of the Gauss chron), but the upper unit is reversed and was placed in chron C2r.2r (the lower Matuyama; Lindsay et al. 1975). Cita Canyon includes the earliest occurrence of Miracinonyx inexpectatus.

The Beck Ranch Fauna in Scurry County, Texas, includes a diverse assemblage of mammals (58 species; Dalquest 1978). It shares *Felis lacustris, Ogmodontomys poaphagus, Hypolagus regalis,* and *Nannippus* with the Rexroad faunas in Kansas and *Sigmodon minor* (originally identified as *Sigmodon medius,* but see Harrison 1978; R. Martin 1986), *Borophagus diversidens,* and *Platygonus bicalcaratus* with the Blanco Fauna (Dalquest 1978). Dalquest (1978) considered the Beck Ranch Fauna to be older than the Rexroad and Blanco faunas and younger than the Fox Canyon Fauna. A report of a rhinoceros tooth fragment from Beck Ranch (Madden and Dalquest 1990) remains to be verified.

The Donnelly Ranch Fauna in southeastern Colorado was recovered from normally magnetized sediments and includes Sigmodon minor, Sigmodon curtisi, Paramylodon, "Equus (Dolichohippus) simplicidens," Tapirus haysii (originally identified as Tapirus copei, but see Ray and Sanders 1984), Hemiauchenia blancoensis (originally listed as Tanupolama, but see Webb 1974b), Gigantocamelus, and an unidentified gomphothere (Hager 1975). The fauna was correlated with the Wolf Ranch Fauna in the St. David Formation of Arizona. The age assessment of 2.5 Ma given by Hager (1975) was derived from paleomagnetic correlations; Hager considered the fauna to be derived from normally magnetized sediments in the Gauss chron (chron C2An.1n). New paleomagnetic age calibrations yield an age of slightly older than 2.58 Ma (Berggren et al. 1995).

The Java Fauna of South Dakota generally is considered early Irvingtonian (R. Martin 1989a; Repenning 1992). No external age control is available. The Java Fauna includes *Allophaiomys, Guildayomys, Hibbardomys marthae, Ondatra annectens, Pliophenacomys, Mimomys dakotaensis* (closely related to and possibly synonymous with *Mi*- *momys virginianus*), *Mictomys kansasensis*, and several zapodid rodents (R. Martin 1973, 1975, 1989a, 1989b). *Mammuthus* is absent. The Java Fauna contains a unique association of taxa, and recent reanalysis suggests that the fauna may be mixed (R. Martin, pers. comm., 2002). For now we consider the fauna to be latest Blancan, but it may be early Irvingtonian. It includes the earliest known occurrence of *Ondatra annectens* (another early record is in the Kentuck Fauna).

Florida A number of important Blancan faunas were traditionally recognized from localities in Florida (Santa Fe River 1, Haile 15A, Macasphalt Shell Pit, Kissimmee River, and Haile 7C; Morgan and Ridgway 1987; Morgan and Hulbert 1995). Many additional faunas that are elsewhere considered Irvingtonian (Morgan and Hulbert 1995; Ruez 2001) are here considered to be latest Blancan (based on our adoption of Mammuthus as the defining taxon for the Irvingtonian). These faunas include Inglis 1A, Inglis 1C, De Soto Shell Pit, and Haile 16A. Low topographic relief results in a lack of exposed extensive stratigraphic sequences, and suitable material for radiometric dating is lacking (a possible exception is helium-uranium dating applied to corals that was used to help bracket the age of the Leisey Shell Pit Fauna; Bender 1973; Morgan and Hulbert 1995). External age control is possible for some faunas by use of the relationship of fossiliferous deposits to eustatic sea level changes supplemented by paleomagnetic data and strontium isotopic data (Webb 1974a; Webb et al. 1978, 1989; Jones et al. 1991).

A diverse assemblage of species is known from these faunas (see summary in Morgan and Hulbert 1995). The characteristic taxa provided by Morgan and Hulbert for the faunas they considered to be Blancan includes Dasypus bellus, Holmesina floridanus, Glyptotherium arizonae, Glossotherium chapadmalense, Megalonyx leptostomus, Eremotherium eomigrans, Trigonictis macrodon, Sigmodon minor (originally reported as Sigmodon medius, but see Harrison 1978; R. Martin 1986), Neochoerus dichroplax, Platygonus bicalcaratus, Hemiauchenia blancoensis, and Nannippus peninsulatus. Cormohipparion emsliei is an endemic Florida species known from the Macasphalt Shell Pit and Haile 15A faunas, the only known post-Hemphillian records of that hipparionine taxon (Hulbert 1987). The De Soto Shell Pit Fauna includes the youngest record of Megalonyx leptostomus, and Glossotherium chapadmalense makes its latest known appearance in the Macasphalt Shell Pit Fauna. Two Florida Blancan faunas (Haile 15A, Santa Fe River 1) contain associations of taxa such as Smilodon gracilis and Nannippus peninsulatus that are not known to overlap chronologically in the western United States. The Santa Fe River 1 record of *S. gracilis* is the oldest in North America. It was identified as *Ischyrosmilus* by Churcher (1984b) and was included in *Megantereon* by L. Martin (1980, 1998); we follow Berta (1985, 1987) for its taxonomic placement.

Nannippus occurs in several Florida Blancan faunas (Haile 15A, Santa Fe River 1, Macasphalt Shell Pit, and Kissimmee River) along with South American immigrant taxa (Holmesina floridanus, Dasypus bellus, and Glossotherium chapadmalense). The ages of these faunas are estimated to between 2.5 and 2.0 Ma (Jones et al. 1991; Morgan and Hulbert 1995), and the youngest occurrence of Nannippus is in the Macasphalt Shell Pit at approximately 2.1 Ma. According to Tedford (1981), the last appearance of Nannippus and the first appearance of South American taxa in New Mexico were nearly synchronous at the Gauss-Matuyama (chrons 2An/2r) boundary (2.58 Ma; Berggren et al. 1995). Nannippus disappears from the 111 Ranch sequence just below that boundary, and South American species first appear 20 m lower in the section (Galusha et al. 1984). The concurrent range is entirely of normal geomagnetic polarity and probably corresponds to chron C2An.1n (Galusha et al. 1984).

"Earliest Irvingtonian" faunas of Morgan and Hulbert (1995) and Ruez (2001) were provisionally interpreted to range in age between approximately 2.0 and 1.6 Ma and are here considered to be latest Blancan. These faunas include the Inglis 1A, Inglis 1C, and De Soto Shell Pit localities; their temporal range is based on correlations with faunas outside Florida that have radiometric dates. They contain several characteristic Blancan taxa such as Megalonyx leptostomus, Trigonictis macrodon, Chasmaporthetes ossifragus, Capromeryx arizonensis, and Ondatra idahoensis. Taxa such as Smilodon gracilis, Platygonus vetus, Paramylodon harlani, and Canis edwardii are found in latest Blancan faunas but are generally more characteristic of Irvingtonian faunas. The records of Paramylodon harlani and Platygonus vetus in Inglis 1A are the earliest known in North America. The Inglis 1C Fauna (Ruez 2001) appears to be intermediate in age between the older Inglis 1A and younger De Soto Shell Pit faunas. It contains the earliest Florida records of Peromyscus polionotus, Reithrodontomys humulis, and Atopomys texensis; late records of Reithrodontomys wetmorei and Ondatra idahoensis in Florida are also recorded in the fauna (Ruez 2001). The fauna also contains the youngest North American record of Platygonus bicalcaratus. Dasypus bellus, Holmesina floridanus, Paramylodon harlani, Sylvilagus webbi, Sigmodon curtisi, Orthogeomys propinetis, Smilodon gracilis, Palaeolama mirifica, Hemiauchenia macrocephala, Platygonus bicalcaratus, and Tapirus haysii are also present. Based on biochronologic data, Ruez (2001) gave a likely chronologic span of 2.01–1.78 Ma, with an age of approximately 1.9 being most likely.

The Haile 16A Fauna is allied with the other latest Blancan faunas based on the shared presence of *Sylvilagus webbi*, *Orthogeomys propinetis*, and *Atopomys texensis*, all of which are confined to the Blancan in Florida. Our removal of Haile 16A from the group of "late early Irvingtonian" faunas proposed by Morgan and Hulbert (1995) is consistent with the opinion of Morgan and White (1995), based on examination of the microfauna. The fauna records the earliest known occurrences of *Megalonyx wheatleyi* and *Synaptomys*.

CHRONOLOGIC ASPECTS OF THE GREAT AMERICAN BIOTIC INTERCHANGE

As noted earlier, a number of southern United States localities produce assemblages of several genera of late Blancan land mammal immigrants from source areas in South America. These southern species, their affiliations with sister groups in South America, and the chronologic evidence regarding the reciprocal cohort that moved southward across the Panamanian land bridge were treated by Marshall et al. (1979), Webb (1985, 1991), and Webb and Rancy (1996). The absence of radiometric dates from Florida sites leads to some loose correlations of key sites, based largely on biostratigraphy and aided, in some cases, by paleomagnetic evidence. For that reason it is fortunate that several of the late Blancan Neotropical taxa extend geographically beyond Florida, appearing concurrently in western sites, thus supporting and refining the biostratigraphic control on the Florida record. These immigrants and their earliest known North American records include Glossotherium in the Lower Cita Canyon (G. Schultz 1977) and Blanco (Dalquest 1975) faunas of Texas, the 111 Ranch Fauna in Arizona (Galusha et al. 1984), the Donnelly Ranch Fauna of Colorado (Hager 1975), and the Haile 15A and Santa Fe River 1 faunas of Florida (Webb 1974a; Robertson 1976); *Glyptotherium* in Upper Cita Canyon (Johnston and Savage 1955), Blanco (Meade 1945), Hudspeth (Strain 1966), and Red Light (Akersten 1972) faunas of Texas, the 111 Ranch Fauna in Arizona (Gillette and Ray 1981 as "Tusker Fauna," but see Galusha et al. 1984), and Santa Fe River 1 in Florida (Gillette and Ray 1981); Holmesina floridanus (originally described as Kraglievichia but transferred to Holmesina by Edmund 1987) and Dasypus in Haile 15A and Santa Fe River 1B faunas in Florida (Webb 1974a; Robertson 1976); Neochoerus at 111 Ranch, Arizona (Lindsay and Tessman 1974; Ahearn and Lance 1980; Galusha et al. 1984); and
Erethizon in the Grand View Fauna in Idaho (Wilson 1935), the Haile 7C and Inglis 1A faunas in Florida (Frazier 1982; Morgan and Hulbert 1995), the Wolf Ranch Fauna in Arizona (Harrison 1978; Frazier 1982), and the San Timoteo Badlands of California (Albright 1999). The records listed here suggest that these immigrants were in southwestern faunas by the end of chron C2An (Gauss) at approximately 2.5 Ma (Berggren et al. 1995).

It is noteworthy that late Blancan Neotropical land mammals of North America provide the best available datum establishing the existence of a functional Panamanian land bridge in the Pliocene. Studies of tectonism and volcanism in the isthmian region (Coates and Obando 1996) provide local observations and cannot demonstrate continuous terrestrial terrain on a convincing scale. On the other hand, although marine micropaleontology and molluscan studies indicate decreasing water depth in Pacific and Atlantic sediments during the Miocene and Pliocene (Cronin and Dowsett 1996), they approach but cannot record the final establishment of a land bridge that would permit the passage of terrestrial mammals. Subaerial exposure of the isthmus may have occurred sporadically between approximately 3.1 and 2.0 Ma (Cronin and Dowsett 1996; Webb and Rancy 1996). For that reason, the marine studies give older estimates, usually between 3 and 4 Ma, than do the mammal data. The main thrust of the Pliocene migration of North American taxa into South America occurred by the early Uquian South American mammal age. South American faunas containing the immigrants closely postdate the Gauss-Matuyama (chron C2An/2r) boundary (Webb and Rancy 1996) at 2.58 Ma (Berggren et al. 1995).

IRVINGTONIAN

HISTORICAL CONTEXT

The Irvingtonian mammal age was originally defined by Savage (1951) based on a fauna recovered from gravel pits southeast of Irvington, Alameda County, California (Stirton 1939; Savage 1951; Firby 1968). These gravel pits now are abandoned, and portions are overlain by Interstate Highway 680. Strata adjacent to the pits and at the level where the fossils were recovered are reversely magnetized, and the fauna was referred to the upper part of the Matuyama chron below the Jaramillo subchron by Lindsay et al. (1975; the placement would now presumably be in chron C1r.2r). The primary criteria proposed by Savage for recognition of the Irvingtonian were the absence of *Bison* and the presence of mammalian species less advanced than related forms from the Rancholabrean and the Holocene. Savage used the appearance of *Bison*, among other criteria, to define the subsequent Rancholabrean. This usage effectively meant that two consecutive mammal ages were defined by the presence or absence of a single taxon, *Bison*. This situation is further complicated by the difficulty in establishing an adequate chronology for the arrival of *Bison* in North America (see "Rancholabrean" later in this chapter).

HISTORICAL DEFINITION AND CHARACTERIZATION

The ambiguity of the original definition of the Irvingtonian ("the Irvingtonian is marked by the absence of *Bison*"; Savage 1951:289) led to unstable and inconsistent approaches to defining the Irvingtonian. Several authors proposed alternative definitions based on either the composite fauna from the type Irvington locality (Firby 1968) or on one or more members of the fauna (e.g., *Mammuthus*; Kurtén and Anderson 1980). No explicit definition was recommended by Lundelius et al. (1987), but they provided a discussion of advantages and disadvantages of using alternative taxa.

CURRENT DEFINITION AND CHARACTERIZATION

Definition In our committee deliberations we failed to reach unanimous consensus on the definition of the Irvingtonian. The majority decision was that the Irvingtonian is best defined by the first appearance of *Mammuthus* in North America south of 55°N latitude. This definition previously was not proposed explicitly but is in keeping with a widespread use that emerged among Pleistocene mammalian paleontologists over the last 20 years. It is also in keeping with the historical context of the Irvingtonian; the presence of *Mammuthus* was considered by Savage (1951:236) to "offer some of the best evidence for assignment of a Pleistocene age to Irvington," but he did not include *Mammuthus* in his discussion of the initial proposal for the Irvingtonian mammal age (Savage 1951:289).

We recognize the benefits of single-taxon boundary definitions (Woodburne 1977, 1987) but also acknowledge the complications that can arise from such definitions. The use of *Mammuthus* to define the Blancan–Irvingtonian boundary certainly suffers from deficiencies, but advantages of using *Mammuthus* to define the Irvingtonian include the facts that it was widespread in North America, is easy to identify, and is difficult to miss (because of its large size) in faunas where it is present. However, although *Mammuthus* was widespread in North America in the Pleistocene it often is absent from faunas that are known or taken to be Irvingtonian based on radiometric dating or biochronologic correlation. Important examples include many cave deposits (where *Mammuthus* probably is absent for taphonomic reasons) and the San Pedro Valley (Arizona) and Meade County (Kansas) sequences, portions of which generally are interpreted to be Irvingtonian. In these cases assignment of faunas to the Irvingtonian must rely on characterizing taxa, especially those that are limited to the Irvingtonian.

With the adoption of Mammuthus to define the base of the Irvingtonian, many faunas elsewhere considered to be early Irvingtonian (based on alternative definitions) are here considered to be latest Blancan. These include the Inglis 1A, Inglis 1C, Haile 16A, and De Soto Shell Pit faunas in Florida; the Curtis Ranch Fauna in the San Pedro Valley sequence in Arizona; the Nash, Aries A, Rick Forester, and Aries B faunas in the Meade Basin of Kansas; the Sappa Fauna in Nebraska; the Java Fauna in South Dakota; the Froman Ferry faunal sequence in Idaho; the El Casco Fauna in California; and the lower portion of the Cedazo faunal sequence in Mexico. Not only do these faunas lack Mammuthus, but their known (or inferred) temporal ranges predate the established arrival of Mammuthus elsewhere (accepted herein as 1.35 Ma). The informal designation latest Blancan can be used to refer collectively to the faunas affected by the new definition. Because of uncertainties in their correlation, the Haile 16A, Rick Forester, Aries B, Sappa, and El Casco faunas may be either late Blancan or earliest Irvingtonian (they may or may not predate the earliest arrival of Mammuthus).

Characterization The characterization of the Irvingtonian includes a few taxa that are limited to the Irvingtonian, many that appear in earlier mammal ages but are common in Irvingtonian faunas, and many that make their first appearance in the Irvingtonian but persist into the younger Rancholabrean. These are listed separately later in this chapter, followed by comments justifying our treatment of certain taxa and relevant faunas.

Taxa limited to the Irvingtonian include *Microtus lla*nensis, Microtus meadensis, Microtus paroperarius, Canis armbrusteri, and Tetrameryx irvingtonensis.

Taxa that make their first appearance in the Blancan (or earlier) but persist into the Irvingtonian include *Glyptotherium*, *Blarina*, *Sylvilagus*, *Miracinonyx inexpectatus*, *Smilodon gracilis*, *Arctodus pristinus*, *Ursus*, and *Mammut americanum*. Taxa that first appear in latest Blancan faunas (those that are elsewhere often considered to be early Irvingtonian) include Nothrotheriops, Paramylodon harlani, Holmesina, Lepus, Allophaiomys pliocaenicus, Microtus with five closed triangles on the lower first molar, Mictomys kansasensis/meltoni, Neofiber, Ondatra annectens, Phenacomys, Synaptomys, Sciurus, Canis edwardii, Lutra canadensis, Homotherium, and Platygonus vetus.

Taxa that first appear in the Irvingtonian and persist into Rancholabrean or younger faunas include Didelphis, Brachylagus idahoensis, Sylvilagus palustris, Clethrionomys, Lemmiscus curtatus, Ondatra zibethicus, Marmota flaviventris, Marmota monax, Cynomys gunnisoni, Cynomys ludovicianus, Panthera onca, Smilodon populator, Mustela erminea, Brachyprotoma, Conepatus, Canis latrans, Canis lupus, Arctodus simus, Euceratherium, Oreamnos, and Mammuthus.

The *Canis* in the Cudahy Fauna in Kansas was described by Getz (1960) as "*Canis* sp."; the identification was changed to *Canis edwardii* by Nowak (1979). *Rangifer tarandus* was reported from the Cape Deceit Fauna in Alaska, here considered an Irvingtonian temporal equivalent (originally identified as "*Rangifer* sp." by Guthrie and Matthews 1971, but see McDonald et al. 1996). The earliest known records from south of 55°N latitude are in the Rancholabrean Medicine Hat and Carlton Bar faunas, both in southern Canada (J. McDonald et al. 1996). The first Irvingtonian record of *Oreamnos* was recently discovered in Porcupine Cave, Colorado (Mead and Taylor 1998; originally identified as "cf. *Oreamnos harringtoni*," but the "cf." was dropped by Jass et al. 2000).

THE ARRIVAL OF MAMMUTHUS

The oldest reported reliable date for *Mammuthus* is from the Leisey Shell Pit Fauna from the Bermont Formation in Florida, which includes the largest sample of early Pleistocene mammoths in North America (Webb and Dudley 1995). An evaluation of strontium isotope data, paleomagnetic data, and biostratigraphy (Webb et al. 1989; Hulbert et al. 1995) yielded an age range for the Bermont Formation of between 1.55 and 1.1 Ma; the major vertebrate-bearing units are considered to be less than 1.3 Ma (Morgan and Hulbert 1995:30), the age we accept for the *Mammuthus* material.

A series of vertebrate fossil localities in the vicinity of Tijeras Arroyo in Bernalillo County, New Mexico, include both Blancan and Irvingtonian faunas (Logan et al. 1984; Lucas et al. 1993; Morgan and Lucas 2000b). The geologic formation from which the faunas were recovered is uncertain (but was tentatively referred to the Sierra Ladrones Formation by Lucas et al. 1993). Reworked pumice fragments deposited in strata containing Irvingtonian faunas were interpreted to be derived from the Guaje Pumice, the lower bed of the Otowi Member of the Bandelier Tuff, dated elsewhere to approximately 1.61 Ma (Izett and Obradovich 1994; Spell et al. 1996). The Irvingtonian component has a fauna including *Mammuthus*, *Glyptotherium arizonae*, and *Equus scotti* and dates to between 1.0 and 1.6 Ma (Morgan and Lucas 2000b). Three localities in Tijeras Arroyo were reported to contain *Mammuthus*; the oldest recorded occurrence from this area was interpreted to be "no older than 1.61 Ma" (Lucas et al. 1993:8), but a more precise age is not available.

Another early record of *Mammuthus* was reported from the Rock Creek Fauna in the Tule Formation, Briscoe County, Texas. *Mammuthus* remains are in close stratigraphic association with a volcanic ash identified as the Cerro Toledo X Ash, with an age of 1.2 to 1.3 Ma (Izett 1977; G. Schultz 1986). The stratigraphic section illustrated by G. Schultz (1986:83) plots *Mammuthus* below the Cerro Toledo X ash bed (the section was republished with minor modification by G. Schultz 1990b).

Until recently, there were no specimens of *Mammuthus* from the Vallecito Creek–Fish Creek sequence in the Anza-Borrego Desert (Cassiliano 1999), but molar fragments referred to *Mammuthus* are now reported from three localities in that sequence, with a maximum age of 1.2 Ma (McDaniel and Jefferson 1999). Additional material is known from the Borrego Badlands in the northern part of the Anza-Borrego Desert State Park. The oldest possible age for this material is between approximately 1.0 Ma and 1.25 Ma (Remeika and Jefferson 1993; Jefferson and Remeika 1994).

Another often-cited early occurrence of Mammuthus is from the Bruneau Formation in Idaho, where Malde and Powers (1962) reported Mammuthus tooth fragments from a gravel bed 3.2 km (2 miles) southeast of Glenn's Ferry. Based on their map (Malde and Powers 1962, plate 1), these tooth fragments were recovered from an area of "sediments and interbedded basalts." The age of the "Bruneau Basalt Mammuthus-bearing fauna" is traditionally given as 1.36 Ma, an age derived from a K-Ar date reported by Evernden et al. (1964); magnetic polarity data are unavailable for the deposit that yielded the Mammuthus (Neville et al. 1979:519). Additional work by Armstrong et al. (1975) yielded a variety of ages for Bruneau Basalt flows, with an average of approximately 1.4 Ma. The complex stratigraphic relationships of former stream channels and the lava flows that dammed them were discussed by Malde (1991). The dates on the lava flow dams range in age from 2.06 Ma to 0.78 Ma, making the history of deposition and the age of associated discrete mammalian fossil deposits difficult to assess (Repenning et al. 1995).

Controversial reports of Mammuthus from the Merced Formation at Thornton Beach, California, are more problematic (Madden 1980, 1995; Lucas 1995). The age, stratigraphic position, and taxonomic affinities of the Thornton Beach mammoth are disputed. The mammoth material from Thornton Beach apparently was collected about 10 m below a horizon dated at 1.5 \pm 0.8 Ma (Hall 1965; Lucas 1995; Madden [1995] stated that the fossil came from above the dated horizon, but this appears to be an error), but much younger age estimates for the Merced Formation $(0.45 \pm 0.08 \text{ Ma})$ were reported by Meyer et al. (1980) from localities to the north and east of Thornton Beach itself. Other reported early occurrences include a single tooth from New Bern, North Carolina, with unknown stratigraphic and age determinations (Madden 1985) and a record from Santa Fe River 1B in Florida that was reported to be in association with Blancan taxa (Lambert et al. 1995; according to Cassiliano [1999] the association may be the result of mixing of fossils of different ages).

The appearance of *Mammuthus* in North America therefore appears to have been essentially contemporaneous over much of what is now the United States and can be bracketed at approximately 1.3 to 1.4 Ma. The differences in age between the first appearances in various regions are small enough to be attributable to discontinuous deposition and the vagaries of association between good fossil sites and good dates. Slightly older ages are possible for the *Mammuthus* material from Leisey Shell Pits in Florida and the Tijeras Arroyo in New Mexico.

An additional early report of *Mammuthus* in the Wellsch Valley faunal sequence from southern Saskatchewan (Stalker and Churcher 1972, 1982; Churcher 1984a; Barendregt et al. 1991, 1998) may represent the earliest North American appearance. Detailed stratigraphic data for the vertebrate species from Wellsch Valley are not published yet, and the stratigraphic position of *Mammuthus* must be confirmed. The fossils were reported from reversely magnetized sediments attributed to the upper part of the Matuyama (chron C1r.1r) by Barendregt et al. (1991).

A Need for a Small Mammal Definition? A small mammal definition for the Irvingtonian is also possible (and perhaps advisable) but is not endorsed here. If such a definition were adopted, the first appearances of *Allophaiomys* and *Microtus* (*sensu* Repenning 1992) seem to be the best choices for defining taxa; both are listed earlier in our characterization of the Irvingtonian. The earliest purported Allophaiomys associated with external age control is from Hansen Bluff (Colorado) and was recovered from a core hole. The specimens in question are not definitively diagnostic; referral to Allophaiomys was based on the general morphology of nondiagnostic molars and stratigraphic position near chron C2n (the Olduvai), dated to approximately 1.9 Ma (Rogers et al. 1992). The Nash Fauna in Kansas may be slightly older (R. Martin et al. 2000), and the specimens permit a more reliable identification. We now consider both records to be latest Blancan. Other early records include Java, South Dakota (R. Martin 1975, 1989a), and Wellsch Valley, Saskatchewan (Churcher 1984a; Barendregt et al. 1991; Repenning 1992). Allophaiomys is fairly common in faunas from the Great Plains but is known from only three localities in or west of the Rocky Mountains: Porcupine Cave, Colorado (Bell and Barnosky 2000); Little Dell Dam, Utah (Gillette et al. 1999); and Cathedral Cave, Nevada (Bell 1995; Bell and Barnosky 2000). The earliest reported occurrence of *Microtus* (sensu Repenning 1992) is from the Anza-Borrego Desert (Zakrzewski 1972), where its earliest occurrence may be between approximately 1.4 and 1.6 Ma (Repenning 1992:59; Repenning et al. 1995). Additional very early Microtus material was reported from the El Casco Fauna in southern California (Albright 1999), with a reported age of between 1.3 and 1.4 Ma. Microtus persists into the modern fauna and includes a diverse assemblage of extant species (Hall 1981).

Alternative Hypotheses There are at least five operational (though not necessarily explicit) definitions of the Irvingtonian in the recent literature, many of which were specifically proposed to account for provinciality in restricted geographic areas. Because these various alternative methods for defining the Irvingtonian continue to be used, we provide a brief summary in the following sections.

Savage's initial reliance on the absence of *Bison* as a primary means of recognizing Irvingtonian faunas was itself provincial in nature and specifically addressed faunas in the San Francisco Bay area in California (to quote Savage, *"Bison* is not represented in the Irvington Fauna. In view of this fact it may seem rather strange that this genus should enter into a discussion of the age of the assemblage. I believe, however, that the dating of the Irvington and all other terrestrial Pleistocene vertebrate faunas in the Bay region must hinge on the presence or absence of this genus"; Savage 1951:277). This method of recognizing Irvingtonian faunas is still occasionally invoked in California (Dundas et al. 1996; Pajak et al. 1996:38), but it does not appear to be used extensively elsewhere.

The first appearances of one or more of the following taxa also are used sometimes to mark the beginning of the Irvingtonian: Smilodon, Lepus, Soergelia, and Euceratherium (Johnson et al. 1975; Lundelius et al. 1987; Cassiliano 1999). There are problems associated with each. Most of them (Smilodon, Soergelia, and Euceratherium) are of limited utility because they are not common in fossil faunas (Lundelius et al. 1987; Cassiliano 1999). Lepus recently was proposed as the best taxon for defining the Irvingtonian in the Vallecito Creek-Fish Creek sequence in the Anza-Borrego Desert (Cassiliano 1999), but it is difficult to distinguish from other leporid taxa (e.g., Sylvilagus; White 1984, 1991b). The earliest occurrence of Smilodon is in the Santa Fe River 1 Fauna in Florida, reported to be between 2.5 and 2.0 Ma by Morgan and Hulbert (1995). Lepus first appears in the Borchers Fauna at approximately 2.0 Ma. The oldest known Soergelia is from the Rock Creek Fauna, younger than 1.2 Ma. The earliest known occurrence of Euceratherium is in the Vallecito Creek-Fish Creek sequence in Anza-Borrego at approximately 1.1 Ma.

Three additional definitions were proposed by Repenning (1992; Repenning et al. 1995) and differ in philosophy from others in that they explicitly seek to recognize provincial changes in faunal compositions as the basis for definition. In Repenning's approach, these perceived provincial changes would result in diachronous boundaries for the Irvingtonian. The first appearance of Allophaiomys (sensu Repenning 1992) was proposed to define the Irvingtonian for faunas east of the Rocky Mountains (Repenning 1992; Fejfar and Repenning 1992; Repenning et al. 1995) at approximately 1.9 Ma (based on the core hole specimen from Hansen Bluff; Rogers et al. 1992; Repenning 1992); the Nash Fauna in Kansas may be somewhat older, and the presence of Allophaiomys there is based on definitively identifiable material (the Hansen Bluff core specimens are nondiagnostic teeth; see Rogers et al. 1992). The first appearance of Phenacomys was proposed to define the Irvingtonian for the portion of the northern United States west of the Rocky Mountains (Repenning 1992; Fejfar and Repenning 1992; Repenning et al. 1995). Its first appearance there is marked by the appearance of P. gryci in the Froman Ferry sequence in Idaho, at approximately 1.7 Ma (Repenning et al. [1995] gave the age as approximately 1.6 Ma, based on their use of 1.65 Ma as the end of the Olduvai event [chron C2n], now dated at 1.77; Berggren et al. 1995). That species is known from much earlier deposits in Fish Creek, Alaska (reported to be approximately 2.4 Ma by Repenning et al. 1987), and also from younger localities in Porcupine Cave, Colorado, and Cathedral Cave, Nevada (Bell and Barnosky

2000). The beginning of the Irvingtonian in the southern part of the United States west of the Rocky Mountains was recognized by Repenning (1992; Repenning et al. 1995) based on the first appearance of *Microtus* (*sensu* Repenning 1992) in the Anza-Borrego sequence at approximately 1.4 Ma to 1.6 Ma (Repenning 1992; Fejfar and Repenning 1992; Repenning et al. 1995; also see Pajak et al. 1996).

External age control for the three taxa in the various provinces indicates that there is as much as 0.5 Ma (1.9 Ma to 1.4 Ma) difference in their first appearance; therefore, based on these records, the Irvingtonian would not begin at the same time in every province, and provincial definition would be based on different taxa. Tentative faunal provinces were outlined by Fejfar and Repenning (1992; see map in Bell 2000) but must be critically reevaluated. Major additional complications with this framework include the determination of temporal and spatial boundaries for provinces and the establishment of rigorous criteria on which such determinations should be based. These proposals warrant additional study and evaluation and highlight an important arena for new research into the nature and scope of mammal ages in the context of faunal provinciality.

TEMPORAL EXTENT

As defined here, the Irvingtonian begins with the earliest appearance of Mammuthus in North America south of 55°N latitude. The actual first appearance is almost undoubtedly earlier than our oldest reliably dated fossil, but as currently understood the early records of Mammuthus place the boundary at approximately 1.35 Ma. The end of the Irvingtonian is marked by the beginning of the subsequent Rancholabrean age (currently defined by the first appearance of Bison). Our understanding of the timing of arrival of Bison is inadequate; the end of the Irvingtonian may be as old as 210 ka or as young as 160 ka (discussed under "Rancholabrean" later in this chapter). The varied provincial definitions proposed by Repenning and his colleagues (based on Microtus at 1.4 Ma, Phenacomys at 1.7 Ma, and Allophaiomys at approximately 1.9 Ma; Repenning 1992:59; Repenning et al. 1995; Phenacomys age modified to conform to Berggren et al. 1995) provide slightly to considerably older ages for the beginning of the Irvingtonian.

TEMPORAL DIVISIONS OF THE IRVINGTONIAN

Sappan, Cudahyan, and Sheridanian Various efforts to refine temporal resolution in the Irvingtonian have

been proposed (figure 7.3). Two divisions of the Irvingtonian, the Sappan (older) and the Sheridanian (younger), were proposed by C. Schultz et al. (1977, 1978) and were based primarily on faunas from the Great Plains. Faunas considered to be Sappan (C. Schultz et al. 1978; Lundelius et al. 1987) include the type Sappa Fauna in Harlan County, Nebraska, situated 2 m beneath the Mesa Falls Ash, dated to between 1.27 and 1.29 Ma (C. Schultz and Martin 1970; Naeser et al. 1971; Izett 1981; Izett and Wilcox 1982; L. Martin and Schultz 1985; Gansecki et al. 1998; this fauna lacks Mammuthus and may be more properly considered latest Blancan); the Nash and Aries faunas (the latter now Aries A, both here considered to be latest Blancan) in Meade County, Kansas; the Wathena Fauna in Doniphan County, Kansas (Van der Meulen 1978); the Kentuck Fauna in McPherson County, Kansas (Hibbard 1952; Semken 1966; R. Martin 1975), deposited in a channel fill cut into the Huckleberry Ridge Ash (Izett 1981); and the Java Fauna, Walworth County, South Dakota (R. Martin 1973, 1975, 1989a, 1989b). These faunas were grouped together originally because they included the earliest known records of the arvicolines Mictomys and Allophaiomys and because of a low diversity of arvicoline rodents (C. Schultz et al. 1978). That the faunas seem dominated by heteromyid and cricetine rodents was suggested by Lundelius et al. (1987), who noted that the subage could be characterized by Ondatra annectens, Allophaiomys, and Mictomys kansasensis. Mammuthus also was reported to appear during the Sappan (e.g., Gilliland Fauna in Texas), and Stegomastodon made its last appearance (C. Schultz et al. 1978). At least some of the faunas traditionally considered to be Irvingtonian (e.g., Sappa, Nash, Aries A) are here considered to be latest Blancan. The Sappan division therefore spans the latest Blancan and early Irvingtonian as they are used here.

The recognition that some Irvingtonian faunas were intermediate in age between the Sappan and the younger Sheridanian (C. Schultz et al. 1978) led Lundelius et al. (1987) to propose the term *Cudahyan* for these faunas. Cudahyan faunas in the Great Plains include Cudahy Ash Pit, Sunbright Ash Pit, Tobin, and Wilson Valley (all in Kansas) and the Vera, Gilliland, Woody Draw, Bull Draw, and Deadman's Creek faunas (all in Texas). These faunas are closely associated with the Lava Creek B Ash (formerly Pearlette Type O Ash), dated between 0.60 and 0.67 Ma (Izett and Honey 1995; Gansecki et al. 1998), and are characterized by the following arvicoline species: Microtus paroperarius, Microtus meadensis (= Pitymys or Terricola of some authors), Microtus llanensis (= Pedomys), Mictomys meltoni, Ondatra annectens, and Phenacomys. Cudahyan faunas also can be recognized outside the Great Plains; examples include Conard Fissure, Arkansas (Brown 1908; Graham 1972); Cumberland Cave, Maryland (Gidley 1913, 1920a, 1920b; Gidley and Gazin 1933, 1938; Nicholas 1953; Van der Meulen 1978); Trout Cave No. 2, West Virginia (Pfaff 1990, 1991); and possibly Port Kennedy Cave, Pennsylvania (Wheatley 1871; Cope 1871; Daeschler et al. 1993; Hibbard 1955b). The Pit Fauna in Porcupine Cave, Colorado (Bell and Barnosky 2000); Cathedral Cave, Nevada (Bell 1995; Bell and Barnosky 2000); and some of the faunal components of Hansen Bluff, Colorado (Rogers et al. 1985, 1992), and SAM Cave, New Mexico (Rogers et al. 2000), may also be considered to be Cudahyan.

The Sheridanian subage (C. Schultz et al. 1977, 1978) primarily was based on the Hay Springs, Rushville, Gordon, and Angus faunas (Nebraska; C. Schultz et al. 1978). These faunas were characterized by Ondatra nebracensis (often erroneously spelled "nebrascensis"; see type description in Hollister 1911; now considered a junior synonym of Ondatra zibethicus; see Stephens 1960; R. Martin 1996) rather than Ondatra annectens, Microtus pennsylvanicus rather than Microtus paroperarius, Microtus ochrogaster (= Pedomys) rather than Microtus llanensis (= Pedomys), and Smilodon populator (formerly Smilodon fatalis; see Berta 1985) rather than Smilodon gracilis (Lundelius et al. 1987). Although the Irvington Fauna was also included in the Sheridanian by C. Schultz et al. (1978), its preservation in reversely magnetized sediments of the upper Matuyama chron (Lindsay et al. 1975) argues for an older age than other Sheridanian faunas, all of which are found in the Brunhes chron (chron C1n). Other faunas considered by Lundelius et al. (1987) to be Sheridanian include Kanopolis (Hibbard et al. 1978), Rezabek (Hibbard 1943), Sandahl (Semken 1966), and Adams (G. Schultz 1969) from Kansas, Berends (Starrett 1956) from Oklahoma, and Slaton (Dalquest 1967) from Texas. The Kanopolis, Rezabek, and Slaton faunas contain Neofiber leonardi and were considered to be approximately the same age (Hibbard and Dalquest 1973; Hibbard et al. 1978; Lundelius et al. 1987). These faunas lack external age control, and their placement on figure 7.1 is tentative. The Kanopolis and Rezabek records of Ondatra zibethicus are among the earliest known occurrences.

Divisions Based on Arvicoline Rodents As discussed earlier in this chapter, Charles Repenning and Larry Martin gave alternative proposals for dividing the Irvingtonian on the basis of changes in taxonomic composition and stage of evolution in arvicoline rodents. However, unlike the Blancan, the two proposals for the Irvingtonian are more similar. Each recognized three temporal divisions based on the appearance of new immigrant taxa or changes in species of endemic North American lineages and used similar taxa to recognize temporal divisions, but they differed in their intended geographic scope. Martin's proposal was centered on the biostratigraphy of Great Plains faunas and is not widely used outside that region. Repenning's original proposal was intended to encompass most of North America and was centered on developing a North American system that corresponded to a similar European biochronology. Repenning's initial proposal was subsequently modified extensively in light of new discoveries and interpretations (Repenning 1980, 1983, 1984, 1987, 1992, 1998, 2001; Repenning et al. 1990, 1995; Bell and Repenning 1999; Bell 2000). Because the taxa used in both schemes are so similar, many of the changes applied to the Repenning scheme have equal impact on the Martin proposal (although this has never been explicitly stated or explored in the literature). For that reason, we center our discussion on the Repenning chronology. The relationships of the two proposals are illustrated in figure 7.3.

Initially Repenning's proposal (1984, 1987) recognized three divisions of the Irvingtonian, numbered consecutively from oldest to youngest: Irvingtonian I, and II, and "Rancholabrean I." "Rancholabrean I" faunas were noted to predate the arrival of Bison in the United States (Repenning 1987). The formal adoption of Bison as the defining taxon for the Rancholabrean (established by Lundelius et al. 1987) led Repenning et al. (1990) to change "Rancholabrean I" to "Irvingtonian III." Only the Irvingtonian I and Irvingtonian II are recognized here. To facilitate ready interpretation of the literature, we provide a complete review of the Repenning proposal in its full form, including brief discussion of the rejected Irvingtonian III. Temporal divisions of the Irvingtonian, like those of the Blancan, were based on purported immigration events, but not all taxa have a documented presence in Asia or North American Beringia.

IRVINGTONIAN I (APPROXIMATELY 1.9 MA OR 1.72 MA TO APPROXIMATELY 0.85 MA)

Three provincial definitions of the Irvingtonian I are currently in use, and the defining taxa and initiation time are different in all three provinces. In the southern United States west of the Rocky Mountains it is defined on the first appearance of a *Microtus* with five closed triangles on the lower first molar (*'Microtus californicus'* of Repenning 1987, but many North American species show an essentially identical morphology; see Bell and Barnosky 2000) between 1.4 and 1.6 Ma (Repenning 1992; Repenning et al. 1995). In the northern United States, west of the Rocky Mountains, it is defined by the first appearance of Phenacomys at approximately 1.72 Ma (Repenning et al. 1995). The age given here is somewhat older than that of Repenning et al. (1995), whose age of 1.6 Ma was based on an age calibration of 1.65 Ma for the top of the Olduvai event (chron C2n), which we calibrate at 1.77 Ma (following Berggren et al. 1995). The earliest appearance of Phenacomys was said to be approximately 0.05 Ma younger than the top of the Olduvai, hence our age of 1.72. East of the Rocky Mountains it is defined by the first appearance of Allophaiomys, possibly as early as 1.9 Ma in Colorado (Rogers et al. 1992; Repenning et al. 1995), but the Nash Fauna in Kansas may be slightly older (R. Martin et al. 2000). The Irvingtonian I is characterized by Mictomys kansasensis, Ondatra annectens, and Proneofiber guildayi.

IRVINGTONIAN II (APPROXIMATELY 0.85 MA TO APPROXIMATELY 0.4 MA)

The Irvingtonian II was originally defined on the first appearance of Microtus meadensis (= Pitymys or Terricola of some authors) and the first Clethrionomys. Lasiopodomys (sensu Repenning 1992) was added as a defining taxon by Repenning et al. (1990). All of these taxa were considered by Repenning et al. (1990) to have entered North America as immigrants at approximately 850 ka. All of the purported early records of *Clethrionomys* that were originally cited to support its presence in the Irvingtonian II subsequently were shown to be misidentified specimens of Ophiomys parvus (southern California records; see Scott and Cox 1993) or Phenacomys (Hansen Bluff; see Bell and Barnosky 2000:124). The report of Clethrionomys from Cumberland Cave (Guilday 1971; reiterated by Repenning 1987) has not been verified since the recognition of Mimomys virginianus in Irvingtonian deposits in the eastern United States (Repenning and Grady 1988). The two taxa are superficially similar in that both have rooted molars with cementum in the reentrant angles, and the Cumberland Cave material may represent Mimomys. The recent report of Clethrionomys from reversely magnetized sediments in SAM Cave, New Mexico (Rogers et al. 2000), confirms its presence in the western United States before about 780 ka, but additional records are lacking.

Lasiopodomys was reported from several localities in the eastern and central United States including Hamilton Cave, West Virginia (Repenning and Grady 1988), Cumberland Cave, Maryland (Repenning 1992), and the County Line Fauna in Illinois (B. Miller et al. 1994). Each of the three records from the western United States is based on a single isolated lower first molar; these are from the Anza-Borrego Desert (Repenning 1992), the Pit locality in Porcupine Cave, Colorado (Bell and Barnosky 2000), and Cathedral Cave, Nevada (Bell and Barnosky 2000). The paucity of material and the possibility that these specimens are actually population variants of *Microtus paroperarius* (see Repenning 1992; Bell and Barnosky 2000) reduces our confidence in the use of this taxon. *Lasiopodomys* was reported originally from Cape Deceit, Alaska (as *Microtus deceitensis*; Guthrie and Matthews 1971).

The complications with Clethrionomys and Lasiopodomys suggest that they are inadequate for defining the Irvingtonian II, and they are here considered as characterizing taxa of the Irvingtonian II. We therefore consider this interval to be defined by the first appearance of *Microtus meadensis* (= *Terricola* or *Pitymys* of others). The history of this species in North America was discussed at length by Repenning (1983, 1992). It is widespread throughout the central and western United States but appears never to have crossed the Mississippi River. The earliest records appear to be from the Hansen Bluff and Porcupine Cave faunas in Colorado (Rogers et al. 1985; Bell and Barnosky 2000), but an occurrence in the Anza-Borrego Desert in reversely magnetized sediments of unknown age (Repenning 1992) may predate the Colorado records. The Hansen Bluff material was assigned an age of approximately 820 ka (Repenning 1992:72); the older specimens from the Pit locality in Porcupine Cave are interpreted to be between 750 and 850 ka (Bell and Barnosky 2000).

Recognition of a *Mimomys*-like arvicoline in the North American Pleistocene came as early as 1972 (L. Martin 1972) with the description of *Loupomys monahani* (originally named *Mimomys monahani*; see Koenigswald and Martin 1984). *Loupomys* is known only from the type locality in the Mullen assemblage in Nebraska (L. Martin 1972). It has a unique enamel microstructure (Koenigswald and Martin 1984; R. Martin 1989a), and although its relationships are poorly understood, it seems best to consider it a late *Mimomys*-like immigrant into North America (Repenning and Grady 1988; R. Martin 1989a).

Another arvicoline lineage appears in North America during the Irvingtonian II and is presumed an immigrant from Asia. Members of this lineage are classified as *Mimomys* (Repenning and Grady 1988 placed them in the subgenus *Cromeromys*), and two species are currently named. *Mimomys virginianus* was described from Hamilton Cave in West Virginia (Repenning and Grady 1988) and was tentatively identified in the Pit Fauna from Porcupine Cave and from Cathedral Cave in Nevada (Bell and Barnosky 2000). *Mimomys dakotaensis* was first described from the Java fauna in South Dakota (R. Martin 1989a) and was tentatively identified from Little Dell Dam in Utah (Gillette et al. 1999).

The Irvingtonian II is characterized by the presence of Atopomys, Clethrionomys, Lasiopodomys, Lemmiscus curtatus, Mictomys kansasensis, Mictomys meltoni, Mimomys virginianus, Mimomys dakotaensis, Neofiber leonardi, Ondatra annectens, Pedomys llanensis, Phenacomys sp., and Synaptomys cooperi.

IRVINGTONIAN III (APPROXIMATELY 0.4-0.15 MA)

The Irvingtonian III (originally named Rancholabrean I but changed by Repenning et al. 1990) was originally defined by the first appearance of the sagebrush voles of the genus Lemmiscus and by three species of Microtus: M. mexicanus, M. montanus, and M. pennsylvanicus (Repenning 1987; Repenning et al. 1990). These taxa were thought to have entered North America between 400,000 and 450,000 years ago (Repenning 1987; Repenning et al. 1990). The recognition of Lemmiscus in faunas predating the Brunhes (chron C1n; 780 ka) (e.g., SAM Cave, New Mexico [Repenning 1992; Rogers et al. 2000], and the Pit Fauna in Porcupine Cave [Bell and Barnosky 2000]) indicates that this taxon first appears in the North American fossil record much earlier than previously thought (its immigrant status is unconfirmed). The purported Irvingtonian occurrence of M. mexicanus cannot be verified (Bell and Repenning 1999); the oldest material tentatively identified as such is from Papago Springs Cave, Arizona (Skinner 1942), with a maximum age of approximately 246,000 years (Czaplewski et al. 1999b), but these specimens were recently reevaluated, and species-level identification was not possible (Czaplewski et al. 1999a). The other two Microtus species in question share common dental morphologies with each other and with several other North American species and cannot be identified reliably from isolated dental elements (Bell and Repenning 1999; Bell and Barnosky 2000). The traditional Irvingtonian III interval is thus undefined and was rejected by Bell and Repenning (1999) as a meaningful and distinct temporal interval. That interpretation is followed here.

Arvicoline rodent biochronology deteriorates by the late Irvingtonian, and effective temporal resolution declines. The arvicoline fauna is taxonomically modern by the end of the Irvingtonian, and an undifferentiated Rancholabrean was included in the schemes of both L. Martin (1979) and Repenning (1987; Repenning et al. 1990). The appearance of *Dicrostonyx* and *Lemmus* outside the Beringian region was used by Repenning (1987) as a means of recognizing Rancholabrean faunas on the basis of arvicolines, but these taxa never penetrate deeply into southern latitudes (Foley and Raue 1987; E. Mead and Mead 1989; Eger 1995; R. Slaughter and Jones 2000). Their utility therefore is quite limited.

We accept the Irvingtonian I as discussed earlier and accept an extended Irvingtonian II that extends temporally from approximately 0.85 Ma to what we consider the latest occurrence of the characteristic Irvingtonian arvicolines *Microtus paroperarius* and *Microtus meadensis*, both of which last appear in the Salamander Cave Fauna at approximately 252 ka (Mead et al. 1996; an additional reported Rancholabrean record of *M. meadensis* in the Kennewick sequence in Washington [Rensberger et al. 1984; Rensberger and Barnosky 1993] is here considered Irvingtonian).

GEOGRAPHIC DISTRIBUTION

Irvingtonian faunas are distributed widely across much of North America (figure 7.5). In contrast to Blancan faunas, many important Irvingtonian faunas were recovered from cave and fissure fill deposits. These deposits are in many respects mixed blessings: Although providing valuable information, they are also subject to complex stratigraphy, and it is often difficult to obtain reliable external age controls and paleomagnetic samples from friable cave sediments. Many Irvingtonian cave faunas lack reliable external age control, and their age estimates rely on varying interpretations of biochronology.

Snake River Plain Apart from the Bruneau Basalt *Mammuthus*-bearing locality discussed earlier in this chapter (see "Current Definition and Characterization"), there are no significant Irvingtonian faunal sequences in the Snake River Plain region. The sequence near Froman Ferry in Idaho was reported to be earliest Irvingtonian by Repenning et al. (1995). Their assessment was based on Repenning's arvicoline divisions of the mammal ages, in which the earliest appearance of *Phenacomys* defined the lower boundary of the Irvingtonian in the northwestern United States. The Froman Ferry sequence is here considered to be latest Blancan and is discussed earlier under "Blancan."

California The most extensive stratified sequence of Pliocene and Pleistocene sediments in North America is



FIGURE 7.5 Irvingtonian localities and their temporal equivalents discussed in the text. The bold line represents 55°N latitude. Independent biochronologies should be established for the region north of this line, and the term *Irvingtonian* should not be applied to faunas there. Localities with external chronologic control indicating an age between approximately 1.35 and 0.21 Ma are considered to be temporal equivalents of Irvingtonian faunas elsewhere in North America. 1, Old Crow Basin, Yukon, Canada; 2, Medicine Hat sequence (in part), Alberta, Canada; 3, Wellsch Valley (in part), Saskatchewan, Canada; 4, Kennewick sequence (in part), WA; 5, Bruneau Formation, ID; 6, Little Dell Dam, UT; 7, Cathedral Cave, NV; 8, Irvington, CA; 9, Fairmead Landfill, CA; 10, San Timoteo Badlands (in part), CA; 11, Elsinore Fault Zone, CA; 12, Anza-Borrego Desert (in part), CA; 13, El Golfo, Sonora, Mexico; 14, Mesilla Basin, NM; 15, Tijeras Arroyo, NM; 16, SAM Cave, NM; 17, Hansen Bluff, CO; 18, Porcupine Cave, CO; 19, Salamander Cave, SD; 20, Meade County faunas (in part), KS; 21, Woody Draw and Bull Draw, TX; 22, Rock Creek, TX; 23, Slaton, TX; 24, Holloman, OK; 25, Vera and Gilliland, TX; 26, Fyllan Cave, TX; 27, Conard Fissure, AR; 28, Hamilton Cave and Trout Cave No. 2, WV; 29, Cumberland Cave, MD; 30, Hanover Quarry No. 1, PA; 31, Port Kennedy Cave, PA; 32, Haile 21A, FL; 33, McLeod, FL; 34, Coleman 2A; 35, Pool Branch, FL; 36, Payne Creek Mine, FL; 37, Rigby Shell Pit, FL; 38, Leisey Shell Pit, FL; 39, Crystal River, FL; 40, La Goleta (in part), Michoacan, Mexico.

beautifully preserved in the Anza-Borrego Desert State Park in southern California. Despite a long, apparently continuous and closely sampled sequence demonstrating that a characteristic Irvingtonian fauna overlies a Blancan fauna, the Blancan–Irvingtonian boundary in this

area is still uncertain. This problem was discussed in detail by Cassiliano (1999), who pointed out that this uncertainty is the result of the lack of a defining taxon for the boundary. Some of the taxa that are used to characterize the Irvingtonian, and some that are proposed as

taxa to define the boundary, have their lowest known stratigraphic appearance (LSD₁, of Walsh 1998) in the Vallecito Creek-Fish Creek section at different places. The inferred times associated with these appearances are summarized here: Navahoceros early in the reversed chron (chron C2r.1r) below the Olduvai subchron at approximately 2.05 Ma, Equus (Equus) early in the reversed chron (chron C2r.1r) below the Olduvai event at approximately 2.09 Ma (this may be the earliest appearance in North America), *Lepus* at the base of the Olduvai (chron C2n) at approximately 1.95 Ma, Smilodon at the top of Olduvai at 1.77 Ma, and Euceratherium at approximately 1.13 Ma. At the time Cassiliano completed his report, mammoths were not present in the section, but molar fragments referred to Mammuthus are now reported from three localities in the sequence, with a maximum age of about 1.2 Ma (McDaniel and Jefferson 1999). Additional material from the Borrego badlands may be as old as 1.25 Ma (Remeika and Jefferson 1993; Jefferson and Remeika 1994).

Two faunas in the San Timoteo Formation were assigned to the Irvingtonian by Albright (1999). One of these, the El Casco Fauna, contains "*Plesippus francescana*" and lacks *Mammuthus*; it is here considered to be latest Blancan in age. The Shutt Ranch Fauna is stratigraphically much higher than the El Casco Fauna. It contains *Sorex, Microtus californicus*, and *Neotoma* close to *N. fuscipes* and was recovered from sediments that appear to be reversely magnetized. Albright interpreted this, along with the faunal data, to indicate placement in chron C1r.1r below the Brunhes. The only record of *Mammuthus* in this area is one tooth that is not well placed stratigraphically but is above the top of one transect that ends in chron C1r.1r (0.78–0.99 Ma) and is therefore below the Brunhes.

The Irvington Fauna is the type fauna for the Irvingtonian mammal age. A preliminary report of the fauna was given by Stirton (1939) and a more elaborate treatment by Savage (1951). Surprisingly, portions of this fauna have yet to be formally published (see Firby 1968). The original collection localities are now beneath Highway 680 and are inaccessible. Sediments adjacent to the original localities and at the stratigraphic level where fossils were originally recovered are reversely magnetized, and the Irvington Fauna was interpreted to be in the upper part of the Matuyama chron (chron C1r) by Lindsay et al. (1975). The fauna includes Megalonyx, Mammuthus, Equus, Camelops, Hemiauchenia (originally listed as Tanupolama), Tetrameryx irvingtonensis, Euceratherium, and Microtus with five closed triangles on the lower first molar (Savage 1951). Mammut americanum, Arctodus, Capromeryx, Sorex, Scapanus, Paramylodon harlani,

Taxidea taxus, Panthera, Smilodon, Homotherium serum, and an otariid seal were identified by Firby (1968) in an unpublished master's thesis.

An extensive and taxonomically diverse Irvingtonian fauna from near Fairmead in Madera County, California, provides an important complement to the type Irvington Fauna (Dundas et al. 1996). The Fairmead Landfill locality produced thousands of vertebrate fossils recovered from normally magnetized sediments tentatively correlated with the upper Turlock Lake Formation (Dundas et al. 1996). The fauna includes *Paramylodon harlani, Nothrotheriops, Megalonyx, Canis armbrusteri, Smilodon, Homotherium, Mammuthus columbi, Camelops, Hemiauchenia, Tetrameryx irvingtonensis,* and *Capromeryx*.

A sedimentary sequence from an unnamed sandstone in the Elsinore Fault Zone in Riverside County, California, produced many vertebrate fossil localities that included Blancan and Irvingtonian faunas (Reynolds et al. 1991; Scott and Cox 1993; Pajak et al. 1996). The Irvingtonian faunas were identified by the presence of Mammuthus and Microtus and included Scapanus, Equus bautistensis, Arctodus simus, Camelops, and Hemiauchenia. Several earlier reports (Reynolds et al. 1990, 1991; Repenning 1987) of Clethrionomys in the Elsinore Fault Zone were in error; the specimens are Ophiomys parvus (see discussion in Pajak et al. 1996). The Elsinore Fault Zone faunas were recovered during salvage operations to mitigate impact of construction activities on fossil resources; the deposits from which the fossils were collected are gone.

Great Basin The Topaz Lake Fauna from Douglas County, Nevada, contains few taxa but was considered an Irvingtonian fauna based on the presence of Euceratherium (Kelly 1997). The fauna also includes Ondatra cf. O. idahoensis and was discussed earlier with the Blancan Wellington Hills Fauna. The only known Great Basin Irvingtonian assemblage is from Cathedral Cave in White Pine County, Nevada (Bell 1995, 2000). A complete description of the fauna is not published, but the arvicoline rodent fauna is almost identical to that from the Pit Fauna in Porcupine Cave, Colorado, and includes Mimomys cf. M. virginianus, Phenacomys gryci, Phenacomys sp. (not P. gryci), Mictomys meltoni or Mictomys kansasensis (an earlier identification of Mictomys borealis was in error; Mead et al. 1992; Bell 1995), Allophaiomys, Lemmiscus curtatus (with both four and five closed triangles on the first lower molar), Microtus paroperarius, Microtus meadensis, and complex Microtus first lower molars with five closed triangles (Bell 1995; Bell and Barnosky 2000).

Rocky Mountain Region One of the most significant newly discovered Irvingtonian localities is Porcupine Cave in Park County, Colorado. The cave is situated in a large intermontane basin at 2900 m elevation. At least 26 discrete fossil localities are known in the cave (Barnosky and Bell in press), and a fantastically diverse vertebrate fauna is now recorded by tens of thousands of specimens recovered from the cave. A preliminary faunal list was provided by Barnosky and Rasmussen (1988), and reports of the arvicoline rodents and carnivorans from various localities are published in some detail (Barnosky and Rasmussen 1988; Anderson 1996; Barnosky et al. 1996; Bell and Barnosky 2000). At present, external age control is published only for the Pit locality, where paleomagnetic data indicate that the Pit sequence straddles the Brunhes-Matuyama boundary (Bell and Barnosky 2000). A unique assemblage of taxa was reported from the Pit locality (Barnosky and Rasmussen 1988; Anderson 1996; Bell and Barnosky 2000), and this is especially true for the arvicoline rodents. At least 10 arvicoline species were found in the Pit: Phenacomys gryci, Phenacomys sp. (not Phenacomys gryci) Mimomys cf. M. virginianus, Ondatra, Mictomys cf. M. meltoni, Allophaiomys pliocaenicus, Microtus paroperarius, Microtus meadensis, Microtus sp. (not M. paroperarius or M. meadensis), and Lemmiscus curtatus (with both four- and fiveclosed-triangle forms). Nine of these taxa were found in direct association in a single stratigraphic level of that deposit (the only one absent from level 4 was Phenacomys sp.). There is no evidence that the deposit is mixed, but the association of these taxa is unique. Attempts to reconcile paleomagnetic and biochronologic data resulted in an age estimate of 750-850 ka for the middle section of the Pit (levels 4-8; Bell and Barnosky 2000). The fauna includes the youngest known occurrence of Allophaiomys pliocaenicus and the earliest known records of Microtus meadensis (another early record is from the Hansen Bluff sequence) and Lemmiscus curtatus (an additional early record is from SAM Cave, New Mexico). The high elevation of the site and the species assemblage from the Pit suggest the possibility that high-elevation sites may warrant independent biochronologies. This hypothesis cannot be tested until additional high-elevation sites are discovered and studied.

The Hansen Bluff sequence includes a diverse faunal assemblage recovered from the Alamosa Formation in the San Luis Valley, south-central Colorado. The valley sits at 2300 m, and fossils were recovered primarily from five sections along a 4-km stretch of the bluff (Rogers et al. 1985). External chronologic control was established primarily by paleomagnetic data and the presence of the Bishop Ash in two of the sections (the average age of the Bishop Ash is now calculated at 758.9 \pm 1.8 ka; Sarna-Wojcicki et al. 2000). Paleomagnetic samples were analyzed from Section A and from isolated portions of other sections. All sediments above unit A-14c have normal polarity and were interpreted to represent the Brunhes (chron C1n); those from A-14c and below have reversed polarity and represent the Matuyama (chron Cır) (Rogers et al. 1985). The Bishop Ash is present in sections C-9 and E-9 at Hansen Bluff. No mammalian fossils were found in association with the Bishop Ash. Mammals recovered from reversed sediments include Spermophilus, Geomys, Reithrodontomys, Mictomys meltoni, Microtus meadensis, Microtus paroperarius, Ondatra annectens, and Equus cf. E. scotti. The record of M. meadensis is among the earliest known occurrences of the species.

A 127-m core was drilled beneath section D at Hansen Bluff in 1986 (Rogers et al. 1992). The Huckleberry Ridge Ash (2.0-2.1 Ma) was intersected at 78.3 m depth in the core. Paleomagnetic data indicate that the sediments in the core preserve the Jaramillo (chron C1r.1n), Olduvai (chron C2n), and Reunion (chron C2r.1n) normal polarity events and the top of the Gauss chron (chron C2An.1n). Mammalian fossils were scarce in the core samples, but the recovery of Spermophilus, Reithrodontomys, and two arvicoline rodent teeth was reported (Repenning 1992; Rogers et al. 1992). The arvicoline teeth were assigned to Allophaiomys (Rogers et al. 1992; neither tooth is diagnostic of Allophaiomys, and the referral to that taxon was based on the ever-growing condition and the overall dental pattern; see Repenning 1992; Rogers et al. 1992). The oldest of the two arvicoline specimens from the core was recovered from a depth of 73.1 m, just above the base of the Olduvai event (chron C2n; Rogers et al. 1992).

SAM Cave is a lava tube cave located at 2737 m elevation in Rio Arriba County, New Mexico. Six discrete faunas were reported from the cave by Rogers et al. (2000). The four oldest of these localities have no external age control but contain Allophaiomys, Lemmiscus curtatus, Microtus (with five closed triangles on m1), Mictomys kansasensis, Cynomys, and Spermophilus tridecemlineatus. The "LB" locality, interpreted to be somewhat younger, was excavated following natural stratigraphy and preserves the Brunhes-Matuyama boundary. Biochronologic interpretation of the basal portion of the sequence yielded an age estimate of 820-840 ka. Based on biochronology and paleomagnetics, the middle section of the sequence (the lowest part with normal polarity) was interpreted as dating between 780 and 740 ka (Rogers et al. 2000). Clethrionomys was recovered from both above and below the Brunhes-Matuyama (chron C1n-1r) boundary; this record represents the only confirmed Irvingtonian occurrence of *Clethrionomys*. *Mictomys kansasensis*, *Microtus*, and *Lemmiscus* are found only in the reversed sediments, but sample sizes appear to be small (the upper levels contained no mammalian fossils).

Two small Irvingtonian faunas were recently reported from the Little Dell Dam site in Salt Lake County, Utah (Gillette et al. 1999). Locality 1 contained Peromyscus, Lemmiscus curtatus, Microtus paroperarius, and an unidentified species of Equus. Locality 2 included Mimomys cf. M. dakotaensis (a Mimomys with roots and cementum in the reentrant angles, elsewhere known only from the Java Fauna in South Dakota; R. Martin 1989a), Allophaiomys, Mictomys meltoni or Mictomys kansasensis, and Phenacomys cf. P. gryci. The Little Dell faunas lack Mammuthus but are considered to be Irvingtonian based on the presence of Microtus paroperarius, a species limited to the Irvingtonian. The recovery of Mimomys, Microtus paroperarius, and Allophaiomys at Little Dell and Cathedral Cave in Nevada provides the first evidence of these taxa west of the Rocky Mountains in the contiguous United States. Similar Mimomys material is known from the Beringian region at the Old Crow Basin in the Yukon and Cape Deceit, Alaska, and at several localities east of the Rocky Mountains (Repenning, pers. comm., 1999).

Southwestern United States The Mesilla Basin in south-central New Mexico was divided into three biostratigraphic zones by Vanderhill (1986). "Faunules" A and B were discussed earlier in this chapter (under "Blancan"). Faunule C in Mesilla Basin was derived from sediments that span the time from just after the Olduvai event to the early part of the Brunhes (i.e., chron C1r), but most of the specimens were reported to come from sediments that predate the Jaramillo event (in chron C1r.2r; 1.77-1.21 Ma). It contains Mammuthus and the characteristic Irvingtonian taxa Paramylodon harlani, Smilodon, and Canis armbrusteri. It also contains Glyptotherium, Equus scotti, Equus calobatus, Cuvieronius, and Stegomastodon. The Mammuthus and Stegomastodon material was recovered from sediments in chron C1r.2r, Smilodon from reversed sediments below the Olduvai (chron C2n). The presence of Stegomastodon in association with Mammuthus is unusual but not unique.

The Tijeras Arroyo locality in New Mexico was discussed earlier and includes an early record of *Mammuthus*. The Curtis Ranch Fauna from the San Pedro Valley in Arizona is traditionally considered to be Irvingtonian. The fauna lacks *Mammuthus* and straddles the base of chron C2n (the Olduvai). It is here considered to be latest Blancan.

Mexico The El Golfo Fauna in Sonora contains a diverse vertebrate assemblage and provides an important perspective on mammalian faunas from northern Mexico during the Irvingtonian. The fauna includes *Myrmecophaga tridactyla*, *Megalonyx wheatleyi*, *Nothrotheriops*, *Sigmodon curtisi*, *Neotoma* (*Hodomys*) sp., *Chasmaporthetes johnstoni* (the only Irvingtonian record of this genus), "*Cuvieronius*" sp., *Mammuthus imperator*, *Equus*, *Tapirus*, *Camelops*, *Hemiauchenia*, and *Odocoileus* (Shaw 1981; Shaw and McDonald 1987). Radioisotopic and paleomagnetic information are not available for the El Golfo Fauna.

Great Plains In our usage here, the Great Plains is an extensive physiographic province that covers much of the midcontinent region of North America and extends southward to include faunas on the Edwards Plateau region in Texas (Atwood 1940). Many Irvingtonian faunas are reported from the Great Plains region, but thick superposed stratigraphic sequences are few, and this lack hindered the establishment of a reliable faunal sequence. Although some superposed sequences of faunas can be demonstrated, much of the early work ordered the faunas through time on the basis of stage of evolution of mammals and the climatic interpretation of the faunas that was used to relate them to the classic glacial sequence. The use of the now-outdated "four glacial stage" scheme and the mistaken interpretation of multiple ashes as a single "Pearlette" ash led to many problems that only recently began to be sorted out. The understanding that the "Pearlette ash" is in fact three ash beds (Huckleberry Ridge, Mesa Falls, and Lava Creek B; see table 7.1 for dates) and the identification and dating of additional ash beds (e.g., those associated with the eruptions that produced the Cerro Toledo Rhyolites; table 7.1) led to major advances in our understanding of Irvingtonian faunas in the region. Ongoing paleomagnetic and faunal analyses by R. Martin and colleagues promise to clarify the faunal sequence in this region. Some of the most important Irvingtonian localities in the Great Plains are discussed in this section, but a more thorough discussion must await new data.

A sequence of six tills with interbedded sands, silts, and clays exposed along the South Saskatchewan River near Medicine Hat, Alberta, Canada, produced a superposed sequence of Pleistocene faunas that extend from the Irvingtonian into the Rancholabrean (Stalker and Churcher 1970, 1972, 1982; Stalker 1996). The base of the Pleistocene sequence rests unconformably on late Cretaceous rocks. The two units at the base of the section (originally referred to the "Kansan") contain few taxa but include *Mammuthus, Equus calobatus, Equus scotti, Camelops minidokae*, and a ground sloth questionably referred to *Nothrotheriops*. Although it is a small assemblage, the presence of mammoth and the absence of *Bison* suggest an Irvingtonian age.

Wellsch Valley is another fossiliferous sequence, approximately 220 km east of Medicine Hat. It contains a diverse assemblage of faunas and a complex stratigraphy that have hindered attempts to interpret the faunal sequence. The association of Borophagus, Hypolagus, and Mammuthus was reported in the first published discussion of the fauna (Stalker and Churcher 1972). Allophaiomys, Microtus paroperarius, Mictomys kansasensis, and Pliophenacomys osborni were added by Stalker and Churcher (1982). The Wellsch Valley Fauna appears to have been derived from several outcrops, and reworking of fossils is possible in some instances (Barendregt et al. 1991, 1998), but a detailed summary of vertebrate paleontological data is lacking. The Jaw Face section of the Wellsch Valley locality is the best studied (Barendregt et al. 1991). Vertebrate paleontological data are published in part, but summary charts lack sufficient detail to resolve important questions. The Jaw Face section as a whole spans the lower Brunhes (chron C1n) and upper Matuyama (chron C1r.1r; Barendregt et al. 1998). Rodent bones were reported to be concentrated in units II and III of the section, stratigraphically below the large mammal bones from unit IV (in the upper portion of the reversely magnetized part of the section; Barendregt et al. 1991). Without detailed data on the stratigraphic positions of the mammalian taxa, especially of Mammuthus, Borophagus, Allophaiomys, and Microtus, biochronologic significance of this section cannot be evaluated adequately. The faunal sequence appears to include both Blancan and Irvingtonian components, but faunal, stratigraphic, and paleomagnetic data are not consistent and are difficult to reconcile with radiometric dates (Westgate et al. 1978; Westgate and Gorton 1981) and electron spin resonance dates (Zymela et al. 1988).

The Horse Room Fauna from Salamander Cave in the Black Hills of South Dakota produced a small fauna including *Mictomys* cf. *M. meltoni, Microtus paroperarius, Microtus meadensis, Canis* cf. *C. dirus, Equus, Antilocapra americana,* and *Camelops* (Mead et al. 1996). The three arvicoline species suggest a possible Cudahy-equivalent age for the deposit (ca. 602–670 ka), but a uranium series date from the stratigraphic layer that produced the fauna yielded an age of 252 ± 30 ka. In this chapter, we accept that the date is correct (see discussion in Mead et al. 1996:463–464), and consider the fauna latest Irvingtonian. Therefore the fauna includes the youngest radiometrically dated material of *M. paroperarius* and *M. meadensis*, and possibly the youngest record of *Mictomys meltoni*. The record of *Canis* cf. *C. dirus* is the only potential Irvingtonian record of that species (Dundas 1999).

The Hall Ash and Courtland Canal faunas (Jewell County, Kansas) were reported by Eshelman and Hager (1984). The Hall Ash Fauna was recovered from below an ash dated at 0.706 ± 0.017 Ma and tentatively correlated with the Hartford Ash dated elsewhere at approximately 0.74 Ma (Boellstorff 1973, 1978). It contains *Ondatra annectens, Mictomys* cf. *M. meltoni, Microtus paroperarius, Phenacomys* cf. *P. intermedius, Geomys,* and *Zapus sandersi.* The Courtland Canal Fauna may be somewhat older and includes *Castoroides* cf. *C. ohioensis, Ondatra annectens, Mictomys meltoni,* a tentatively identified specimen of *Allophaiomys, Platygonus* cf. *P. vetus, Titanotylopus* sp., and *Soergelia mayfieldi.*

The Holloman gravel pit located near Frederick, Oklahoma, produced a fauna containing *Mammuthus, Gigantocamelus* (= *Titanotylopus*) *spatula, Platygonus vetus*, several horse species, and possibly *Stegomastodon* (Dalquest 1977). This locality is another in which both *Mammuthus* and *Stegomastodon* may co-occur, but the identification of *Stegomastodon* from Holloman probably is in error, and the material may actually represent *Teleobunomastodon* (= *Cuvieronius*; see Madden 1980, 1983). The only small mammal recovered was *Cynomys* sp. External age control is not available, but the fauna closely resembles the Gilliland Fauna in Texas (Dalquest 1977).

The Cudahy Fauna in Meade County, Kansas, is situated immediately beneath the Lava Creek B Ash (= "Cudahy Ash" of Hibbard 1944, "Pearlette Ash" of Paulson 1961, and "Pearlette-O" of Izett et al. 1981), the source of which is variably dated to between 602 and 670 ka (table 7.1). This close association of the fauna with a radiometrically dated ash bed made the Cudahy an important fauna for regional correlations for many years. Details of the excavation were provided by Hibbard (1976). The mammalian fauna was discussed by Hibbard (1944), Paulson (1961), and Bell and Repenning (1999) and includes Geomys tobinensis, Ondatra annectens, Mictomys meltoni, Microtus paroperarius, Microtus meadensis, Microtus llanensis, Equus scotti, Megalonyx sp., and Mammuthus. This fauna includes the youngest well-dated and definitive occurrences of Megalonyx wheatleyi (an additional young record is in the McLeod Fauna in Florida), *Ondatra annectens*, and *Mictomys meltoni*, but that species was tentatively identified in a significantly younger fauna in Salamander Cave, South Dakota (Mead et al. 1996).

Several localities with similar faunas in Kansas (Sunbright Ash Pit, Tobin, Wilson Valley) and Texas (the Vera Fauna) were united by Hibbard (1976) into an expanded "Cudahy Fauna"; that term was later restricted to the type Cudahy locality at the Cudahy Ash Pit (Dalquest and Carpenter 1988; Bell and Repenning 1999). The Vera Fauna is also directly beneath Lava Creek B Ash in Knox County, Texas. The depauperate Vera Fauna includes *Geomys tobinensis, Microtus paroperarius, Microtus llanensis*, and *Ondatra annectens* (Dalquest and Schultz 1992).

The Gilliland Fauna was recovered from the Seymour Formation in Knox and Wilbarger Counties, northcentral Texas (Hibbard and Dalquest 1966). The fossils of the Gilliland Fauna were recovered from sands and gravels below the level of the Vera Fauna, but the age of the Gilliland deposits is difficult to assess (Hibbard and Dalquest 1973; Dalquest and Carpenter 1988; Dalquest and Schultz 1992). The most recent age estimate suggests that the Gilliland Fauna may predate the Vera Fauna (which is situated immediately beneath the Lava Creek B Ash) by as much as 400,000 years (Dalquest and Schultz 1992:18). The fauna includes Nothrotheriops shastensis, Paramylodon harlani, Geomys tobinensis, Sigmodon curtisi, Microtus paroperarius, Microtus llanensis, Proneofiber guildayi, Canis armbrusteri, Miracinonyx, Homotherium, Cuvieronius, Stegomastodon, Mammuthus imperator, Tapirus haysii (originally identified as Tapirus copei, but see Ray and Sanders 1984), Equus scotti, Platygonus vetus, Camelops, Hemiauchenia, Capromeryx, and Tetrameryx (Dalquest and Schultz 1992).

Fossils have been known for years along Rock Creek (Briscoe County, Texas), and were derived from several discrete localities during a complicated excavation history (see Dalquest and Schultz 1992); more recent work showed that there are several faunas and two volcanic ash beds in superpositional relationship in the Tule Formation (G. Schultz 1990b). At the base of the sequence is the Martin Ranch Fauna, with Mammuthus, Stegomastodon, Paramylodon harlani, "Equus (Dolichohippus) simplicidens," and Camelops (Dalquest and Schultz 1992). Elements of this fauna were collected from both below and above the Cerro Toledo X Ash Bed (1.2-1.3 Ma; Izett 1977). The locality is significant because Mammuthus is present as early as 1.2-1.3 Ma. About 27 m above Martin Ranch is Gidley's Horse Quarry (Gidley 1900), and 5 m above that level is the Sloth–Camel quarry that produced the other elements of the Rock Creek Quarry reported by Troxell (1915a, 1915b). This material includes *Paramylodon harlani* (originally identified as *Mylodon*), *Canis armbrusteri, Arctodus simus, Platygonus vetus* (the original report of *Platygonus compressus* was in error; see Dalquest and Schultz 1992), *Mammuthus* (originally identified as *Elephas*), *Soergelia* (originally identified as *Preptoceras*), and several camelids and equids. At the top of the section, 5 m above the Horse Quarry, is a bed of the Lava Creek B Ash (602–670 ka) that directly overlies the Mayfield Ranch Fauna, a fauna reported by G. Schultz (1990b) and Dalquest and Schultz (1992) to contain *Geomys tobinensis, Peromyscus cragini, Ondatra annectens, Microtus paroperarius, Microtus meadensis, Microtus llanensis, and Mictomys meltoni.*

Several additional faunas are now known to occur directly beneath the Lava Creek B Ash in Texas. The Woody Draw Fauna (Randall County, Texas) includes *Geomys tobinensis*, *Microtus paroperarius*, *Microtus meadensis*, *Mammuthus*, *Equus*, and *Camelops* (Dalquest and Schultz 1992). The Bull Draw Fauna (also Randall County) includes *Geomys tobinensis*, *Ondatra annectens*, *Microtus paroperarius*, *Microtus llanensis*, *Microtus meadensis*, *Mictomys meltoni*, *Mammuthus*, *Platygonus vetus*, and *Camelops*; the Deadman's Creek Fauna is slightly older (4 m below the Lava Creek B Ash) and produced the same rodents (except *M. llanensis*), *Equus conversidens*, and *Camelops* (Dalquest and Schultz 1992).

The Fyllan Cave Fauna in Travis County, central Texas, is the only Irvingtonian fauna from that region (Patton 1965; Taylor 1982; Winkler and Tomida 1988; Winkler and Grady 1990). Fossils were recovered from a narrow fissure fill exposed in a quarry wall and include Didelphis, Dasypus bellus, Sylvilagus cf. S. hibbardi (see White 1991a), Aztlanolagus agilis (Winkler and Tomida 1988), Ondatra hiatidens or Ondatra annectens, Microtus guildayi (= Allophaiomys or Pedomys or Pitymys), Atopomys texensis, and Sigmodon cf. S. curtisi. The sediments are reversely magnetized, which places a minimum age of 780 ka on the fauna (predating chron C1n). The co-occurrence of Didelphis with Sylvilagus cf. S. hibbardi, Atopomys texensis, and Sigmodon cf. S. curtisi is unique. Other records of Didelphis are confined to the latest Irvingtonian (e.g., Coleman 2A in Florida; R. Martin 1974) or Rancholabrean. The temporal ranges of the various taxa include late Blancan (if the Sigmodon and Sylvilagus identifications can be strengthened) through Rancholabrean. We consider the fauna Irvingtonian based primarily on the co-occurrence of Didelphis, Ondatra, Microtus, and Atopomys.

The Slaton locality (Lubbock County, Texas) produced a diverse mammalian fauna including *Holmesina septen*-

trionalis, Lepus, Geomys bursarius, Canis latrans, Canis armbrusteri, Homotherium serum, Mammuthus, Platygonus vetus, Equus, Tetrameryx shuleri, and Neofiber leonardi (Dalquest 1967; Dalquest and Schultz 1992). The absence of Bison and the presence of Mammuthus and Platygonus vetus suggests an Irvingtonian age. The most recent age estimate dated the fauna between 50 and 610 ka (Dalquest and Schultz 1992). The younger age estimate seems too young, based on the presence of Platygonus vetus, Canis armbrusteri, Neofiber leonardi, and Tetrameryx shuleri; we suspect a greater antiquity for the fauna. Previous correlations considered Slaton to be approximately equivalent with the Rezabek and Kanopolis faunas in Kansas (Hibbard et al. 1978; Lundelius et al. 1987).

Florida Several Irvingtonian faunas were recovered from fissure fill, shallow pond, marsh, and stream deposits in Florida. Useful paleomagnetic data are scarce, there are no igneous rocks on which to base radiometric ages, and superpositional sequences are rare. The ages of these faunas were determined based largely on biostratigraphy. Because Florida is a low-lying, tectonically stable region, relationships of fossil localities to sea level can be used to relate the bone-bearing deposits to former sea levels that are related to the glacial–interglacial cycles, with low sea levels being correlated to glacial stages and high sea levels being related to interglacial stages (Webb 1974a).

These faunas were grouped into four major temporal groups by Morgan and Hulbert (1995), but our designations are slightly different (because we use *Mammuthus* to define the Irvingtonian). "Earliest Irvingtonian" faunas of Morgan and Hulbert (1995) and Ruez (2001) were provisionally interpreted to range in age between approximately 2.0 and 1.6 Ma and are here considered to be latest Blancan. These faunas include the Inglis 1A, Inglis 1C, and De Soto Shell Pit localities and were discussed earlier in this chapter. The Haile 16A Fauna was included with other "late early Irvingtonian" faunas by Morgan and Hulbert (1995), but we discussed it earlier under "Blancan."

"Late early Irvingtonian" faunas of Morgan and Hulbert (1995) were provisionally interpreted to range in age between approximately 1.6 and 1.0 Ma and include Leisey Shell Pit, Pool Branch, Crystal River, Payne Creek Mine, Rigby Shell Pit, and Haile 21A. Only the Leisey Shell Pit and Payne Creek Mine faunas include *Mammuthus*. Haile 21A includes *Geomys pinetis*, which is found only in Irvingtonian and Rancholabrean faunas in Florida. The Pool Branch, Crystal River, and Rigby Shell Pit faunas are depauperate but were correlated by Morgan and Hulbert (1995) with the Leisey Shell Pit on the basis of overall faunal similarity. We follow that arrangement here. These faunas are characterized by Nothrotheriops texanus, Ondatra annectens, and Mammuthus hayi. These faunas record the first occurrences of Sylvilagus palustris, Geomys pinetis, Erethizon dorsatum, Castoroides, and Canis armbrusteri. Together with the Haile 16A Fauna, they include early records of Megalonyx wheatleyi, Synaptomys, Tapirus haysii (in all but Rigby; characteristic of Irvingtonian), and Sigmodon libitinus. We treated the Haile 16A Fauna earlier in our discussion of Florida Blancan localities, but its faunal similarities, especially with the Leisey Shell Pit, clearly indicate its proximity to the Blancan– Irvingtonian boundary.

The Leisey Shell Pit Fauna (Webb et al. 1989; Hulbert et al. 1995) was dated by a combination of strontium isotope data, paleomagnetic data, and biostratigraphy. When all relevant data were considered, the age range for the Bermont Formation (containing the Leisey Shell Pit Fauna) was interpreted to be between 1.55 and 1.1 Ma (Morgan and Hulbert 1995:30); the vertebrate sites are considered to be less than 1.3 Ma. *Mammuthus* is present in this fauna and thus is among the earliest occurrences of this taxon in North America.

The only "middle Irvingtonian" fauna (provisionally interpreted to range in age between approximately 1.0 and 0.6 Ma) currently recognized in Florida is the McLeod Fauna. This time interval was characterized by Morgan and Hulbert (1995) by the presence of *Neofiber leonardi* and an advanced *Smilodon gracilis* (probably the youngest North American occurrence) and by the first appearance of *Holmesina septentrionalis*, *Panthera onca*, and *Sigmodon bakeri*. This interval records the last occurrence of *Megalonyx wheatleyi*, *Smilodon gracilis*, and *Tapirus haysii* in Florida; the *M. wheatleyi* and *S. gracilis* records are among the youngest known in North America.

A single "late Irvingtonian" Florida fauna, the Coleman 2A (whose age lies between 0.6 and 0.3 Ma), is recognized. This interval was marked in Florida by the limited occurrence of *Microtus aratai* (= *Pitymys*) and by the first Florida occurrence of *Didelphisvirginiana* (an earlier record exists in Fyllan Cave, Texas; Taylor 1982), *Neofiber alleni*, and *Tapirus veroensis* (also found in the Kanopolis Fauna in Kansas; Hibbard et al. 1978). The Coleman 2A Fauna was considered by Morgan and Hulbert (1995) to be Irvingtonian based on the presence of three taxa: *Arctodus pristinus, Canis armbrusteri* (originally identified as *Canis lupus* by R. Martin 1974, but see discussion in Nowak 1979), and *Platygonus cumberlandensis* (R. Martin 1974; the latter species is now referred to *Platygonus* cf. *P. vetus;* D. Wright

1995). This is one of the youngest occurrences of *C. arm-brusteri* (Berta 1995; another late record is Slaton Quarry in Texas; Dalquest and Schultz 1992).

Eastern Caves A number of faunas from cave deposits in the eastern United States provide an important perspective on the taxonomic composition of Irvingtonian mammalian faunas in that region. External age control is lacking for these sites, and estimates of their age vary widely. Three such deposits were discovered in the late nineteenth and early twentieth centuries and provided early glimpses of middle Pleistocene mammals from the east: Port Kennedy Cave (perhaps more properly considered as a sinkhole) in Pennsylvania (Wheatley 1871; Cope 1871; Daeschler et al. 1993), Conard Fissure in Arkansas (Brown 1908; Graham 1972), and Cumberland Cave in Maryland (Gidley 1913, 1920a, 1920b; Gidley and Gazin 1933, 1938; Nicholas 1953; Van der Meulen 1978). The Port Kennedy Cave Fauna includes Megalonyx wheatleyi, Arctodus pristinus, Panthera onca, Miracinonyx inexpectatus, Smilodon gracilis (possibly the youngest occurrence in North America), Tapirus haysii, Mylohyus nasutus, and Mammut americanum (Berta 1987; Daeschler et al. 1993; Van Valkenburgh et al. 1990; Seymour 1993). The Conard Fissure Fauna contains Microtus paroperarius, Microtus llanensis (= Pedomys), Ondatra annectens, Miracinonyx inexpectatus, Smilodon populator (possibly the earliest known occurrence), and possibly Panthera onca (Graham 1972; Van Valkenburgh et al. 1990; Seymour 1993). The Cumberland Cave Fauna contains Canis armbrusteri, Arctodus pristinus, Miracinonyx inexpectatus, Panthera onca, Smilodon, Platygonus vetus, Microtus paroperarius, Microtus guildayi (= Allophaiomys of Repenning 1987, 1992), Ondatra annectens, Atopomys, Mammut, and Tapirus (Gidley and Gazin 1938; Van der Meulen 1978; Repenning 1987; Van Valkenburgh et al. 1990; Seymour 1993). These cave occurrences of M. inexpectatus are the youngest known records. The Cumberland Cave Fauna records the youngest known occurrence of P. vetus.

Three additional faunas are also noteworthy. The Hanover Quarry No. 1 Fauna (Pennsylvania) was reported to contain *Miracinonyx inexpectatus, Panthera onca, Smilodon gracilis, Microtus paroperarius,* and *Microtus guildayi* (Guilday et al. 1984; Seymour 1993). The Cheetah Room Fauna in Hamilton Cave in West Virginia includes *Miracinonyx inexpectatus, Panthera onca, Mimomys virginianus, Allophaiomys pliocaenicus, Lasiopodomys deceitensis* (= *Microtus* of Guthrie and Matthews 1971), *Ondatra annectens, Synaptomys, Atopomys,* and the earliest known occurrence of *Microtus paroperarius* (Repenning and Grady 1988; Winkler and Grady 1990; Van Valkenburgh et al. 1990; Seymour 1993). Trout Cave Entrance (Guilday 1967b) and Trout Cave No. 2 (Pfaff 1990, 1991) in West Virginia are poorly known faunas. The Trout Cave Entrance (terminology following Pfaff 1990; this locality was previously called "Trout Cave" byGuilday 1967b; Zakrzewski 1975a; and Kurtén and Anderson 1980) Fauna includes *Ondatra annectens* and *Atopomys*. Trout Cave No. 2 includes *Ochotona*, *Microtus paroperarius*, *Microtus llanensis* (= *Pedomys*), *Atopomys*, and *Ondatra annectens* (Pfaff 1990, 1991).

RANCHOLABREAN

HISTORICAL CONTEXT, DEFINITION, AND CHARACTERIZATION

The Rancholabrean was established by Savage (1951) and is named for the Rancho La Brea Fauna of California. Rancholabrean faunas were defined and characterized by Savage (1951) by the presence of the Eurasian immigrant *Bison*, many extinct (late Pleistocene) large mammal taxa (e.g., *Equus, Camelops, Mammut*, and *Mammuthus*), and numerous extant species of smaller mammals, especially carnivorans and rodents.

CURRENT DEFINITION AND CHARACTERIZATION

The Rancholabrean is defined by the first appearance of *Bison* in North America south of 55°N latitude and ends with the extinction of the megafaunal species in the same region. The characterization of the Rancholabrean includes a few taxa that are limited to the Rancholabrean, many that appear in earlier mammal ages but are common in Rancholabrean faunas, and a few that make their first appearance in the Rancholabrean but persist into the modern fauna. The lack of clear distinction between Irv-ingtonian and Rancholabrean faunas was, in at least one instance, used to justify treating the Rancholabrean as a temporal division within an expanded Irvingtonian (L. Martin 1985, 1989), but most authors continue to recognize it as a distinct mammal age.

Taxa that are limited to the Rancholabrean include *Megalonyx jeffersonii*, *Platygonus compressus, Canis dirus, Panthera atrox*, and *Miracinonyx trumani*. A questionable record of *M. jeffersonii* from Holloman (a broken humerus

fragment) was reported by Dalquest (1977); it is not clear whether this specimen is sufficient for reliable species allocation. The Papago Springs Cave specimens of Platygonus are the oldest dated records of the species (age taken here as 107 ka; see Czaplewski et al. 1999b); they were originally identified as P. alemanii (Skinner 1942), which Slaughter (1966) considered a junior synonym of P. compressus. Canis cf. C. dirus is recorded in the Salamander Cave Fauna in South Dakota (Mead et al. 1996) and is associated with a radiometric date of 252 ± 30 ka; if the material actually represents C. dirus, it would constitute a latest Irvingtonian record for the species. There are two records of Ovis that predate the Rancholabrean, but neither can be identified reliably to species. Ovis cf. O. canadensis was reported from the Pit Fauna Porcupine Cave (Barnosky and Rasmussen 1988), and Ovis sp. was reported from the El Golfo Fauna (Lindsay 1984).

Taxa that first appear in earlier mammal ages but are common in Rancholabrean faunas include Didelphis, Nothrotheriops, Paramylodon harlani, Glyptotherium, Brachylagus idahoensis, Sylvilagus, Clethrionomys, Lemmiscus curtatus, Ondatra zibethicus, Marmota flaviventris, Marmota monax, Cynomys gunnisoni, Cynomys ludovicianus, Panthera onca, Smilodon populator, Mustela erminea, Brachyprotoma, Conepatus, Canis latrans, Canis lupus, Arctodus simus, Ursus, Euceratherium, Oreamnos, Mammut americanum, and Mammuthus.

Taxa that first appear in the Rancholabrean and persist into the modern fauna include *Aplodontia rufa*, *Vulpes velox*, *Felis concolor*, *Alces*, *Bison*, *Ovis canadensis*, *Rangifer tarandus* (known from an Irvingtonian equivalent fauna in Cape Deceit, Alaska), and *Homo sapiens*.

ARRIVAL OF BISON

Bison was previously reported to appear in Alaska earlier than in the coterminous United States (Péwé 1975, 1989; Péwé and Hopkins 1967; Harington 1978, 1984). However, the time of first appearance of *Bison* in Alaska is now a confusing issue because of problematic stratigraphic attributions. *Bison* was reported from late Pliocene to early Pleistocene deposits in central Alaska (Péwé 1975, 1989; Péwé and Hopkins 1967). The fossils in question were reported to come from the "Fox Gravel" and the Gold Hill Loess. Recent data, including ages of volcanic ash beds, suggest that the "Fox Gravel" is time transgressive or represents multiple units (Hamilton et al. 1988; Westgate et al. 1990; Preece et al. 1999). Unfortunately, Péwé and Hopkins (1967) and Péwé (1989) did not identify specific localities from which their *Bison* specimens were recovered. To our knowledge, none of these fossils were curated in museums, so it is impossible to identify specific localities or verify the reported identifications.

R. H. Tedford (pers. comm., 2001) indicated that the Frick collection of Alaskan Pleistocene mammals in the American Museum of Natural History contains specimens of *Bison* that were recovered with those of *Xenocyon lycaenoides, Alces* cf. *A. latifrons, Praeovibos recticornis, Praeovibos priscus, Saiga tatarica,* and *Bootherium bombifrons* when the lower sediments of the Cripple Creek Sump were being dredged. These taxa are characteristic of the Olyorian faunas of the Kolyma Lowland of Siberia, which are dated between the late Matuyama and early Brunhes (1.5 to 0.5 Ma; (Repenning 1992; Sher 1986). Although the *Bison* remains could have been mixed with the other taxa when dredged, the association suggests contemporaneity.

Previous attempts to establish a reliable date for the arrival of Bison in the coterminous United States depended to a large extent on the correlation of faunas containing Bison to the classic (four-fold) glacial sequence. Many seemingly early faunas that contain Bison were previously assigned to the late "Illinoian" glacial stage because many workers regarded Bison to have first appeared at that time, an unfortunately circular argument. No Bison are known from any fauna in close association with the 0.60-0.67 Ma Lava Creek B Ash (table 7.1). It probably is significant that Bison remains are not known from the rich "Sheridanian" faunas from either northern (e.g., Hay Springs, Rushville, Gordon) or southern (Angus) Nebraska. These faunas lie below the Loveland Loess (Repenning 1987), for which thermoluminescent (TL) dates indicate an age between 200 and 120 ka (Forman et al. 1992; Muhs et al. 1999). These data strongly suggest that Bison appeared on the central Great Plains after 200 ka.

Several authors recently reported putative *Bison* remains in association with radiometric dates or in sedimentary contexts that suggest that *Bison* entered the coterminous United States sometime before 120 ka. These purported records suffer from dubious identification, unclear stratigraphic position, or unsatisfactory chronologic control. The localities in question include the Macasphalt Shell Pit and Inglis 1A localities in Florida (see J. McDonald and Morgan 1999; the age of Macasphalt Shell Pit was estimated between 2.5 and 2.0 Ma by Jones et al. 1991 and Morgan and Hulbert 1995; the age of Inglis 1A was estimated between approximately 1.9 to 1.6 Ma by Webb et al. 1989, Jones et al. 1991, and Morgan and Hulbert 1995). Additional questionable reports include younger records from Teichert Gravel Pit near Sacramento, California, and the Camp Cady faunas in southern California. The Teichert Quarry material consists of a single isolated second phalanx in the collection of the University of California Museum of Paleontology; the age of the locality was estimated at 130 ka by Repenning et al. (1990). The Camp Cady Fauna ranges in age between 350 and 19 ka (Jefferson 1987); the purported *Bison* material consists of fragmentary vertebral elements that were recently reidentified as belonging to *Camelops* (Scott and Cox 2002). The specimens are from questionable stratigraphic provenience (see discussions and data presented in Jefferson 1968, 1985, 1987, 1991).

A report of early *Bison* from unit c1 at Jones Spring, Missouri, has more reliable stratigraphic control and was in close stratigraphic association with a radiometric date. A uranium series date of 160 ka was obtained by C. R. McKinney from *Mammut* enamel from the contact of unit c1 with underlying gray clay (Haynes 1985:22; Saunders 1988:131).

Perhaps the most reliable early *Bison* date is from layers B and E of the American Falls Formation in Idaho. Twenty-one cranial elements referred to *B. latifrons* from layer E were recovered from a coarse alluvium conformably underlying fine-grained alluvium (Hopkins et al. 1969; Scott et al. 1982; Pinsof 1991). The fine-grained alluvium accumulated behind a lava dam of Cedar Butte basalt, dated at 72,000 \pm 14,000 years B.P. (Scott et al. 1982). This sedimentary package is superposed on Crystal Springs basalt, dated at 210,000 \pm 60,000 yr B.P., thus bracketing the age of these specimens.

TEMPORAL EXTENT

The temporal extent of the Rancholabrean is poorly established. The first appearance of *Bison* in North America south of 55°N latitude defines the beginning of the Rancholabrean, but the exact time of its arrival in this region is not known. The American Falls *Bison* records bracket the time of arrival between 210 ± 60 and 72 ± 14 ka. The Jones Spring (Missouri) date provides a minimum arrival time of 160 ka (Saunders 1988).

Because no younger mammal age has been established, the end of the Rancholabrean is operationally defined by the extinction of large-bodied mammal species near the end of the Pleistocene (e.g., C. Schultz et al. 1978). The date of the end of the Rancholabrean therefore must be based on the youngest radiocarbon dates of now-extinct large mammals. A number of compilations and analyses of these terminal dates are available (Hester 1960, 1967; Kurtén and Anderson 1980; Meltzer and Mead 1983, 1985; Lundelius et al. 1983; Mead and Meltzer 1984; Barnosky 1989; Grayson 1989, 1991), but recent developments in radiocarbon dating technology, primarily using accelerator mass spectrometry ¹⁴C (Stafford 1990), show that many of the previously reported post-Pleistocene dates (i.e., younger than 10 ka) may be erroneous, and all should be viewed with caution.

Using the criteria outlined by Meltzer and Mead (1985), 10 large mammal taxa with "good dates" were identified by Grayson (1991). Available data demonstrate that the extinction of large mammals was time-transgressive, ranging from approximately 23.23 ± 0.49 ka (Glyptotherium; latest record from Laubach 3 in Texas; Lundelius 1985) and 20.45 \pm 0.46 ka (*Paramylodon*; latest reliable record from Rancho La Brea; Meltzer and Mead 1985) to approximately 10 ka for several taxa (Grayson 1991).The youngest good date for eight of these taxa (Palaeolama, Tapirus, Smilodon, Mammuthus, Mammut, Equus, Camelops, and Nothrotheriops) is younger than 12 ka (Grayson 1991). With adequate consideration of the error bar on the youngest of these dates, the latest survivor of an extinct large-bodied mammal could be approximately 9.5 ka. Based on these data, the end of the Rancholabrean can be considered to be as recent as 9500 years ago, a time slightly younger than the 10,000-year date recognized earlier as the lower boundary of the Holocene (see discussion of the Pleistocene-Holocene boundary earlier in this chapter).

Our discussion of the extinction event (and hence the end of the Rancholabrean) does not include the remarkable records of *Mammuthus* from Wrangel Island, where it survived until approximately 4000 years ago (Vartanyan et al. 1993, 1995; Lister 1993b; P. Martin and Stuart 1995; Arslanov et al. 1998). We justify this exclusion not by special pleading but as a direct result of our geographic restriction of use of the term *Rancholabrean* to faunas from latitudes south of 55°N latitude.

Many possible causes of the extinction have been proposed over the last three decades. These include overkill by early humans, seasonally out-of-step mating periods, epidemics, climatic stress, loss of habitat, vegetation changes, and food shortages (P. Martin 1967, 1973; Axelrod 1967; Guilday 1967a; B. Slaughter 1967; Dreimanis 1968; Van Valen 1970; Alford 1974; Mosimann and Martin 1975; L. Martin and Neuner 1978; Graham and Lundelius 1984; Delcourt 1985; Owen-Smith 1987; Barnosky 1989; Webb and Barnosky 1989; Stuart 1991; Flannery 1995; Beck 1996; Alroy 1999, 2001; Klein 2000). A detailed consideration of this subject is beyond the The Blancan, Irvingtonian, and Rancholabrean Mammal Ages 287

scope of this chapter, but recent reviews of the subject can be found in MacPhee (1999).

TEMPORAL DIVISIONS OF THE RANCHOLABREAN

There is no basis for a numeric chronology within the Rancholabrean except for its terminal ("Wisconsinan") phase, which falls within the range of radiocarbon dating techniques. The age lies completely within the Brunhes chron (chron C1n), during which polar wander is recorded (Opdyke and Channell 1996), but there are no known events of reversed magnetic polarity suitable for boundary markers. Recent efforts to document fluctuations in geomagnetic paleointensity (Stoner et al. 1998, 2002) show great promise, but these data are not yet developed sufficiently to permit temporal boundary recognition. Thus for most of the Rancholabrean, chronologic control necessarily relies on faunal relationships, radiometric dates derived from associated igneous deposits, and new dating techniques applied to paleosols and loess deposits. Attempts to fit faunas into the fourfold glacial-interglacial framework previously used were perhaps marginally successful, but climatologists now recognize as many as 20 significant cooling events in the last 2 million years (Shackleton and Opdyke 1976; Richmond and Fullerton 1986; Raymo 1992), and terrestrial mammal faunal correlation should not be made solely on the basis on climatic inferences (see Lindsay 1997 and the following discussion).

Bison Chronology The temporal duration of many mammalian species is greater than the short span of the Rancholabrean. Thus most schemes proposed to divide the Pliocene and Pleistocene mammal ages (C. Schultz et al. 1978; L. Martin 1979; Repenning 1987; Repenning et al. 1990) leave an undifferentiated Rancholabrean. Attempts to divide the Rancholabrean based on perceptions of Bison evolution produced varying results (Hibbard 1955a; C. Schultz and Martin 1970; J. McDonald 1981; C. Schultz and Hillerud 1977), and no one system is generally accepted. The disagreements result from uncertainty in the age relationships of relevant faunas and lack of consensus in the interpretation of Bison phylogeny and taxonomy (Wilson 1974a, 1974b; J. McDonald 1981). Significant sexual dimorphism, intraspecific and individual variation, and the purported presence of shifting geographic and temporal clines (C. Schultz and Hillerud 1977; J. McDonald 1981; Gingerich 1993) combine to form an intractable systematic and taxonomic problem.

Chronologic control for many purported early Bison faunas is derived from alternative techniques such as presumed superpositional relationships and temporal ordering of terrace sequences in the central part of the continent (C. Schultz et al. 1972). Analyses of sequential terrace deposits suggest that large-horned Bison (e.g., B. latifrons, B. alaskensis, and B. alleni) are, in general, older than the short-horned B. bison antiquus or B. b. occidentalis (Skinner and Kaisen 1947; Guthrie 1970; C. Schultz et al. 1972; C. Schultz and Hillerud 1977), and that these, in turn, are older than B. b. bison. However, B. latifrons survived into the latest Pleistocene, at least in California and Idaho, and was contemporaneous with B. b. antiquus (Wyman 1922; Miller 1968, 1971; Miller and Brotherson 1979; Pinsof 1991; Gust 1993). In Florida, B. latifrons was reported to predate the appearance of B. b. antiquus; temporal ordering was based on a eustatic-hydrologic approach (Webb 1974a).

Loess Stratigraphy Recent work on loess stratigraphy in the upper Midwest indicates that the widespread loess deposits across the Great Plains may be used as proxies for glacial advance. Numeric ages on loess deposits beyond the Laurentide ice sheet margin are becoming more reliable and may provide a detailed numeric chronology for the last two glacial–interglacial cycles. TL dates from the Loveland Loess type section in western Iowa suggest that the Loveland Loess accumulated between approximately 180 and 120 ka (Forman et al. 1992). TL ages from eastern Colorado and western Nebraska indicate a similar age for the Loveland Loess (between approximately 200 and 120 ka; Muhs et al. 1999), as do TL ages from the Mississippi Valley (Forman et al. 1992; Markewich et al. 1998; Rodbell et al. 1997).

Application of numeric dating techniques also recently increased the usefulness of paleosols as stratigraphic markers in the midcontinent Quaternary sequence. Several paleosols are widespread, and they developed during both stadial (glacial) and interglacial intervals. Using ¹⁰Be inventories on soils, the beginning of the last glacial in Illinois was placed after 59 ka by Curry and Pavich (1996), the last interglacial was placed between 59 and 130 ka, and the penultimate glacial was placed between 130 and 190 ka. Similar studies were applied to paleosols in the Middle Mississippi Valley loess sequence (Markewich et al. 1998). The potential for dating loess deposits and paleosols associated with vertebrate-bearing sediments offers hope of obtaining a better numeric chronology for Rancholabrean faunas. Relating Rancholabrean faunas to the location of the glacial front is essential for improving

chronology and interpreting glacial and interglacial paleoenvironments.

Radiocarbon Interval The last 40 to 55 ka (Trumbore 2000) of the Rancholabrean is known in greater detail than the earlier part because of the applicability of radiocarbon dating and the greater frequency of specimen recovery. As a result, changes in the fauna during that interval are better dated than for any other part of the Pliocene and Pleistocene, and the most commonly used temporal division of the Rancholabrean is "pre-" versus "post-radiocarbon."

GEOGRAPHIC DISTRIBUTION

Rancholabrean faunas are widespread across North America south of 55°N latitude (see FAUNMAP Working Group 1994; figure 7.6). We center our discussion here on the three available faunal sequences that reveal faunal change through that time in one place. Of the many Rancholabrean faunas known from North America, only a few show a superpositional relationship that spans a sufficient period of time to provide a faunal sequence that could help to subdivide the Rancholabrean.

Medicine Hat Sequence The Medicine Hat sequence (Stalker 1969, 1996; Stalker and Churcher 1970, 1972) is one of the few Rancholabrean sequences in North America. There are seven faunal levels above the Irvingtonian faunas. The lowest of these faunas, separated from the Irvingtonian component by a till, is diverse (33 taxa) and contains *Bison* (therefore, by definition, it is a Rancholabrean fauna). Other taxa include *Ondatra zibethicus, Erethizon dorsatum, Cynomys ludovicianus, Canis latrans, Canis lupus, Canis dirus, Panthera atrox, Equus conversidens, Equus niobrarensis, Cervus canadensis, Ovis canadensis, Rangifer tarandus, ?Alces, and Mammuthus jeffersonii. The fauna was assigned to an interglacial time.*

This fauna is followed by a very small assemblage (three taxa) consisting of *Mammuthus primigenius* (the first appearance of *M. primigenius* in the sequence; it may indicate cold conditions), *Equus giganteus*, and *Antilocapra*. This fauna was assigned to the early "Wisconsinan."

Separated from the first two faunas by two tills and an unconformity are two faunal horizons of 11 and 7 taxa, respectively; the lowest of these includes *Smilodon populator* (formerly *Smilodon californicus*; see Berta 1985), *Mammuthus*, *Equus* cf. *E. giganteus*, *Equus conversidens*, *Hemiauchenia macrocephala* (formerly *Tanupolama stevensi*, but see Webb 1974b), *Camelops hesternus*, *Odocoileus* sp., and *Bison* sp. The upper fauna is separated from the lower by an unconformity and includes *C. hesternus*, *S. populator*, and *E. conversidens*.

Two stratigraphically higher faunas, both assigned to the late "Wisconsinan," are separated from the previous two faunas by a till reported to date to 20 ka. The faunas have similar taxa except for the species of mammoth. The lower has *Mammuthus imperator*, and the upper has *Mammuthus primigenius*. A Holocene assemblage is found at the top of the sequence with *Bison bison* and *Antilocapra*.

Although some of the faunas are small, they clearly show shifts in environmental conditions from bottom to top. At present, reliable numeric age control on this sequence is not extensive (see Stalker 1996). A number of electron spin resonance dates from various units and localities in this area were reported by Zymela et al. (1988), but the results are too variable to be helpful.

Meade Basin, Kansas In the Meade Basin, a sequence of faunas is interpreted to span at least two glacial stages and include one interglacial stage (Hibbard et al. 1965; R. Martin et al. 2000). These are, from oldest to youngest, Adams, Butler Spring, Mt. Scott, Cragin Quarry, Jinglebob, Jones (dated to between 26.7 and 29.0 ka; Hibbard 1970), and Robert (approximately 11.1 ka; G. Schultz 1969). The Butler Spring and Adams microfaunas includes predominantly modern species (G. Schultz 1965, 1967; R. Martin et al. 2000), supporting their placement in the Rancholabrean. Bison first appears in this sequence in the Mt. Scott Fauna, is absent from Cragin Quarry, and reappears in the Jinglebob and Jones faunas. The Cragin Quarry Fauna was previously interpreted to represent an interglacial stage (Hibbard and Taylor 1960; Hibbard 1963), suggesting the possibility that the absence of Bison was somehow related to environmental change.

Kennewick Sequence, Washington A temporally long, stratigraphically superposed sequence of Rancholabrean localities near Kennewick was described by Rensberger et al. (1984; see also Rensberger and Barnosky 1993). The assemblages were assigned a Rancholabrean age based on the large percentage of Recent species. *Bison* is absent. The top of the section is clearly dated by Mazama Ash to around 7 ka. Dating the lowest part of the sequence is more problematic, with the best evidence coming from the estimated rate for formation of calcrete horizons. The calcrete chronology probably brackets the base of the section to between 40 and 328 ka, although using a very slow rate for calcrete formation would make the base of the section up to a few hundred thousand



FIGURE 7.6 Putative early *Bison* localities and significant Rancholabrean localities discussed in the text. The bold line represents 55°N latitude. Independent biochronologies should be established for the region north of this line, and the term *Rancholabrean* should not be applied to faunas there. Localities with external chronologic control indicating an age between approximately 210 and 9.5 ka are considered to be temporal equivalents of Rancholabrean faunas elsewhere in North America. Circles = Rancholabrean faunas; triangles = putative early *Bison* localities; see text for discussion. 1, Medicine Hat sequence (in part), Alberta, Canada; 2, Kennewick sequence (in part), WA; 3, False Cougar Cave, MT; 4, American Falls, ID; 5, Teichert Gravel Pit, CA; 6, Camp Cady Fauna, CA; 7, Rancho La Brea, CA; 8, Ventana Cave, AZ; 9, Papago Springs Cave, AZ; 10, Cedazo, Aguascalientes, Mexico; 11, Cave Without a Name, TX; 12, Howard Ranch, TX; 13, Meade County faunas (in part), KS; 14, Kanopolis, KS; 15, Rezabek, KS; 16, Jones-Miller site, CO; 17, North Cove, NB; 18, Waubonsie, IA; 19, Jones Spring, MO; 20, Little Beaver Cave, MO; 21, Peccary Cave, AR; 22, Cheek Bend Cave, TN; 23, Patton Cave, WV; 24, Ladds Quarry, GA; 25, Inglis 1A (Blancan), FL; 26, Macasphalt Shell Pit (Blancan), FL.

years older. Rensberger and Barnosky (1993) argued against slower-rate calculations for the calcrete and proposed that the entire section be assigned to the Rancholabrean, but their placement of the Rancholabrean– Irvingtonian boundary was at 450 ka (Rensberger and Barnosky 1993:322). *Microtus meadensis* (= *Terricola* or *Pitymys*) is present in the lowest part of the Kennewick sequence. Its youngest known occurrence elsewhere is in Salamander Cave in South Dakota, with an associated date of 252 ± 30 ka (Mead et al. 1996). Using the calcrete calculations that yield ages up to 328 ka and the presence of *M. meadensis* in the basal part of the section, it seems likely that the lower part of the Kennewick sequence is Irvingtonian.

CHRONOCLINES AND EVOLUTION

Phyletic sequences or chronoclines in the Pliocene and Pleistocene have been proposed and evaluated for several mammalian lineages (e.g., Megalonyx, Ogmodontomys, Ondatra, Ophiomys, Mictomys, Microtus pennsylvanicus, Platygonus, Bison, and Mammuthus). Studies on evolutionary changes in these lineages examine morphologic change at various chronologic scales and contribute to temporal divisions in the Pliocene and Pleistocene mammal ages. If they can be calibrated independently or demonstrated to be in superpositional context, evolutionary changes in species help provide regional faunal characterizations. In lineages for which an especially rich fossil record is available, it can be difficult to determine adequate species boundaries (see R. Martin 1996). Studies of such lineages, when considered with other works that establish morphologic stasis over long periods of time (e.g., Barnosky 1987; Lich 1990) contribute significantly to our understanding of the range of morphologic variation within and between closely related species and provide a rich data resource that is now being used to address questions of evolutionary tempo and mode (Barnosky 1987; Gingerich 1993; R. Martin and Barnosky 1993). The phylogenetic affinity of many of these fossils with the modern biota also provides a crucial bridge between paleontology and neontology because the consequences of the incomplete nature of the fossil record can be assessed at least tentatively in comparison with the more adequately understood extant biota. Detailed studies of morphologic variation within and between various lineages thus assume a broader importance in the contexts of determination of mosaic evolution in different morphologic systems (e.g., dentition versus hind limb morphology in muskrats; Viriot et al. 1993; R. Martin 1996; Flint 1998), reliable identification of isolated fossil remains (e.g., teeth), and the interplay of these and other factors in establishing reliable and stable taxon definitions for mammal ages and their temporal divisions (Woodburne 1996). By providing a means for definitive identification of fossils that is independent of modern geographic distribution, these studies also help to offset the use of modern geographic distribution to refine taxonomic identifications. That practice is still common in studies of late Pleistocene and Holocene mammals but should be avoided because it introduces circularity in discussions of faunal response to climatic changes.

Published explorations of morphologic variation in Pliocene and Quaternary mammals encompass a broad range of taxa and provide a crucial database on morphologic change and variation through time and space. The voluminous literature on morphologic variation in Quaternary rodents was reviewed by R. Martin (1993). Studies on additional groups not covered in his review include Holmesina (Hulbert and Morgan 1993), Blarina (Guilday 1957; Graham and Semken 1976; Jones et al. 1984), Sorex (Jammot 1972; Junge and Hoffmann 1981; Carraway 1990, 1995), Allophaiomys (Repenning 1992), Dicrostonyx (Eger 1995), Guildayomys (Zakrzewski 1984), Hibbardomys (Zakrzewski 1984), Microtus (Bell and Repenning 1999), Microtus pennsylvanicus (Barnosky 1993; Gordon 1999), Ogmodontomys (Zakrzewski 1967), Ondatra (Viriot et al. 1993; R. Martin 1996), Ophiomys (Hibbard and Zakrzewski 1967), Pliophenacomys (Hibbard and Zakrzewski 1972; Zakrzewski 1984), Neotoma (Zakrzewski 1993), Zapus (Klingener 1963; R. Martin 1994), Dipodomys (Carrasco 2000), Cynomys (Goodwin 1993), Canis (Nowak 1979), Panthera (Seymour 1993), Smilodon (Berta 1985, 1987), Odocoileus (Purdue and Reitz 1993), and Mammuthus (C. Schultz et al. 1972; Lister 1993a; Webb and Dudley 1995).

GLACIAL CLIMATES: HARMONIOUS AND DISHARMONIOUS FAUNAS

Perceived changes in mammalian biogeography in response to alternating glacial-interglacial environments provide a potential means to refine Pleistocene chronology. The recovery, in deposits south of their modern distribution, of mammal species that today are limited to boreal and tundra environments usually is interpreted as signifying glacial conditions at the time of deposition. Conversely, the presence of southern species in localities north of their present range is interpreted to indicate interglacial intervals (Blair 1958). These geographic shifts sometimes result in direct stratigraphic associations of species that are today entirely allopatric; the apparent sympatry in the fossil record results in species assemblages that have no modern analog. Such species assemblages have been recognized in the Great Plains for decades (Hibbard 1944, 1949a). These nonanalog assemblages, which vary in species richness (Graham and Semken 1976), are variously called intermingled (Graham 1985), disharmonious (Semken 1988; Lundelius 1989), mixed (Markova 1992), mosaic (Guthrie 1982), and extraprovincial (Roy et al. 1995). Conversely, Holocene interglacial faunas with a species richness similar to that in modern biomes are sometimes called depauperate (L. Martin and Hoffmann 1987) or impoverished (R. Martin and Webb 1974; Semken 1974, 1984).

Nonanalog faunas sometimes are used as biostratigraphic tools to separate late Pleistocene glacial faunas from Holocene faunas, the latter of which rarely have more than two allopatric species (Semken 1988). This practice has its origin in the mid-twentieth century when Claude Hibbard, Dwight Taylor, and their colleagues attempted to order a diverse suite of molluscan and mammalian faunas from the Great Plains into a meaningful temporal sequence. In conjunction with stratigraphic position and the perceived stage of evolution of certain species, Hibbard et al. (1965) used the relative abundance of "cool summer" (boreal) and "mild winter" (temperate) faunal elements to place a series of faunas in southwestern Kansas in biostratigraphic succession. The absence of any Meade County Fauna directly comparable to the modern led Hibbard and Taylor (1960) and Hibbard et al. (1965) to regard the Holocene as "geologically atypical" for the Great Plains Quaternary. Pre-Holocene faunas with wholly boreal exotic species (not found today in Meade County; e.g., Jones, Butler Spring, and Cudahy) were assigned to glacial intervals, and those with only temperate exotics (Cragin Quarry and Borchers) were assigned to interglacial times. These faunas generally are regarded as nonanalog faunas now (but see Alroy 1999). Other nonanalog faunas (e.g., Jinglebob and Mt. Scott) were difficult to place because they contained both boreal and temperate exotics. With misgivings (Hibbard, pers. comm., 1965), the Jinglebob Fauna was assigned to an interglacial and the Mt. Scott Fauna to a glacial age based on the relative abundance of boreal and temperate taxa.

An increased reliance on paleomagnetic and radioisotopic data for faunal correlation has reduced the prevalence of such paleoecologic correlations, but faunal paleoecology is still used in some cases to assign strata to or exclude them from certain intervals of time, especially those of the late Quaternary. This practice assumes that factors controlling modern geographic distributions of species are adequately understood and that ecological tolerances and preferences of extant species were static through time. These assumptions were explicitly stated by Hibbard (1949a) but have not received adequate critical evaluation since that time, especially in light of modern alternative philosophical and methodologic approaches to paleoecologic reconstructions (Owen et al. 2000; Bell and Gauthier 2002). Although climatic correlations may be applicable to faunas in the latest Pleistocene and Holocene, their application to older faunas is questionable and should be avoided (see Lindsay 1997).

Radiocarbon dating of late Pleistocene nonanalog faunas with boreal exotics in association with modern residents can be used to test Hibbard's model generally and late Pleistocene faunas specifically. Late Pleistocene nonanalog faunas are defined by the presence of a few totally allopatric species (usually north boreal or tundra); widespread coexistence of boreal, prairie, and deciduous forest species now sympatric only along ecotones separating biotic provinces; and a species richness that may be twice that living around the site today (FAUNMAP Working Group 1996; Graham 1985; L. Martin and Hoffmann 1987; Semken 1988). A recent study of multiple accelerator mass spectrometry ¹⁴C dates conducted by Stafford et al. (1999) demonstrated contemporaneity of nonanalog species assemblages in discrete stratigraphic levels from Peccary Cave, Arkansas (Semken 1984) and Cheek Bend Cave, Tennessee (Klippel and Parmalee 1984).

Although the quantity and quality of radiocarbon dates from different sites vary widely, additional examples of radiocarbon-dated late Pleistocene glacial nonanalog faunas document the wide geographic distribution of such faunas. These include Patton Cave, West Virginia (13.3 ka; Grady 1988); Ladds Quarry, Georgia (10.9-10.3 ka; Lipps and Ray 1967; Holman 1985a, 1985b); Little Beaver Cave, Missouri (11.0 ka; Schubert 1997; Schubert and Graham 2000); the Waubonsie Fauna, Iowa (14.8 ka; Rhodes 1984); Cave Without a Name, Texas (10.9 ka; Lundelius 1967); Howard Ranch, Texas (19.1–16.8 ka; Dalquest 1965; Dalquest and Schultz 1992); North Cove, Nebraska (12.8–11.0 ka; Stewart 1987); False Cougar Cave, Montana (14.6-10.5 ka; M. Graham et al. 1987); Jones-Miller, Colorado (16.6 ka; Graham 1987); and Ventana Cave, Arizona (12.6 ka; Haury 1975; Mehringer 1967).

The significance and interpretation of nonanalog faunas was recently challenged on the basis of both empirical and methodologic concerns (Alroy 1999). These concerns centered primarily on the temporal association of (and possible causal relationships between) climate change, the breakup of nonanalog mammal communities, and the late Pleistocene megafaunal extinction in North America. The arguments raised by Alroy (1999) pose important challenges to traditional interpretations of Quaternary mammal faunal dynamics and provide incentive for reevaluating traditional hypotheses.

NORTH AMERICAN PLIOCENE AND PLEISTOCENE FAUNAL PROVINCES

The mammal ages treated in this chapter, and their proposed temporal divisions, are defined and characterized by appearances and disappearances of certain species. Earlier in this chapter we noted several instances in which perceived geographic differences in faunas play a role in the interpretation of temporal and spatial extent of mammal ages or their temporal divisions. The potential significance of these considerations affords us an opportunity to present some preliminary considerations regarding faunal provinciality and its potential impact on biochronologic interpretations and mammal age boundaries with respect to the Pliocene and Pleistocene.

That species are not distributed uniformly over the surface of the globe but rather can be seen as displaying varying degrees of provinciality is one of the most pervasive ideas in biogeography. Faunal provinciality has important implications for biochronology, some of which were noted by W. D. Matthew early in the twentieth century (Matthew 1915). The complex nature of faunal dynamics throughout the late Cenozoic, combined with the possibility that faunal provinces may persist through long periods of time (FAUNMAP Working Group 1996), forces the consideration that different faunal regions or provinces may need different biochronologies. For example, Repenning et al. (1995:12) recently stated, "The 'North American mammal ages' cannot be used in Alaska without complete redefinition." This difference in the faunal character of Alaska is tacitly acknowledged in much of the literature on North American mammalian biochronology and is one of the primary reasons for our geographic restriction of the Blancan, Irvingtonian, and Rancholabrean. However, few authors have addressed the immense complexities and potential ramifications of temporally variable faunal provinciality.

These issues are perhaps of greatest significance in the late Cenozoic, when temporal resolution may be sufficient to detect (and potentially resolve) the timetransgressive nature of species dispersal. The diverse range of geochronologic techniques available to scientists working in the Pliocene and, especially, the Pleistocene (Noller et al. 2000) affords a unique opportunity to resolve time intervals of short duration.

Climatic perturbations during the Pliocene, Pleistocene, and Holocene triggered varied, often individualistic responses among mammalian taxa. Mammalian faunal dynamics during these times certainly included significant (in some cases dramatic) geographic range adjustments of individual species. Some of the complications and challenges of recognizing faunal provinciality in the late Pleistocene were discussed by L. Martin and Neuner (1978), Graham (1979), and L. Martin and Hoffmann (1987). More recently, the FAUNMAP database documented that the rate, timing, breadth, and direction of geographic range adjustments varied significantly among different mammal species in North America (FAUNMAP Working Group 1996). Despite the response of individual species to changing conditions and the lack of modern analogs for community compositions in the Pleistocene, cluster analyses of species revealed that mammalian faunal provinces of the late Pleistocene were related to moisture and temperature gradients, as were Holocene provinces (FAUNMAP Working Group 1996). The Pleistocene provinces differed because there were as many as twice the number of species in any given area during the Pleistocene as are found at present (Semken 1988).

The extent of North American mammalian faunal provinces during the Pliocene through middle Pleistocene has not been explored in detail (Fejfar and Repenning 1992; Repenning 1987, 1992; Repenning et al. 1995; Bell 2000). The Holarctic arvicoline faunal regions proposed by Fejfar and Repenning (1992) were based on overall faunal similarity across large geographic areas, but the possibility that the regions could be subdivided into smaller faunal provinces was discussed briefly. Five North American arvicoline faunal regions were proposed by Fejfar and Repenning (1992). The Beringian faunal region is in the extreme northwest portion of the continent. The Canadian and Mexican faunal regions essentially follow geopolitical boundaries but were postulated on the basis of latitudinal climatic differences. The eastern United States and western United States faunal regions are divided by the Rocky Mountains (the western United States region was renamed the Pacific faunal region by Repenning et al. 1995). The temporal duration and spatial extent of these faunal regions was not stated explicitly, but the authors implied that the regions were biogeographically pertinent throughout the Blancan and Irvingtonian mammal ages. A preliminary map illustrating the possible geographic limits of these arvicoline regions was provided by Bell (2000), but further critical evaluation of these limits (and their potential change through time) is needed for all relevant time intervals.

The problem is perhaps best illustrated by the complicated state of affairs surrounding current proposed definitions of the Irvingtonian mammal age. At least five operational definitions have been proposed for the base of the Irvingtonian. The differences between them stem from disagreement as to potential defining taxa and their apparently diachronous regional appearances. Three of these definitions were proposed with explicit recognition of diachrony for the beginning of the Irvingtonian on either side of the Rocky Mountains (Repenning 1992; Repenning et al. 1995). The potential complications of this situation are not adequately addressed in the literature (see Repenning et al. 1995; Bell 2000). The presence of faunal provinces with shifting boundaries throughout the Pliocene and Pleistocene raises some fundamental issues regarding the concept of mammal ages, usually considered to be continentwide in scale. In cases where provincial differences include taxa that are considered to define a mammal age, reevaluation of the temporal divisions of the age may be needed. If a mammal age is defined by the appearance of a single taxon that disperses slowly or unevenly, the base of that mammal age will be time-transgressive. A similar argument pertains to the termination of the Rancholabrean mammal age, the upper boundary of which is not defined by a subsequent mammal age but is based instead on the latest occurrence of large-bodied extinct mammals, a similarly timetransgressive phenomenon. The discussions in this chapter pertaining to the appearance of Bison in North America and the late occurrence of Mammuthus on Wrangel Island provide good examples. If provinciality in the past was as well marked as in the present, no single taxon may be suitable to define an isochronous boundary in all regions; in fact, a taxon well suited to mark a boundary in one region may not appear in another region. Perception of such provinciality led to the explicitly diachronous definitions proposed for the beginning of the Irvingtonian (Repenning 1992; Repenning et al. 1995).

These considerations take on special importance when we consider the proposed divisions of the Pliocene and Pleistocene mammal ages. Temporal divisions proposed by C. Schultz et al. (1978) and subsequently modified by Lundelius et al. (1987) were based on changes in the mammalian faunas of the Great Plains and may not have broad application outside that region. The temporal divisions based on taxonomic composition and stage of evolution of the arvicoline rodents proposed by Repenning (1978, 1980, 1984, 1987; Repenning et al. 1990) were established with an implicit or acknowledged recognition of provinciality.

The provincial nature of North American mammalian distribution is best exemplified by the extant biota and by fossils from the most recent geologic time intervals. The Rancholabrean is unique among the mammal ages because of its recency, the fact that many of the species that characterize the age are extant, and the widespread geographic distribution of Rancholabrean faunas. These factors combine to permit a greater understanding of the complexities of mammalian faunal dynamics, the interplay of biotic and abiotic factors in shaping mammalian community structure, the response of mammalian species to changes in local climate or vegetation, and the range of patterns thus potentially discernible in the fossil record. The opportunity to study these issues is especially great for the Holocene and the part of the Rancholabrean that falls within the range of radiocarbon dating. Apart from merely providing a ready means of determining precisely the age, or age range, of a fossil deposit, radiocarbon dating may also permit detailed documentation of the rates of change in faunal communities. Well-dated sites also document the positive and negative aspects of time averaging in fossil deposits (Hadly 1999) and provide a temporal perspective on the persistence (or lack thereof) of faunal communities in time and space (e.g., Hadly 1999; Hadly et al. 1998; Hadly and Maurer 2001).

Late Pleistocene and Holocene biogeographic provinces based on differences in North American mammal faunas were proposed by L. Martin and Neuner (1978), Graham (1979), and L. Martin and Hoffmann (1987). Although different names were applied to the provinces, their geographic boundaries were remarkably similar. The most comprehensive study of Quaternary faunal provinces in North America is that of the FAUNMAP Working Group (1996), which was based on a larger number of taxa than was the case with previous studies. The FAUNMAP database recorded more than 2500 faunas from the late Pleistocene through the late Holocene in the contiguous United States. This database makes it possible to investigate changes in geographic distributions of species in greater detail than for any other period of time (FAUNMAP Working Group 1994, 1996). Shifts in the geographic distribution of species apparently took place individually, resulting in changes in overall community composition throughout the time interval covered by the FAUNMAP database. These data can be used for a preliminary evaluation of the effect of provinciality on biochronology. Examination of the FAUNMAP data set revealed that provincial boundaries at a given time were based on faunal aggregates of various species, but the aggregates on which the provinces were based were different at the two time intervals examined (late Pleistocene and late Holocene). A more robust (denser and richer) record of faunas from relevant time intervals across purported faunal regions must be obtained before reliable provincial definitions of mammal ages (e.g., Fejfar and Repenning 1992; Repenning 1992; Repenning et al. 1995) can be accepted for earlier time intervals (e.g., Irvingtonian and Blancan).

The faunal regions proposed by Fejfar and Repenning (1992) were based on preliminary examination of faunas from throughout the Holarctic and were erected based primarily on perceived provinciality in the arvicoline fauna. For the North American regions (see map in Bell 2000) we accept that the Beringian faunal region is largely valid (for the mammalian fauna generally, not just the arvicolines), but its southern boundary is not defined in time or space. Our use of the 55°N latitude line is an attempt to provide a southern boundary (admittedly arbitrary). The Canadian region is essentially a datadepauperate zone for most of the Pliocene and Pleistocene and therefore should be abandoned. The western and eastern United States boundary must be carefully reevaluated. Comparisons of approximately contemporaneous faunas in Texas, the Great Plains, Arizona, New Mexico, and California will be needed to evaluate the temporal and spatial nature of that boundary. Many important Blancan faunas are situated in Arizona and New Mexico, where the distinction between the eastern and western United States regions is unclear (see map in Bell 2000). The validity of that boundary also must be tested for the Irvingtonian; preliminary analysis suggests that its recognition, based only on arvicolines during that time interval, may be premature. Two of the postulated differences between eastern and western faunas involve Allophaiomys and Microtus paroperarius, taxa that previously were not known west of the Rocky Mountains but are now both known from Porcupine Cave in Colorado (central Rockies), the Little Dell Dam faunas (near Salt Lake City), and Cathedral Cave (east-central Great Basin).

Limits of the Mexican faunal region are not well established or characterized. It was originally postulated on the basis of latitudinal climatic differences rather than faunal character (Fejfar and Repenning 1992). Florida faunas were included in the Mexican region by Bell (2000), but this must be reevaluated. Florida has long been known to contain a unique combination of northern, western, tropical, and endemic taxa (Webb and Wilkins 1984). The FAUNMAP data confirm that Floridian faunas were distinct in the late Pleistocene and Holocene. The similarity between Florida faunas and those in Texas during the late Pleistocene may reflect an effect of the Gulf of Mexico coastal plain, either climatic or simply due to greater subaerial exposure during periods of lowered sea level. Texas coastal plain faunas from earlier time intervals are unknown.

The FAUNMAP Working Group (1996) recognized eight fine-scale provinces for the late Holocene, grouped under two major geographic divisions (essentially breaking out along the hundredth meridian). Geographic limits of faunal provinces in the late Pleistocene and Holocene were similar, despite different species composition and community organization. The study of late Holocene fossil faunas provides the key data for evaluating the complexities of faunal dynamics as they appear in the fossil record because of their proximity in time to the modern biota and their preservation in depositional contexts similar to those of older deposits. With extensive and detailed radiocarbon control and fine-scale stratigraphic excavation it is possible to tease apart details of morphologic and geographic response of mammals to climatic changes of varying intensities and durations. Studies of this nature, conducted by E. Hadly in Yellowstone National Park, provide a valuable insight into the dynamics of mammal communities and their response to short-term climatic changes (E. Barnosky 1994; Hadly 1996, 1997, 1999; Hadly et al. 1998; Hadly and Maurer 2001).

SUMMARY

Approximately the last 5 million years of mammalian evolution are encompassed by three mammal ages, named, from oldest to youngest, the Blancan, Irvingtonian, and Rancholabrean.

Because of their young age and the application of a variety of dating methods independent of faunal composition, these mammal ages are among the best dated in North America. Close phylogenetic affinities with the extant mammalian fauna permit detailed evaluation of faunal dynamics over short time intervals. Mammalian response, especially geographic range adjustments, to climatic changes over the last 2 million years was used extensively in prior correlations of these North American faunas. The advent of independent dating and correlation techniques (such as radiometric dating of volcanic deposits and the development of the Geomagnetic Polarity Time Scale) provide a more reliable basis for establishing age relationships of these faunas. Climatic correlations of faunas from the late Pleistocene and Holocene are still commonly applied, but their application for earlier time intervals is discouraged.

Pronounced faunal provinciality in the extant, Holocene, and late Pleistocene mammalian fauna is well documented. There is now sufficient evidence to demonstrate that Pleistocene faunas from northern latitudes in North America are of a different overall character than their temporal equivalents at lower latitudes, and similar patterns now are emerging for Pliocene faunas. Mammal ages that are defined by faunas at lower latitudes are rendered effectively inoperable at higher latitudes, where independent biochronologies should be developed. For these reasons, we recommend that the terms *Blancan, Irvingtonian*, and *Rancholabrean* be restricted to faunas in North America south of 55°N latitude. Finer-scale faunal provincialism for the Blancan and Irvingtonian was proposed nearly a decade ago but has yet to be demonstrated unequivocally in terms of both faunal character and the recognition of provincial boundaries through time and space. This is a fertile area for future research on Pliocene and Pleistocene biostratigraphy and biochronology.

The Blancan is defined by the first appearance in North America south of 55°N latitude of the arvicoline rodent *Mimomys* or the *Mimomys*-like arvicolines *Ogmodontomys* and *Ophiomys*. The beginning of the Blancan now lies between 5.2 and 4.6 Ma, depending on the arvicoline species used.

The Irvingtonian mammal age is defined by the first appearance in North America south of 55°N latitude of the elephant Mammuthus. The earliest records of Mammuthus with external chronologic control indicate that mammoths appear between 1.25 and 1.36 Ma across most of North America south of 55°N latitude, from California to Florida. An age of 1.35 is accepted here as the lower temporal limit of the Irvingtonian as it is currently understood. Following the adoption of Mammuthus as the defining taxon for the Irvingtonian, no fewer than 14 localities that were previously considered early Irvingtonian are here considered latest Blancan. These faunas include Inglis 1A, Inglis 1C, Haile 16A, and De Soto Shell Pit in Florida; Nash, Aries A, Rick Forester, and Aries B in Kansas; Sappa in Nebraska; Java in South Dakota; Curtis Ranch in Arizona; Froman Ferry in Idaho; El Casco in California; and the lower portion of the Cedazo Fauna in Mexico.

The Rancholabrean mammal age is defined by the first appearance in North America south of 55°N latitude of the bovid Bison. Well-dated early records of Bison are rare, and although several publications suggest the presence of Bison in the United States before 160 ka, we accept the Jones Spring, Missouri (160 ka), and American Falls, Idaho (between 210 and 72 ka), records as the earliest well-dated Bison. No mammal age younger than Rancholabrean is established, but the megafaunal extinction near the end of the Pleistocene represents a significant faunal change that we use to mark the termination of the Rancholabrean and the long sequence of North American mammal ages. The youngest reliable radiocarbon date from extinct megafauna in North America south of 55°N latitude could be as young as 9.5 ka, and that age is used here to mark the end of the Rancholabrean.

Divisions of the Blancan and Irvingtonian mammal ages permit finer-scale faunal correlations and temporal resolution for much of the Pliocene and Pleistocene. Proposals to divide the mammal ages in finer units include one based on overall faunal character and two based on the evolutionary history of the arvicoline rodents. We recognize some, but not all, of the proposed divisions.

The Miocene–Pliocene and Pliocene–Pleistocene boundary stratotypes are now formally designated in Italy, permitting evaluation of the correspondence of North America mammal ages with the epochal boundaries. The base of the Pliocene is 5.335 Ma, and the base of the Pleistocene is slightly younger than 1.77 Ma. The Holocene has no formal boundary definition, but its beginning is here operationally recognized at 10 ka. Thus the Blancan mammal age as defined here is mostly Pliocene, but faunas from the latest Blancan are early Pleistocene in age. The Irvingtonian as defined here is entirely Pleistocene. The Rancholabrean is mostly Pleistocene in age, but its terminal phase extends approximately 500 years into the early Holocene.

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The Blancan, Irvingtonian, and Rancholabrean Mammal Ages 297

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8

Global Events and the North American Mammalian Biochronology

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The prime tasks of modern historical geology are to separate the local signals from the global ones, to plot the relationships of global patterns both to time and to each other, and to search for the forces that drive these varied processes.

—A. G. Fischer 1984, p. 129

ISCHER (1984) INTRODUCES the concept of icehouse and greenhouse worlds to generalize global climatic settings in which glaciations were either preeminent or virtually absent. In the icehouse world, levels of atmospheric CO₂ would be those of preindustrial levels of this century; mean annual sea and land temperatures would be depressed; there would be greater poleward negative gradients in temperature and severity in climatic zonations; convective oceanic circulation would be active, with highly oxygenated oceans; and conditions would be conducive for the development of land and sea ice. In the greenhouse world, atmospheric CO₂ levels would be substantially greater than now; polar temperatures would be more equable and global temperatures elevated, with a decrease in the polar temperature-climatic gradient; oceanic circulation would be sluggish; and marine anoxia would be expected, as would be the absence of glacial ice. In general, sea level would be low during icehouse conditions, higher during greenhouse times.

Fischer (1984) correctly recognized that such cycles were of first-order magnitude (Abreu and Haddad 1998), or on the order of 50–300 m.y. in duration. The net ebb and flow of these global sea level fluctuations has been attributed to cycles in mantle convection (Fischer 1984), to assembly and dispersal of continents (Dewey and Pitman 1998), or to generally eustatic–tectonic origin (Jacquin and Graciansky 1998). Duval et al. (1998 and references cited therein) recognize two subsets of the 50- to 300-m.y. category and describe first-order (>50 m.y.) and second-order (3–50 m.y.) cycles as resulting from major continental encroachment associated with the breakup

of supercontinents and from transgression and regression reflecting changes in the rate of tectonic subsidence, respectively. Hag et al. (1988) and Graciansky et al. (1998, chart 1) suggest that the unconformities that bound these sequence packages can be correlated globally and therefore are potentially important for mammalian chronology. In a recent summary (Duval et al. 1998), third-order cycles (duration of 0.5–3 m.y.) are considered likely to be of glacio-eustatic origin, as are the fourth-order parasequence cycles (0.01-0.5 m.y. duration). The third-order sequence is the basic unit of sequence stratigraphy according to Jacquin and Graciansky (1998). Because of their global extent, such cycles are inferred to have a glacio-eustatic control, even when there is no independent evidence of the presence of major ice caps (Stoll and Schrag 1996; Gale et al. 2002). Jacobs and Sahagian (1993) proposed a mechanism whereby climatically induced fluctuations of major terrestrial lacustrine bodies could affect global sea level in nonglacial times.

Glacio-eustacy is a major factor affecting sea level changes during the Age of Mammals (here used as the time span embraced from the Late Cretaceous to the present), but aspects of tectonism and oceanic circulation also contribute importantly to climatic and other factors that affect the evolution and dispersal of terrestrial mammals. Some of these factors are summarized in figure 8.1.

Woodburne and Swisher (1995) examined the proposal that land mammal dispersals to between North America and other continents were linked to sea level lowstands and found that the tectonically active western margin of North America generally overrode the potential effect of



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FIGURE 8.1 Cenozoic global deep sea oxygen and carbon isotope records, mammal ages, climatic and tectonic events. After Zachos et al. (2001). Dispersal of mammalian taxa indicated by single- or double-headed arrows, with the length and thickness of the bar proportional to the magnitude of dispersal (see figures 8.4–8.7). Mean annual temperature and vegetation summary after Graham (1999). Mammal events from various sources, including chapters 2–7. CIE, carbon isotope excursion; GAI, Great Amercan Interchange; MBE, Mammal Biotic Event; NA, North America; O.W., Old World; SA, South America. the rise and fall of sea level in this regard. On the other hand, see Knox (1998) for a discussion of the interplay between tectonism and sea level change that probably resulted in the mammalian dispersal at the beginning of the Eocene across the northern Atlantic region. In addition to the tectonic influence of the Great American Interchange (GAI) at ca. 2.5 Ma (Iturralde-Vinent and MacPhee 1999), the Late Cretaceous to early Cenozoic exchange of land vertebrates between North and South America (Rage 1978; Gayet et al. 1992) also can be attributed to tectonic evolution of the Caribbean Plate (Pindell 1994; Villamil and Pindell 1998).

Abreu and Haddad (1998) provide a recent summary of the variations of isotopes of oxygen and carbon during glacial or nonglacial times. Fluctuations in isotopic ratios of both elements serve as proxies for glaciation and sea level independent of other methods or criteria.

Briefly, during glacial times the amount of ¹⁸O in sea water (and in foraminifera and other organisms that incorporate oxygen in their CaCO₃ tests) increases as an increased amount of the lighter isotope ¹⁶O (which preferentially flows to the atmosphere) is removed from the oceans and trapped in glacial ice. Thus the δ^{18} O ratio (¹⁸O/¹⁶O) increases. In general, when sufficiently large δ^{18} O ratios are measured in the CaCO₃ of tests of fossil marine organisms, or even in bulk rock analyses of limestone, it is possible to infer that glaciations have taken place on land (see also Graham 1999:86–92).

Regarding carbon, the heavy isotope ¹³C is discriminated against during photosynthesis, so that all organic matter is enriched in the light isotope 12C. Any change in the organic carbon reservoir in sea water alters the ¹³C/¹²C ratio recorded there. During interglacial times, when sea level is high, large amounts of 12C are stored in the terrestrial biomass and in sediments deposited in the flooded shelves; organisms living in the oceans record the concurrently higher (positive) ¹³C/¹²C ratio. In glacial times, when shelves are exposed and eroded, formerly trapped ¹²C is released to the ocean and could show up in, say, bathyal organisms, with a lower (negative) δ^{13} C ratio. Still, this relationship does not always hold true because the deep sea isotopic record commonly shows a positive shift in δ^{13} C during periods of ice growth, coeval with the positive shift shown in the δ^{18} O ratios, apparently caused by ventilation of the deep sea water masses during glacial periods. In the following discussion, ratios of these and other organic elements are considered as proxies for climatic change that could affect the faunal succession of Late Cretaceous and Cenozoic mammals. Figure 8.1 shows the oxygen and carbon isotopic curves for the past 70 m.y.

"MEDIAL" THROUGH LATE CRETACEOUS

Before the Albian, a generally greenhouse world prevailed in the Cretaceous Period. As indicated by Hardenbol et al. (1998), the Late Albian through Late Campanian was overall a time of major sea level high and presumably a greenhouse world without significant polar ice, although sea surface temperatures apparently were lower than at present at 125 Ma (Frakes 1999). Huber (1998) suggests that sea surface temperatures were about 12°C at about 60°S in the Albian, rose to an average of about 24°C in the Turonian-Coniacian (ca. 93-86 Ma), and dropped to about 8°C in the Maastrichtian (ca. 67 Ma), with a rise to about 12°C toward the end of the Cretaceous. In this time interval Hardenbol et al. (1998) show distinctive drops in sea level at ca. 111 Ma and 102 Ma (Early and Late Albian), 95 Ma (Late Cenomanian), 91 Ma (Late Turonian), 79 and 72 Ma (Early and Late Campanian), and 67 Ma (Late Maastrichtian), for which a glacial-eustatic cause would be difficult to propose in a greenhouse world, and Frakes (1999:51) states that "there is no direct evidence for Cretaceous continent-wide glaciation anywhere on the planet." Still, Abreu et al. (1998) suggest that oxygen isotope fluctuations in the Aptian to lower Albian and Campanian to Maastrichtian intervals (also Barrera and Savin 1999) resemble those of the medial Eocene. In that evidence has been marshaled to suggest the presence of Antarctic glaciation in the medial Eocene, the pattern similarity opens the question of a glacial cause for those oxygen isotope fluctuations in the Cretaceous. However, Immenhauser and Scott (1999) demonstrate that at least for the Albian, correlation of sea level fluctuations on a global basis is very difficult, so the pattern should be viewed with caution. Gale et al. (2002) continue to rely on glacio-eustacy as a mechanism to account for shortterm fluctuations in the stratigraphic record of Cenomanian (ca. 98.9-93.5 Ma) marine strata in southeastern India and northwestern Europe, possibly driven by limited high-altitude Antarctic glaciation. And Miller et al. (1999) propose an Antarctic glacial origin for a drop in sea level (ca. 20-40 m; New Jersey) synchronous with a major global increase in δ^{18} O at ca. 71 Ma (base of chron C31r) for the early Maastrichtian. These events apparently are coeval with a negative global δ^{13} C excursion, which Miller et al. (1999) interpret as being caused by increased weathering of organic-rich sediments exposed by sea level lowering on continental shelves. Huber et al. (2002) evaluate deep and surface sea temperatures from the Albian through Maastrichtian from both mid- to high northern and southern paleolatitudes and conclude that both

realms show conditions that were mostly as warm as or warmer than present conditions and too warm to conform to scenarios that invoke Antarctic ice sheets, even for the cooler intervals discussed herein.

Whereas evidence of sea level fluctuation over the time span indicated earlier seems clear, as does the evidence of concurrent isotopic variations in oxygen and carbon, the effect, if any, of sea surface temperatures on continental atmosphere still is tenuous. Frakes (1999) reviews evidence in favor of episodes of cool sea surface temperatures at ca. 97, 89, and 68 Ma but cautions that the admittedly limited data on continental air temperatures do not track the marine record well. Continental air temperature data indicate a warming trend from the Early Cretaceous to a Turonian peak without the cooling in the Cenomanian (97 Ma) seen in the marine record and continued warming thereafter in higher latitudes. Dettman and Lohmann (2000) studied δ^{18} O values of river water in Late Cretaceous and Paleogene basins of western North America and suggest that mountainous relief there was comparable to the 2.5-3 km seen today and that montane snow was present year-round at times, but whether this was controlled by or was only contemporaneous with oceanic cooling remains to be demonstrated. Upchurch et al. (1999) demonstrate the difficulties (and the power) in modeling continental climates in the Late Cretaceous, even when assumptions as to the impact of vegetation are supplied.

The problem remains that a glacio-eustatic solution to a drop in sea level is difficult to reconcile with general greenhouse conditions. This is exacerbated by the lack of independent evidence of glaciations proposed on a combination of eustatic and oxygen isotope data (Barrera and Savin 1999) and the still meager means of correlating atmospheric with sea surface temperatures. The evidence suggests that oceanic temperatures suffered periods of deterioration correlative with sea level drops in the mid-Campanian (ca. 79 Ma), at about the Campanian-Maastrichtian boundary (ca. 72 Ma), and in the late Maastrichtian (ca. 67 Ma) but also that climates warmed just before the beginning of the Cenozoic, possibly in response to Deccan Traps volcanism. Thus, although sea temperatures were cooler in the Maastrichtian than previously, the overall climate still was a cool greenhouse (Huber et al. 2002).

The terrestrial plant record from the Late Cretaceous through early Eocene is summarized from Graham (1999). In the Late Cretaceous, the prevailing epicontinental seaway, sited roughly athwart the present location of the Rocky Mountains, divided the terrestrial flora into an eastern Normapolles pollen group and a western Aquilapollenites pollen group, as summarized in figure 8.2. The Normapolles pollen group extended east of the Cretaceous Sea, the Aquilapollenites group to the west. Sparse megafossil plants were preserved mostly along the margins of the Late Cretaceous Seaway and in the Appalachian region. A polar microthermal broadleaved deciduous forest developed north of about the 60°N paleolatitude (northern Canada and Alaska), with a mean annual temperature (MAT) of 8–15°C; sea surface temperatures are estimated at 6-8°C. The poleward climatic gradient was much shallower than at present, and the deciduous nature of the vegetation suggests a seasonal regime, both as to temperature and as to light, in an overall cool-temperate climate, with north slope areas having a diverse understory and forest habitat. In southern Canada and the Pacific Northwest, this gave way to a mesothermal notophyllous broadleaved evergreen forest (MAT of about 13°C) between about 50 and 60° paleolatitude. South of about 45° paleolatitude, growth rings are absent to poorly developed, consistent with the southern (and southwestern) United States being dominated by a tropical or paratropical forest developed under a subhumid, largely aseasonal climate with an MAT of 20-25°C.

Lancian faunas best represent terrestrial mammal communities of the Late Cretaceous (chapter 2, table 2.3), with approximately 12 genera of multituberculates (cimolodontids, eucosmodontids, neoplagiaulacids, and ptilodontids), a metatherian, 10 marsupials (alphadontids, "pediomyids," and stagodontids), and placentals (cimolestids, gypsonictopids, soricomorphs, and ungulatomorphs), mostly limited to sites along the western margin of the epicontinental sea (latitudinal range comparable to that of the fossil plant sites in figure 8.2). These sites fall within the areas dominated by notophyllous broadleaved evergreen forests on the north and by paratropical rainforest on the south. This appears to be reflected in northern and southern biofacies among the mammals (Weil and Williamson 2000; Clemens 2002), with the northern biofacies characterized by a greater diversity of eutherians. Most of the taxa apparently were derived endemically, with only two, Batodon and Glasbius, being allochthonous (Clemens 2002).

Case et al. (in press) include *Glasbius* as one of a small number of Lancian or Judithian marsupial lineages having a potential southern (equatorial) theater of origin or differentiation. Although the origin of *Batodon* is unclear, it appears unlikely that it was in equatorial America, based on the geographic distribution of potential sister taxa (McKenna and Bell 2000).



FIGURE 8.2 General paleogeographic setting for North America in the Late Cretaceous, with pollen provinces (*Aquilapollenites, Normapolles*), distribution of floral types, Cretaceous Sea, after Graham (1999). Sites are better represented in the western than in the eastern facies but still sparse. Both show a polar broadleaved deciduous forest (D) and a southern tropical (T) or paratropical (P) forest in the south, with an intervening notophyllous broadleaved evergreen forest (N) documented in the west. This is summarized as ranging from a microthermal to mesothermal transition and megathermal climate. Isotherms and paleolatitudes are approximate. After Wolfe (1977), the polar broadleaved deciduous forest has a mean annual temperature (MAT) of ca. 8–15°C, with large, thin-textured leaves inhabiting a mesothermal to microthermal moist climate. The notophyllous broadleaved evergreen forest reflects an MAT of about 13° C and a mean coldest-month temperature of ca. 1° C, with sclerophyllous vegetation lacking dip tips and having 40-60% entire-margined leaves. The paratropical rainforest has an MAT of $20-25^{\circ}$ C, lacks a dry season, and is composed mainly of broadleaved evergreen trees, with some deciduous and with 50-75% entire-margined leaves. The tropical forest has an MAT of about 25° C in a subhumid, aseasonal climate, with broadleaved evergreen, single-tiered open-canopy vegetation, mostly entire-margined leaves. F, fossil plant site.

PALEOGENE

As indicated in figure 8.1, oceanic temperatures generally rose across the Cretaceous-Tertiary boundary and progressed toward the early Eocene climatic optimum, by which time the sea temperature was about 12°C. Kennett and Stott (1995, figure 5.1) indicate that the temperature of Antarctic surface waters was ca. 8–10°C based on δ¹⁸O data in planktonic foraminiferans in the early Paleocene and increased to ca. 13-14°C just before the late Paleocene thermal maximum (LPTM; Zachos et al. 1993), associated with the global carbon isotope excursion (CIE), dated at 55.5 Ma (Bains et al. 1999). During the LPTM, deep ocean water temperatures were more than 15°C, surface waters in the high latitudes more than 20°C (Corfield and Norris 1998). The oceanic carbon isotope (δ^{13} C) values dropped about 2.5 per mil during the CIE, perhaps in three steps during an interval of about 10,000-20,000 years (Bains et al. 1999). The CIE implies that the global ocean experienced an abrupt input of a large amount of isotopically light carbon at this time, which Rea (1998) and Bains et al. (1999) suggest having resulted from the release of large amounts of biogenic methane into the ocean. The best candidate for this gas is proposed to be methane hydrates preserved in sediments beneath the sea floor in the subtropical western North Atlantic Ocean, with release promoted by erosion- or impact-triggered failure of the sea floor along continental slopes, perhaps aided by warming of deep ocean temperatures, which converted the once-solid hydrates to the gaseous state. Hudson and Magoon (2002) propose a second but not necessarily alternative source for the generation of atmospheric methane: heating of subducted hydrocarbonproducing sediments along coastal Gulf of Alaska from about 65 to 55 Ma. However, Clift and Bice (2002) elaborate that methane was not the sole trigger for global warming in the late Paleocene to early Eocene, with an increase of atmospheric CO₂ being a likely candidate from volcanic or tectonic sources. Thomas et al. (2002) favor a model wherein a general late Paleocene trend in warming of oceanic surface and intermediate-depth waters led, by downwelling or subduction, to thermally induced dissociation of methane hydrates in an unspecified deeper source location. In any case, the onset of the CIE was associated with the Benthic Foraminiferal Extinction (BFE), the Kaolinitic Event (KE), and the Eolian Dust Event (EDE) and coincided with the Mammal Biotic Event (MBE) mammal dispersal event at Wao (Berggren et al. 1998; Zachos et al. 2001).

Thomas (1998) describes the BFE as a major, rapid global extinction wherein 30–50 percent of benthic

foraminifera at middle bathyal or greater depths became extinct in a few thousand years. Factors contributing to the extinction include changes in deep sea circulation, increased corrosion of CaCO₃ related to the strong increase in isotopically light carbon, increased temperatures, low oxygenation, and changes in productivity patterns.

As discussed by Rea (1998), a dramatic reduction in size of eolian dust grains (the EDE) from North Atlantic and southern Indian oceanic deep sea cores at the time of the LPTM signifies a strong reduction in global wind intensity, in sharp contrast to the vigorous atmospheric circulation patterns interpreted for the Late Cretaceous and all but latest Paleocene. Based on these data, atmospheric circulation remained sluggish for most of the Eocene, apparently reflecting a significant reduction in the pole-to-equator temperature gradient, but began to reinvigorate in the icehouse world of the later Eocene and Oligocene. The KE is the sharp increase of kaolinitic clays that occurred globally in synchrony with the LPTM, apparently indicating and episode of even higher humidity and intensity of chemical weathering than otherwise characteristic of the early Eocene (Sloan and Thomas 1998:139).

Thus the LPTM saw a major reorganization of global patterns largely attributed to global warming but also to the CIE as isotopically light carbon was released into the oceans and then into atmosphere. Depending on the definition of the series—epoch boundary, these events transpired at the end of the Paleocene or beginning of the Eocene (see chapters 2 and 3).

The bolide impact at the K–T boundary (Alvarez et al. 1980) probably contributed to but arguably was not the major cause of the mammalian extinctions at that time, with impact dust-induced curtailment of photosynthesis viewed with some skepticism (Pope 2002; also see Clemens 2002 for an important review). Regardless of cause, Clemens (2001, 2002) records that the mammal fauna of the beginning Puercan (Pu1) was reduced in diversity by about 60 percent and that about 18 percent of the mammalian fauna survived from the Lancian. Early Paleocene floras in the vicinity of the southern Rocky Mountains (New Mexico) show the fern spike, followed by Paleocene recolonization by angiosperms (Wolfe 1987; Wolfe and Upchurch 1987), indicating a paratropical rainforest with an MAT of about 22°C, whereas farther north (Alberta) plant diversity decreases across the K-T boundary, but a fern spike is absent. The notophyllous broadleaved evergreen forest (figure 8.2) of the Late Cretaceous was replaced in those paleolatitudes by the broadleaved deciduous forest, although the climate still was mesothermal. Still, the overall climatic setting of the

Late Cretaceous was not markedly different from that of the early Paleocene, at least in the areas represented by fossil mammals, with rainfall on the order of 1000 mm annually. Graham (1999, table 5.5) indicates that the southeastern United States supported a tropical rainforest, with an MAT of 27°C, that gave way to the northeast to a notophyllous broadleaved evergreen to polar broadleaved deciduous forest, with an MAT of 15-20°C. Farther inland, early to late Paleocene floras of the eastern Rocky Mountains ranged from polar broadleaved deciduous forests in the north to paratropical rainforest and notophyllous broadleaved evergreen forests in the south (MAT 13-15°C to 18°C). In Alberta and the Yukon, polar broadleaved deciduous and notophyllous broadleaved evergreen forests lived under an MAT of 10-15°C. In general, a warming trend extends from the Tiffanian (MAT of 10°C) to the Clarkforkian (MAT of ca. 13.5°C) in the Rocky Mountains district (e.g., Bighorn Basin, Wyoming, figure 8.3), with mesothermal-megathermal broadleaved deciduous vegetation giving rise to megathermal evergreen tropical forests. The earlier Paleocene floras from the Ravenscrag Formation (figure 8.3) of Saskatchewan (i.e., north of about 50° paleolatitude) indicate a microthermal climate with near-freezing temperatures reached in January. Overall, floral indicators show a discernible north-south zonation in the Paleocene but also are consistent with the general warming trend toward the early Eocene climatic optimum (figure 8.1). From a tectonic standpoint, Jerzykiewicz and Sweet (1988) indicate pulses of uplift in at least the northern Rocky Mountains during the interval from 80 to 60 Ma, and by the early Eocene the range generally had been elevated to about half its present height (Graham 1999), so the previous lowlands and epicontinental sea were disrupted. A comparable scenario can be applied to the Front Range and southern Rocky Mountains as well (Pazzaglia and Kelley 1998; see also Dettman and Lohmann 2000).

As indicated in chapter 3 (table 3.2), early Puercan faunas continue to share with Lancian ones the ptilodontid, eucosmodontid, and taeniolabidid multituberculates, didelphid and glasbiid marsupials, and cimolestid didelphodontan, cimolestan, and lipotyphlan placentals (also Clemens 2002; classification follows McKenna and Bell 1997). The marsupials declined strongly from the Lancian in Pu1, with only *Peradectes* representing the group that formerly included alphadontines (*Alphadon, Protalphadon,* and *Turgidodon*), pediomyids ("*Pediomys*"), glasbiids (*Glasbius*), and stagodontids (*Didelphodon*). New groups for Pu1 include leptictids (*?Prodiacodon*) and a variety of ungulates (*Oxyprimus, Protungulatum, Baioconodon,* and *Mimatuta*), although their novelty may be more local than revolutionary. Clemens (2001) indicates that about 70 percent of the Pu1 mammals of northeastern Montana were aliens (lineages not known in the Lancian of the western northern interior), so their point of origin is not clear; they include Acheronodon, Catopsalis, Stygimys, ?Prodiacodon, Protungulatum, Oxyprimus, Baioconodon, and Mimatuta. Stygimys may be represented in the Campanian El Gallo Fauna (Baja California del Norte), so the group to which it belongs can be considered to be known from pre-Pu1 faunas of North America generally, but not in the western northern interior. Similarly, Protungulatum, Oxyprimus, Baioconodon, and Mimatuta also have Campanian representatives in southern districts (Baja California and Utah; Clemens 2002). The multituberculate Catopsalis and primitive ungulates of possible Lancian age occur in Saskatchewan, suggesting that western interior faunas were different from precursor or possibly contemporaneous suites in peripheral areas such as these. Whereas climatic indicators may indicate a biofacies contribution from that source, the factors that contributed to the Baja California element are less clear. Lying outside the San Andreas fault zone, Baja California was at least 300 km southeast of its present location in the Late Cretaceous. Thus, although immigration played a role in the development of early Puercan mammal faunas in the western interior, the home of the immigrants may not have been outside of North America in most (possibly all) cases.

About 400,000 years later, Pu2 saw the most dramatic increase in mammal diversification for the Paleocene, and, again, a major component of this increase resulted from immigration. Compared with Pu1, new taxa cited in chapter 3 for Pu2 are as follows (**= alien, R = resident, U = unknown in Clemens 2002; * = immigrant in 1987 volume). The multituberculates include Neoplagiaulax U, Ectypodus**, Parectypodus**, Kimbetohia, Ptilodus**, Xyronomys U, and Microcosmodon R. Eutherians include the cimolestid Alveugena; the taeniodonts Onychodectes, Schochia, and Wortmania; the primates Purgatorius* and Pandemonium*; the oxyclaenids Carcinodon*, Chriacus*, and Oxyclaenus*; the arctocyonids Platymastus, Desmatoclaenus, Loxolophus, and Mimotricentes; the hyopsodontid Litomylus**; the mioclaenids Ellipsodon, Choeroclaenus, Bubogonia**, Tiznatzinia, and Promioclaenus; and the periptychids Anisonchus, Haploconus, Mithrandir, Hemithlaeus, Ectoconus, Alticonus, Periptychus, Tinuviel, Oxyacodon, and Conacodon. Based on Clemens (2002) it appears that cimolestids, periptychids, mioclaenids, arctocyonids, and taeniodonts were generally endemic to North America, but other taxa



abla

FIGURE 8.3 Map of western North America showing location of paleofloral sites discussed in the text. After Graham (1999). Also shows south coastal region of California that yields Eocene mammals.

(multituberculates, primates, oxyclaenids, hyopsodontids, and mioclaenids) were immigrants, probably from elsewhere in North America, if not Holarctica. The (neoplagiaulacoid and eucosmodontid) multituberculates are otherwise endemic to North America in the Late Cretaceous and early Paleocene (including Torrejonian). Primates, oxyclaenids, and hypsodontids are shared with other regions (McKenna and Bell 1997), but still may have their earliest Paleocene records in North America. Pu2 records a strong immigration pulse at a time (1, figures 8.1, 8.4) between major episodes of lowered sea level. If that pulse is relative only to interior North America, sea level may be irrelevant. For Pu3, the multituberculate *Taeniolabis*** apparently is an immigrant, but the eutherians (the leptictids *Prodiacodon* and *Palaeictops*, the cimolestan *Ravenictis*, the hypsodontid *Haplaletes*, and the triisodontid *Goniacodon*) are not.

In the Torrejonian and Tiffanian, cimolestids, apatemyids, pantolestids, and arctocyonids are diverse; hyopsodontids undergo a radiation from the Puercan; pantodonts, erinaceomorphs, soricomorphs, plesiadapid primates, paromomyid dermopterans, carpolestid euprimates, and phenacodontids diversify in the Tiffanian (from Torrejonian first occurrences); and periptychids diminish relative to their Puercan abundance (e.g., chapter 3, table 3.2). Immigration was of minor importance in the Torrejonian and Tiffanian (figures 8.1 and 8.4), despite a major sea level drop (Ta2) at about Ti3. As for

TIME (Ma)	CHRONS	РОГАВІТУ			AGE	OTHER DATA	MAMMAL AGES	DISPERSAL/TAXA
52	C23		ENE	-۲	AN	Early Eocene Climatic Optimum	Lostcabinian Wa7	Lambdotherium, Eotitanops
54 -	C24		EOCE	EARI	YPRESI		Lysitean Wa6 Wasatchian Wa5 Greybullian Wa2	Heptodon Homogalax
56					ETIAN	Carbon isotope excursion; Late δ ¹³ C_ Paleoc. Thermal Max.	Sandcoulean wa2 wa0Wa1 Clarkforkian Cf1 Ti6	 Apatemys*, Macrocranion, Cantius, Palaeosinopa*, Didelphodus, Arfia, Prototomus, Didymictis*, Palaeonictis*, Miacis, Pachyaena**, Hyopsodus*, Hyracotherium, Diacodexis Rodentia, Tillodontia, Coryphodon
58	C25		111	LATE	N THAN			Prodinoceras, Arctostylops (Asia)
60	C26		EOCENI		SELANDIA	Ta2 -	Tiffanian	Chiromyoides
			PALI				Ti1 To3	Plesiadapis
62	C27			ARLY	NIAN		Torrejonian <u>To2</u>	Dissacus, Ankalagon, Pantolambda, Deltatherium
64	C28			E/	DA		$\frac{63.90 \pm 0.04}{Puercan} \xrightarrow{63.90 \pm 0.04}_{Fu} \frac{100}{Pu3}$	– Taeniolabis 1 ?Purgatorius, Pandemonium, Carcinodon, Chriacus, Litomylus? - ?Oxvclaenus
66	C30				AESTRICHTIAN	Ta1 - Major Sea Level Fall	Lancian	1, 2 = major dispersal event

FIGURE 8.4 Paleocene time scale, mammal ages, and dispersal of mammalian taxa. Time, chrons, polarity, epochs, and ages after Berggren et al. (1995). Mammal ages and dispersal/taxa after chapters 2–4. Ta1 and Ta2 are times of major sea level fall, after Haq et al. (1988) for terminology and Hardenbol et al. (1998) for chronology. * = taxa known from the Paleocene of North America, ** = from the Paleocene of Asia but involved in Holarctic dispersal at Wao.

324 Michael O. Woodburne

North America, the Paleocene faunas of Asia are largely endemic (Ting 1998). Following chapter 3, members of the Mesonychia (Ankalagon, Dissacus), Pantodonta (Pantolambda), and Tillodontia (Deltatherium) are likely immigrants from Asia during the Torrejonian (To2), suggesting a correlation with the Shanghuanian mammal age (Ting 1998). The Nongshanian mammal age (Ting 1998) includes the first occurrence in Asia of Arctostylopida, Dinocerata, Phenacolophidae, and Ernanodontidae (?Edentata), and the first two of these groups first appear in Ti5 of North America at ca. 57 Ma, about 2 m.y. later than the time of a major sea level lowstand (Ta2; figures 8.1 and 8.4). As indicated in chapter 3, the Asian first occurrence of these taxa may not be synchronous with the North American record, but their immigrant status seems clear in North America. The Clarkforkian heralds a major dispersal event from Asia, with Rodentia, Tillodontia, and Pantodonta (Coryphodon) making a dramatic appearance (2, figures 8.1 and 8.4). According to chapter 3 (table 3.2), Rodentia include Alagomys, Acritoparamys, Paramys, and Apatosciuravus; Tillodontia include Esthonyx. Other elements of Clarkforkian faunas record persistence of groups that occurred earlier, but oxyaenids, nyctitheriids, micromomyids, and pauromomyids are more diverse than in Tiffanian faunas, and new hyopsodontid condylarths appear.

Eberle and Lillegraven (1998) point out that in the Puercan, mammal species of the Hanna Basin, Wyoming (figure 8.3), were more similar (54 percent) to those of southern districts than to those to the north, exemplified by both multituberculates and eutherians ("ungulatomorphs"). This is approximately coincident with the boundary between the paratropical dry forest and evergreen tropical rainforest in the southern part of the United States and the northern microthermal polar broadleaved deciduous forest (see P in the Cretaceous Sea on figure 8.2 for location of that boundary, if not marine conditions in the Paleocene). As indicated in chapter 3, the geographic distribution of North American Paleocene mammal faunas younger than Puercan is limited, so currently there is little documentation of paleozoogeographic facies for this time frame. In Torrejonian interval To3 plesiadapid and carpolestid primates may be dominant in northern faunas, whereas Tetraclaenodon, Periptychus, and Mixodectes may dominate in southern faunas.

Chapter 4 illustrates that there is some disagreement about the location of the Paleocene–Eocene boundary not only with respect to stratotypic relationships in the London/Paris Basin but also with respect to the continental mammal record in North America. Figures 8.4 and 8.5 indicate that the base of the Eocene corresponds to the base of the Ypresian Stage/Age at ca. 54.7 Ma, whereas the Clarkforkian–Wasatchian boundary corresponds closely with the CIE, dated at ca. 55.5 Ma. Under that scenario, the earliest Wasatchian (Wao) is latest Paleocene in age. Alternatively, if the Paleocene–Eocene boundary is correlated to the CIE, then Wao would be earliest Eocene (see also Aubry et al. 1999; Aubry 2000). Regardless of a decision on this topic, Wao faunas witnessed a major intercontinental dispersal between North America and Europe and Asia, to which a combination of plate tectonic and local geologic events contributed (McKenna 1983a, 1983b; Knox 1998), but apparently was not coincident with a major sea level lowstand (figure 8.5).

The early Eocene is warmest period in the Paleogene, culminating the trend from the later Paleocene. Sea temperatures around Antarctica still are warm (Ehrmann and Mackensen 1992), and in Australia this is the time of maximum development of nonseasonal megathermal rainforests and year-round high humidity consistent with global warming (MacPhail et al. 1994:242–246). The interpretation for a generally broad interval of warmth during the early Eocene (ca. 55–49 Ma, early Eocene climatic optimum, figure 8.1) is based on low δ^{18} O global sea water values (Browning et al. 1996:639, 640; Zachos et al. 2001).

As summarized in Graham (1999), tropical, subtropical, and warm temperate forests dominate the United States interior in the early Eocene. Gunnell (1997) indicates that the Wasatchian climate was characterized by warm, subtropical MATs (12–18°C) and forests and by closed conditions in the Bighorn Basin, Wyoming (figure 8.3). This climatic setting was at least conducive to the wave of dispersals that resulted in the greatest similarity of Holarctic mammal faunas ever achieved (Savage and Russell 1983:67), apparently along with a significant immigration of floral elements from Europe (Frederiksen 1988), with both possibly coeval with the LPTM.

Wasatchian faunas reflect an early phase in the progressive modernization of land mammals in North America and a reduction in some typical Paleocene groups. Thus these faunas show a loss of about 50 percent of multituberculate families, a diminution of archaic giants and primitive Paleocene elements (taeniodonts, pantodonts, and pantolestans), the last oxyclaenid and arctocyonine, and diminished hyopsodontid condylarths. These changes were countered by an increase in herpetotheriine marsupials; a development of more modern rodent groups (castorimorphans, sciruravids, and cylindrodontids); a radiation of new creodonts, miacid carnivores, phenacolemurine dermopterans, and notharctine and omomyoid primates; and the beginning of the artiodactyl and perissodactyl radia-



FIGURE 8.5 Eocene time scale, mammal ages, and dispersal of mammalian taxa. Time, chrons, polarity, epochs, and ages after Berggren et al. (1995). Mammal ages and dispersal/taxa after chapters 4–5. Ta3 and Ta4 are times of major sea level fall. * = taxa known from the Paleocene of North America, ** = from the Paleocene of Asia but involved in Holarctic dispersal at Wa0). *Palaeogale* is first known from the Chadronian but apparently dispersed to Europe at about the Whitneyan (Baskin and Tedford 1996; also see this reference for *Parictis*). Nimravidae as immigrants suggested by Bryant (1996). *Patriomanis* after and Gaudin and Emry (2002).

tions, including the first equids, brontotheres, chalicotheres, hyracodontid rhinos, and helaletid and isectolophid tapiroids.

According to Gingerich (1989, 2001) and Strait (2001), Artiodactyla (*Diacodexis*), Perissodactyla (*Hyracotherium*), Primates (*Cantius*), and hyaenodontid Creodonta (*Prototomus, Arfia*) appear in Wao faunas (**3**, figures 8.1, 8.4, and 8.5), have no local precursors, and probably are of European origin. Bowen et al. (2002) suggest an Asian origin for those groups, however, so the North Atlantic avenue to Europe (McKenna 1983a, 1983b) may not have been the sole or most important dispersal pathway at this time. Other Wao novelties include *Macro*- *cranion* (erinaceomorph lipotyphlan), *Miacis* (miacid carnivoran), and *Pachyaena*** (mesonychid), all of which are shared with Europe. Additional Wao taxa(*Apatemys**, *Palaeonictis**, and *Didymictis**) are known from the Paleocene of North America but apparently dispersed to Europe at Wao time (* = taxa known from the Paleocene of Asia). Wao taxa *Hyopsodus** and *Diacodexis* also occur in Asia (Ting 1998). In chapter 4, Wasatchian taxa, *Didelphodus*, and *Palaeosinopa** are indicated as shared with Europe. To summarize, the early Wasatchian witnessed a major overland dispersal across Holarctica, but the vectors are not always clear. Subsequently, *Homogalax* (Graybullian) is

shared with Asia at that time (Ting 1998); *Heptodon* is shared with Asia in the Lysitean (Ting 1998), so the very limited late Wasatchian Holarctic dispersals reflect European isolation relative to North America.

In the medial and later Eocene (49-36 Ma), a general cooling trend culminated in the early Oligocene with a reduction in surface Antarctic water temperatures by 10–12°C (figure 8.1) and deeper waters by 3–5°C (Ehrmann and Mackensen 1992). In Australia this is the time of maximum development of nonseasonal mesothermal rainforests, associated with global cooling (MacPhail et al. 1994), and at 46 Ma (early medial Eocene), ice-rafted debris in cores adjacent to East Antarctica indicate at least alpine glaciation with ice down to within 1000 m above sea level (Ehrmann and Mackensen 1992). In New Jersey (Browning et al. 1996), hiatuses at 48 and 46.5-44 Ma apparently are associated with increases in δ^{18} O levels, indicating glacial action and cooler sea temperatures. Sea level falls at these times are considered to have had an Antarctic glacial origin, as are sea level drops at ca. 43-41 Ma (indicated as times of glaciation, but not major sea level drops on figure 8.5). All of these would significantly predate the generally accepted date of the opening of the Drake Passage at ca. 34-36 Ma but would be approximately consistent with the evidence of Ehrmann and Mackensen (1992).

Whereas the present Rocky Mountain region was a seaway or otherwise lowland from the Cretaceous (e.g., figure 8.2) into the Paleocene, the growth and development of a continental divide are manifested by floras at least by Bridgerian time. The Green River flora (figure 8.3; ca. 47 Ma) of northwestern Colorado and adjacent areas was a woodland-savanna with affinities to seasonally dry subtropical forests of the Gulf region, in contrast to the Germer flora of Idaho (figure 8.3), which is a mixed deciduous hardwood-conifer forest with affinities to more western associations. Altitudinally zoned elements of the Green River flora indicate the presence of lake margins, swamps, and floodplains at about 300 m elevation (according to MacGinitie 1953, but see Wolfe et al. 1998 for an estimate of 2.9 km), giving way to drier, better-drained savanna oak-pine woodland, followed by broadleaved deciduous forest, overlapped with a final mixed hardwoodconiferous forest zone from 1000 m to about 1700 m. Seasonal rainfall is thought to have reached ca. 700 m (Graham 1999). According to Graham (1999) the Germer flora (ca. 46 Ma) was deposited at about 600 m (but possibly three times as high) and shares elements (Abies [fir] and Picea [spruce]) of the present western montane coniferous forest with other sites to the west (Thunder Mountain, figure 8.3), where the MAT is as low as 8.5°C at elevations of ca. 2200 m at treeline and precipitation of summer rain and light winter snow reaches 1100-1500 mm annually. Wolfe et al. (1998) indicate that the Salmon flora (figure 8.3), dated at ca. 41 Ma (and from the same Challis volcanics as the Germer flora), is estimated to have lived at elevations up to about 2 km with an MAT of 2-10°C. This elevation is compatible with the MAT for the Thunder Mountain flora, Idaho, and Wolfe et al. (1998) reconstruct paleoelevations of 2.0–2.9 km for sites ca. 48-50 m.y. old on both sides of the modern continental divide, with MATs ranging from 8.3°C on the northwest (One Mile Creek, southern British Columbia, figure 8.3) to 15-17°C on the southeast (Kisinger Lakes, western Wyoming, figure 8.3). With elements of the Green River flora (Ephedra [Mormon tea], Celtis [Hackberry], and Ocotea [Laurel]) having affinity with those from subhumid habitats more characteristic of subsequently more arid settings, both provinces record the continuing modernization of regional floras during the later Eocene.

In addition to the inauguration of a continental divide, the middle Eocene also witnessed a diversification of floral associations as compared with the earlier Eocene. Graham (1999) indicates that an important modernization of North American land plant communities begins in the medial Eocene during the initial phases of transition from greenhouse to icehouse climates (figure 8.1). In the later part of the Bridgerian (Br₃), MATs decreased somewhat (still in the range of 11–19°C; Gunnell 1997), possibly coincident with the Antarctic alpine glaciations recorded about then (figures 8.1 and 8.5), and more open wooded conditions may have prevailed. Graham (1999) describes the pollen record as indicating episodes of change about synchronous with the Antarctic alpine glaciations at about 46 and 42 Ma (figure 8.5), with the second interval recording not only the first grasses (pollen) but also the elimination of many of the previously common arborescent taxa (see also Frederiksen 1988 but use time scale calibrations of Berggren et al. 1995).

In general a semideciduous tropical dry forest occupied much of the continental interior as a reflection of reduced and more seasonally distributed rainfall than previously. The eastern coastal region (southeastern United States) experienced a middle Eocene MAT of 24°C, which decreased to about 13°C at Ellesmere Island, a gradient of 0.28°C/1° latitude (comparable to that of the Late Cretaceous but somewhat lower than for the early Eocene). This is generally comparable to the western coastal gradient, where an MAT of 27°C in northern Pacific California (Susanville, figure 8.3) decreased to 15–16°C in northern lowland Alaska (or even cooler: 12–13°C in montane Washington State; Graham 1999). In Vancouver, British Columbia, mixed conifer, paratropical rainforest, and notophyllous broadleaved forests prevailed, with more northern regions (Alaska) clothed in a polar, broadleaved deciduous forest.

Tropical rainforest occupied west coastal California and Washington in the medial Eocene. The Susanville flora reflects a coastal rainforest environment, with such conditions persisting to the end of the Eocene. In central Oregon, the Clarno flora (ca. 44 Ma) is a paratropical association (e.g., above) with only a few temperate forms, living under humid conditions that lack a coastal influence (Coast Ranges and Cascade Mountains not yet present). The upper part of the Clarno Formation (ca. 44 Ma; figure 8.3) begins the base of a succession interpreted (Bestland et al. 1997) as recording a transition in soilforming regimes that track the onset and development of more arid conditions from originally nearly tropical climates reflective of the early Eocene climatic optimum. The sequence is developed mostly in the lower part of the John Day Formation (figure 8.3), which unconformably overlies the Clarno, but the upper Clarno Formation records deeply weathered paleosols developed under a tropical to paratropical climate (Bestland et al. 1997:165) at ca. 44 Ma. Subsequently, subtropical conditions prevailed at ca. 43-42 Ma, followed by paleosols developed in the John Day Formation from ca. 40 Ma that show that subtropical to humid temperate climates obtained by 34 Ma and humid temperate to subhumid temperate conditions by 30 Ma (Bestland 2002). Bestland et al. (1997) interpret the paleosol evidence as reflecting a climatic change to drier and cooler conditions coincident with glacially controlled global cooling during the 44-30 Ma interval, comparable to the summary of Wolfe (1992, 1994b).

Middle Eocene floras of coastal southern California reflect the drying trend seen in the continental interior, with rainfall in the range of 500–1000 m annually, supporting a savannalike vegetation with an understory of shrubs and herbs rather than grasses (the first megafossil evidence of which is of Miocene age, late middle Eocene grass pollen notwithstanding; figure 8.5), and a diversity of mesic trees in gallery forests. In contrast to southeastern U.S. floras, grass pollen was not represented in the southern California associations in the late Eocene, and at the very end of the Eocene these floras show the beginning of the Madrean scrubland or chaparral, woodland, and savanna vegetation characteristic of the present arid southwestern United States and adjacent Mexico.

Although Bridgerian mammal faunas still are almost nonexistent in southern California, the climatic settings discussed here apparently set the stage for provincial differentiations found in the Uintan (below). The few taxa of late Bridgerian Clarno Nut Bed Fauna, Oregon (figures 4.1 and 8.3), show correspondence with those of the continental interior (Hanson 1996) and therefore do not illuminate mammalian response to the regional floral differentiation under way at that time, as summarized earlier in this chapter. The geographic clustering of existing Bridgerian faunas apparently leads to general discussion of faunal dynamics in a temporal rather than geographic context (Prothero and Heaton 1996; Janis et al. 1998a–1998c; Prothero 1999).

Bridgerian faunas can be contrasted with those of the Wasatchian by having the last pantodonts and the first leptochoerid artiodactyls, along with a radiation of dichobunids, a diversity of sciuravid rodents, omomyid and notharctine primates, hyaenodontid creodonts, and brontotheriids, along with oxyaenid procreodi, tillodonts, helaletid tapiroids, and hyracodontid rhinos.

Middle Eocene mammalian dispersals were generally sporadic, except for pulses in the early Bridgerian (ca. 50 Ma; Smith et al. 2003) and latest Bridgerian–early Uintan (ca. 46 Ma). Correspondence between early Bridgerian dispersals (4, figures 8.1 and 8.5) and a major sea level lowstand (Ta3) is suggested. Most Bridgerian immigrants show affinities with Asian faunas.

By the late Eocene, vegetation records an overall shift to drier forests, at least in the United States, with the climatic setting in areas east of the Rocky Mountains reflecting seasonally dry, if tropical, conditions. The generally more arid conditions in the Clarno-John Day region (but still humid-temperate) have been reviewed earlier in this chapter. Graham (1999) and Wolfe et al. (1998) suggest that segments of the Rocky Mountains and Basin and Range provinces had achieved modern elevations at that time, if not in the medial Eocene. In that context, the more northerly situated Copper Basin flora of northeast Nevada (ca. 40 Ma; figure 8.3) contrasts with the approximately coeval Florissant flora of Colorado (ca. 35 Ma; figure 8.3) to the southeast. The Copper Basin flora is a microthermal mixed deciduous-conifer association that apparently occupied a montane, lakeside setting, with an interpreted MAT of 11°C at an elevation of ca. 1200 m (MAT 10.5°C, elevation ca. 2.0 km; Wolfe et al. 1998), and rainfall estimated between ca. 1300-1500 mm annually. The Florissant flora is summarized (Graham 1999) as a stream and lake margin mesic forest with a drier evergreen oak-pine woodland on the higher ground, comparable to the dry savanna associations of western Texas and adjacent Mexico. Annual rainfall (mostly in summer, with a dry winter) is estimated at 500-635 mm, with an MAT of 18°C. Even though the Florissant has been subsequently interpreted as having an MAT 11.8°C and an elevation ca. 3.1 km (Wolfe et al. 1998, with an inferred high elevation for the southern Rocky Mountains at that time), the more southern and arid-adapted affinity of its taxa is compatible with floral and topographic diversity having been achieved by the Uintan and Duchesnean.

In addition to containing the first sespedectine erinaceomorphs; soricids; lagomorphs; eomyine rodents; muroid rodents (in North America); leptochoerine, agriochoerid, hypertragulid, and camelid artiodactyls; and hyracodontine, amynodontine, and metamynodontine rhinos, Uintan faunas are characterized by a diversity of miacoid carnivores, bunomerycine dichobunid, oromerycid tylopod, and protoceratid artiodactyls. Collectively these more selenodont forms (especially artiodactyls) apparently evolved in reflection of the transition from the previous megathermal tropical rainforests to an overall semideciduous tropical dry forest, including a mosaic of paratropical and warm temperate taxa and upland temperate forms (Graham 1999:195). As indicated at 5 in figures 8.1 and 8.5, an immigration pulse at about the Bridgerian-Uintan boundary included uintatheres, brontotheres, amynodontine and hyracodontid rhinos, and eomoropine chalicotherioids. Limited later dispersals include omomyine primates and eomoropines shared with Asia at Ui2, lagomorphs at Ui3.

Walsh (1996) summarizes the mammal faunas of the Uintan and Duchesnean of California, the Rocky Mountains, and Texas. He suggests that the two distal regions are about equally distinct relative to the Rocky Mountains region (ca. 60 percent Simpson coefficient) but even more distinct relative to each other (ca. 49 percent Simpson coefficient).1 California faunas contain a number of holdover taxa from the Bridgerian (e.g., Scenopagus, Pantolestes, Palaeictops, Pauromys, and Lophiohyus), but they are not unique to California. Antiacodon (dichobunid artiodactyl), Aethomylos ("proteutherian"), and Crypholestes (erinaceimorph) are unique to California, which, with Stockia and Washakius (and with the possible absence of otherwise common early Uintan groups such as peraceratheriine, triplopodine, and hyracodontine rhinos, isectolophid tapiroids, and bunomerycine homacodontines), appears to reflect a western facies distinct from more interior regions, but the faunas west of the Rocky Mountains are poorly known. The synopsis of floral distributions in this chapter is consistent with Walsh's (1996) finding that the later Uintan faunas of California differed (mainly at the species level; Lillegraven 1979) from those of the interior largely because of vegetational and climatic patterns. For the later Uintan, washakiine

omomyid primates apparently persisted (*Dyseolemur*), which, with the presence of ailuravine (*Eohaplomys*) and simimyid (*Simimys*) rodents and the absence of otherwise key groups such as rabbits and hypsodontid condylarths (*Hyopsodus*), continues to suggest a western facies during that time.

Duchesnean faunas continue the Uintan renovations in that the sciuravid rodents, taeniodonts, oxyaenid and limnocyonine creodonts, viverravid carnivores, microsyopid and notharctine primates, Dinocerata, helohyid and homacodontine artiodactyls, and hyrachyine rhinos are no longer present. Heliscomys is the first geomyoid rodent, Hyaenodon, Ischyrognathus, and Hemipsalodon the first hyaenodontine creodonts, Hesperocyon the first canid, and Heptacodon the first anthracothere. Selenodont artiodactyls (e.g., agriochoerid and merycoidodontine oreodonts and hypertragulids) and other advanced groups persist, and later in the Duchesnean, taxa having affinities with Chadronian faunas occur as early elements of the White River Chronofauna. In chapter 4, faunal provincialism is highlighted for the West Coast, West Texas, Gulf Coastal Plain, Great Basin, and Rocky Mountains (based mostly on rodents; Storer 1989), and this seems to be a part of the regional endemism also recognized for the Uintan as based on other mammalian groups also (Walsh 1996). This provincialism apparently does not persist in Chadronian and younger elements of the chronofauna (Storer 1989).

As far as Duchesnean dispersals are concerned (figure 8.5), *Hyaenodon* shows affinity with Europe and *Pterodon* with Europe and Asia (McKenna and Bell 2000). Leptomerycidae refers to *Hendryomeryx* (chapter 4), with potential Asian affinities (*Archaeomeryx*; Webb 1998; Webb and Taylor 1980); Anthracotheriinae is a likely Asian immigrant (Kron and Manning 1998), of which *Heptacodon* is the oldest North American representative (also chapter 4).

In the late Eocene (Chadronian), the White River Chronofauna persisted. As indicated in chapter 4, Chadronian innovations include Sciuridae, Nimravidae, Tayassuidae, and Ursidae (Baskin and Tedford 1996). Limited immigration from Asia produced the bothriodontine anthracothere *Bothriodon* (Emry et al. 1987; Kron and Manning 1999) and the amphicynodontine ursid *Parictis* (Emry et al. 1987; Hunt 1996, 1998b). The major sea level lowstand at ca. 37 Ma (Ta4; figures 8.1, 8.6) was largely unremarked by the North American indigenous fauna (*Ardynomys* being another immigrant about this time), but a coeval early phase of climatic cooling may correspond with the faunal turnover that marked the beginning of the White River Chronofauna, in the context of general increase in climatic aridity and concomitant more modern, open floral associations. The chronofaunal turnover begins in the late Duchesnean and is manifested by archaic groups such as microsyopid, adapid, and omomyine primates, ailuravine rodents, oxyaenid and mesonychid creodonts, hyopsodontid condylarths, uintatheres, and viverravid carnivores giving way to more modern elements: Leptictis (leptictid epithere), *Eutypomys** (eutypomyid castorimorph; *=but also in the Lac Pelletier Lower Fauna of the Cypress Hills, Saskatchewan [figure 8.3], which is arguably older than late Duchesnean; Storer 1996, 1998), Ischyromys (ischyromyine rodent), Pseudocylindrodon* (cylindrodontine rodent), Adjidaumo*, Yoderimys (eomyid rodents), *Hyaenodon*^{**} (creodont, ^{**}=also from early Duchesnean; chapter 4), Daphoenus** (amphicyonid carnivore), Toxotherium** (amynodontine rhino), Hyracodon** (hyracodontine rhino), Mesohippus (miohippine equid), Agriochoerus** (agriochoerid oreodont), Poabromylus,

Heteromeryx (protoceratid artiodactyls), *Eotylopus*** (oromerycid artiodactyl), *Aclistomycter*** (oreodontine oreodont), *Hendryomeryx** (leptomerycid artiodactyl), *Sinclairella** (apatemyid rodent), *Hesperocyon** (canid), *Heptacodon** (anthracotheriine artiodactyl), and hypertragulids** (Prothero and Emry 1996).

This long interval of faunal integrity began in the late Duchesnean, as seen in the Porvenir (figure 8.3) and related units (Emry et al. 1987; Prothero and Emry 1996), coincident with the dispersal of *Ardynomys* (figure 8.5) between North America and Asia (Emry and Korth 1996). A second limited Asian dispersal in the Chadronian (figure 8.6) is represented by *Patriomanis* (Gaudin and Emry 2002) and Nimravidae (Bryant 1996).

The present icehouse world is heralded by the opening of the Drake Passage and onset of the modern regime of Antarctic continental glaciation at the beginning of the Oligocene (figure 8.1). The circum-Antarctic current was established at about 34–36 Ma. In Australia, this is coeval



FIGURE 8.6 Oligocene time scale, mammal ages, and dispersal of mammalian taxa. Time, chrons, polarity, epochs, and ages after Berggren et al. (1995). Mammal ages and dispersal/taxa after chapter 5. Tb1 is time of major sea level fall. Other notes as for figure 8.4.

with the last occurrence of mesothermal–megathermal rainforests and the beginning of the dominance of *Nothofagus* as cooler climates prevail (MacPhail et al. 1994) and open forests are developed (Woodburne and Case 1996). In North America, the early Oligocene is a period of cooling and increased seasonal aridity (Graham 1999) with stable conditions reflected in the presence and persistence of the White River Chronofauna for contemporary mammals.

The Oligocene begins with the Priabonian-Rupelian boundary, at about 33.7 Ma, slightly below chron C13n and correlative with sequence boundary TA4.4 of Haq et al. (1988; Woodburne and Swisher 1995) and with oxygen isotope event Oi1 of Miller et al. (1991; Abreu et al. 1998:251), a major cooling event attributed to Antarctic glaciation. Global cooling continues during chron C13n (Brinkhuis 1994; sea surface data based on dinoflagellates, ca. 33.7 Ma; Hardenbol et al. 1998), with oxygen isotope event Oi2 (C11.1n, ca. 29.4 Ma; Abreu et al. 1998:252). In this context, sea level fluctuations from the late Eocene into the Oligocene appear to correspond to the Haq et al. (1988) intervals TA4.1-4.5, or from about 37.0 to 31.8 Ma (Hardenbol et al. 1998) as being glacially controlled. Abreu et al. (1998) continue this analysis further into the Miocene and Pliocene, but the main episode of sea level lowering concomitant with glaciation focused mainly on the Oligocene. Although oxygen isotope values fluctuate in the Miocene, consistent with glacially controlled climate and sea level, they regain the high levels of the late Oligocene only in the medial Miocene.

The modernization of paleofloras begun in the late Eocene proceeds in the Oligocene as far as ascertained from limited evidence. The late Oligocene Creede flora of southwestern Colorado (ca. 27 Ma; figure 8.3) is estimated to have lived under an MAT of ca. 4.5°C (compared with about 2°C at present) and consisted of a fir-spruce forest, a fir-pine forest, a pine-juniper forest or woodland, and a mountain mahogany chaparral community, with affinities to species in eastern and western North America and eastern Asia. Wolfe et al. (1998) indicate a paleoelevation of ca. 2.6 km for the Creede flora. Although the Creede flora is not considered to have a direct modern analog (Graham 1999), it shows that the modern montane deciduous forest continued to develop from middle Eocene forerunners in the Pacific Northwest (Washington, British Columbia) and Rocky Mountains (Green River). Prior tropical elements were absent by the Oligocene in interior North America.

The earlier Oligocene (ca. 32 Ma) Bridge Creek flora (and adjacent sites in central Oregon; same general locality as the middle Eocene Clarno flora, figure 8.3) is a tem-

perate broadleaved deciduous hardwood forest, indicating an MAT of 9-11°C, and reflects a cooler, drier, and more seasonal climate than inferred from the Clarno, possibly in part because of the early phase of Cascade Mountain elevation. Contemporaneous and later Oligocene floras of more western Oregon preserve the more humid warm temperate to temperate maritime conditions, with MATs ranging from 12–13°C (upland) to ca. 16°C (coastal). Farther northwest, cooler climates support temperate deciduous and coniferous forests (Graham 1999). The Oligocene mammalian record is biased toward that from the eastern flank of the Rocky Mountains (Montana, Wyoming) and adjacent plains (Dakotas, Nebraska), with an outlier in the Texas panhandle and another in Death Valley, California. The mammalian record thus does not yet reflect the geographic diversity seen in paleofloras of the time, so faunistics are couched mostly in temporal terms (Prothero and Heaton 1996; Janis et al. 1998a–1998c; Prothero 1999).

The mammalian record for the Orellan and Whitneyan is characterized by persistence of the White River Chronofauna, with assemblages dominated by hyaenodontids (Hyaenodon), rabbits (Archaeolagus, Gripholagomys, and Megalagus), rhinos (hyracodontine, Hyracodon; diceratheriine, Amphicaenopus, Subhyracodon, and Diceratherium; amynodontine, Metamynodon), and miohippine horses (Miohippus and Mesohippus). Oreodonts are represented by leptauchenines (Pseudocyclopideus, Hadroleptauchenia, Leptauchenia, and Pithecistes), oreodontines (Aclistomycter, Merycoidodon, Otionohyus, and Paramerycoidodon), miniochoerines (Stenopsochoerus and Miniochoerus), desmatochoerines (Prodesmatochoerus and Subdesmatochoerus), and promerycochoerines (Promesoreodon). Camelids include the poebrodontines (Poebrotherium, Paralabis, and Paratylopus) and pseudolabines (Pseudolabis), with oromerycids represented by Eotylopus, Malaquiferus, and Montanatylopus. Ruminants are represented by leptotraguline (Poabromylus and Heteromeryx) and protoceratine (Protoceras) protoceratids, the hypertragulids (Hypertragulus, Nanotragulus, and Hypisodus), and leptomerycids (Leptomeryx; Lucas 1992). Canids include the hesperocyonines (Prohesperocyon, Hesperocyon, Parenhydrocyon, Mesocyon, and Cynodesmus), the borophagine Otarocyon, the daphoenine amphicyonids (Daphoenus), and nimravids (Dinictis and Nimravus). A diverse group of rodents includes the ischyromyids (Ischyromys and Titanotheriomys), the allomyines (Prosciurus and Pelycomys), the sciurine Protosciurus, the eutypomyoid Eutypomys, an eumyid (Eumys), the eomyids Paradjidaumo and Eomys, the geomyoids Heliscomys, Tenudomys, and Proheteromys, and

the sciuravid *Pipestoneomys*. Limited mammal dispersal during the Oligocene is suggested by eumyine rodents in Or2 (*Eumys elegans*) and *Elomeryx* (Fossil Bush Local Fauna, possibly about this age; Storer 1996; Kron and Manning 1999). The carnivore *Palaeogale* (Baskin and Tedford 1996) is known from the Chadronian of North America but apparently dispersed to Eurasia in the Orellan (**6**, figure 8.5, which otherwise signals the time of the Eurasian Grand Coupure).

In chapter 6, a general similarity is noted for the late Oligocene (early Arikareean) mammal faunas from the Great Plains (and Montana) to the southwest (Great Basin), in contrast to those from the John Day region of Oregon. Among these differences is a lack of leptauchenine oreodonts and protoceratids and abundance of Entoptychus species in Oregon, along with a diversity of aplodontid rodents, a characteristic group of small hypercarnivores, the presence of gentilicameline and paratylopine camels, and persistence of White River Chronofaunal relicts. The causes of this regional endemism are unclear. The John Day region was part of a major volcanic province that, along with the rising continental divide to the east, may have provided background for these faunal differences, as could the rising Cascade Mountains evidenced by the Rujada flora (below) and relatively arid conditions indicated by the Bridge Creek flora and John Day paleosols (above). The early Arikareean faunas of the Albuquerque area, New Mexico, and the Big Bend area, Texas, also illustrate endemism relative to those of the Great Plains, as do those of the Texas Gulf Coastal Plain, which flourished under subtropical to tropical conditions that contrast with the drier upland environments envisioned for the Great Plains (chapter 6).

Faunas from the early part of the Arikareean (figure 8.6) generally include the last elements of the White River Chronofauna. Members of persisting but dwindling to outgoing lineages include cylindrodontids, heterosoricine soricids (e.g., Domnina), hesperocyonine canids (Munthe 1998), daphoenine amphicyonids (Hunt 1998a), entelodonts (Effinger 1998), anthracotheres (Kron and Manning 1998), miniochoerine oreodonts (Lander 1998), hypertragulids and leptomerycids (Webb 1998), brachydont horses, early tapirids (Colbert and Schoch 1998), hyracodontid rhinos (Prothero 1998a), and diceratheriine rhinos (Prothero 1998c). Chapter 6 identifies Geolabis, Centetodon, Domnina, Proscalops, Protosciurus, Eutypomys, Agnotocastor, Palaeocastor, Scottimus, Arikareeomys, Heliscomys, Palaeolagus, Megalagus Leptomeryx, Elomeryx, and Diceratherium annectens as among the White River relicts.

Early Arikareean faunas also record the first allomyid, mylagaulid, marmotine, and entoptychine rodents, as

well as canine (Leptocyon; Munthe 1998) and procyonid carnivores, characteristic of the Runningwater Chronofauna that begins in the late Arikareean (Webb and Opdyke 1995). Also during this interval an expansion of groups important to the Runningwater Chronofauna include beavers (Xu 1996), borophagine canids (Wang et al. 1999), mustelids (Baskin 1998), synthetocerine protoceratids (Prothero 1998b), and stenomyline camels (Honey 1998). Ar2 witnessed the major immigration of the Arikareean (7, figure 8.6), represented by erinaceids (Amphechinus and Parvericius), a brachyericine (Metechinus), an ochotonid (Gripholagomys), an aplodontid (Parallomys), an eomyid (Pseudotheridomys), and the mustelid Promartes. As indicated in chapter 6, faunas of the earlier part of the Arikareean were undergoing an incompletely documented revolution that probably was under way by about 24 Ma. By the time of the Runningwater Chronofauna of Janis et al. (1998a-1998c), in the later Arikareean, almost all remnants of the White River Chronofauna had been replaced.

NEOGENE

Shackleton et al. (2000) suggest that the age of the Oligocene–Miocene boundary is revised to 22.1 ± 0.1 Ma, 0.9 Ma younger than the usually accepted date of 23.8 \pm 1 Ma. For present purposes, the Miocene (23.8-5.3 Ma) includes the early occurrence of major phosphogenic episodes (21-20, 19-18, and 17-16 Ma) on the southeastern coast of the United States, apparently in response to changes in sea level, upwelling intensity, northward-aging Atlantic deep water, and high phosphorus burial rates possibly reflecting rapid uplift and erosion of the Himalayan-Tibetan plateau between 21 and 15 Ma (Raymo 1994; Compton and Mallinson 1996; figure 8.1 herein) and delivery of phosphorus to the North Atlantic ocean via deepwater formation in the northern Indian Ocean (Woodruff and Savin 1989), according to Mallinson and Compton (1997).

As indicated in figures 8.1 and 8.6, a period of climatic warming began in the late Oligocene at about 25 Ma and culminated in the medial Miocene climatic optimum at about 15 Ma. This interval generally witnessed a continuation of the warm temperate to subtropical conditions of the Oligocene. Erosion of the Rocky Mountains that began in the Oligocene continued to shed debris to the east in support of a diversity of stream border communities, open interfluves, and savanna–parkland environments (Hunt 1990).

332 Michael O. Woodburne

Sparse early Miocene floras record a northern and Arctic element of mixed hardwood and coniferous forests with an MAT of 11-14°, giving way in the northeastern United States (Vermont; Brandon flora, ca. 24 Ma) to a warm temperate to subtropical climate with an MAT of about 17°C (frost free). Farther south, in the Great Plains, limited evidence suggests the presence and persistence of a shrubland-savanna community including the first megafossil evidence of grasses. For the Rocky Mountains, higher elevations resulted in the persistence of a western montane forest, with streamside components of broadleaved deciduous angiosperms living under conditions that fluctuated from dry to wet in the late early Miocene, from wet to dry in the early middle Miocene, and dry to wet in the late Miocene-Pliocene (Graham 1999), apparently synchronous with the oceanic oxygen isotope record for that interval (figure 8.1). The warm temperate conditions interpreted for the west coastal Rujada flora (Oregon; figure 8.3) reflect its maritime location, but the presence of fir trees in the assemblage suggests derivation from the possibly rising Cascade Ranges to the east, contributing a rain shadow effect (Graham 1999) represented by the more arid conditions inferred from the paleosols of the Clarno-John Day region (figure 8.3), conditions that plausibly persisted into the time of the Arikareean John Day faunas as well (Bestland et al. 1997; Bestland 2002).

The initiation of extensional faulting in the Basin and Range province about 17 Ma resulted in its elevation via isostatic processes (Wolfe et al. 1997). Floras from this region (Buffalo Canyon, ca. 15.6 Ma [figure 8.3]; Eastgate, ca. 15.5 Ma; Middlegate, ca. 15.5 Ma) are considered to have lived at elevations ranging from 2.8 to 3.2 km, under an MAT of ca. 10°C, made up of a mixed conifer-deciduous hardwood forest, with drier, south-facing slopes supporting a chaparral vegetation. The more arid, subtropical influence also is recorded by the Tehachapi flora (figure 8.3; ca. 17 Ma) to the southwest, in California, even at lower elevations. The Sierra Nevada still was low at this time as well, as reflected by the ca. 21 Ma Sutro flora (mixed mesophytic broadleaved evergreen and conifer) in westernmost Nevada (figure 8.3; Graham 1999). By the end of the early Miocene, the previous tropical dry forest and notophyllous broadleaved evergreen vegetation of the middle and late Eocene had been replaced by a southern coastal tropical community, a southern deciduous forest having a pine woods and southern mixed hardwood floodplain component; an Appalachian montane coniferous forest; a shrubland-chaparral woodland, savanna, and mixed hardwood-conifer forest in the interior; and a montane coniferous forest in the northwest (Graham 1999).

As indicated in chapter 6, faunas of Hemingfordian age generally show reasonable similarity across North America, even though those of the southern Great Basin and adjacent coastal California tend to be composed of fewer taxa than Great Plains contemporaries. This includes the sharp reorganization of the Miocene Chronofauna in the second part of the Hemingfordian. The new chronofauna persists to about the Hemphillian, but its Barstovian segment shows a sharp separation of Great Basin faunas relative to those of the Great Plains (and even in Montana on the west and the Florida Gulf and East coasts). The great diversification of midcontinent lineages such as mylagauline rodents, dromomerycids, cervids, and antilocaprids, the radiation of equine horses, and other features documented in chapter 6 only marginally affect Great Basin faunas of the late Hemingfordian through Barstovian, in contrast to the Great Plains affinities seen the faunal elements of the early Clarendonian Dove Spring Formation of California. These observation may reflect the elevation of the Great Basin at about 17 Ma and its collapse by about 13 Ma as discussed by Wolfe et al. (1997).

The Runningwater Chronofauna (from late Arikareean [Ar3] through early the Hemingfordian [He1]) reflects the opening floral landscape characterized as sustaining riparian forests, woodland, park savanna by Webb et al. (1995) and Webb and Opdyke (1995). This chronofauna is characterized by derived anchitherines (Archaeohippus, Desmatippus, and Parahippus) and diceratheriine, aceratheriine, and teleoceratine rhinos (immigrants are *Menoceras* [Ar3], *Floridaceras* [He1], and Brachypotherium [He1]). Paleomustelids immigrate (Zodiolestes; Ar3) and diversify, specialized hesperocyonine canids persist, and borophagines diversify. Amphicyonine amphicyonids undergo a minor radiation, aided by immigrants Ysengrinia (Ar3) and Cynelos (Ar4). The expanding ungulate component is represented by new and diverse camelids (protolabines, miolabines, and floridatragulines), which show their greatest breadth in the Barstovian and diminish subsequently (Webb et al. 1995). Leptauchenine oreodonts persist, and ticholeptines are new. Synthetocerine protoceratids first appear. Blastomerycines (Problastomeryx, Ar4) and aletomerycine (Aletomeryx, He1) and cranioceratine dromomeryids (Barbouromeryx, Ar3) immigrate and diversify; merycodontine antilocaprids appear in the late Arikareean (Paracosoryx, Ar4) and early Hemingfordian, with the dromomerycids achieving greatest diversity in the early Barstovian, the merycodontines in the late Barstovian. Dwindling groups include entelodonts, anthracotheres, and hypertragulids, and leptauchenine, merycochoerine, and phenacocoeline oreodonts do not

survive, or barely survive, the Arikareean (Janis et al. 1998a–1998c).

Minor immigrant pulses at Ar3 and Ar4 in the late Arikareean (figure 8.7) bracket a strong (and apparently ineffectual) sea level lowstand (Tb2) and predate a major pulse at the beginning of the Hemingfordian (8, figure 8.7). As indicated in chapter 6, this contingent of immigrants is dominated by mustelids (Potamotherium, Craterogale, Leptarctus, and Miomustela) but includes a soricid (Antesorex), plesiosoricid (Plesiosorex), rabbits (Desmatolagus and Oreolagus), a castorine beaver (Euroxenomys), procyonids (Amphictis and Edaphocyon), an amphicyonid (Amphicyon), a hemicyonine (Phoberocyon), an ursid (Ursavus), aceratherine (Floridaceras) and teleoceratine (Brachypotherium) rhinos, and aletomerycine artiodactyl (Aletomeryx) and merycodont antilocaprids (Janis and Manning 1998), suggesting a variety of habitats ranging from streamside or pond through more open country settings consistent with the vegetational changes summarized earlier.

The second Hemingfordian immigration episode is contemporaneous with the beginning of the mid-Miocene climatic optimum (Flower and Kennett 1995), recorded between 17 and 15 Ma (figure 8.1); it includes the time of major radiation of North American mesodont to hypsodont equids (Hulbert and MacFadden 1991) and presumed spread of grasslands (Wang et al. 1994), and it heralds the beginning of the Clarendonian Chronofauna as used by Janis et al. (1998a–1998c), which persisted until the Hemphillian at ca. 9 Ma. After about 15 Ma, climate began to deteriorate, as reflected in floral and faunal change.

The 17–15-Ma warm interval is reflected in the eastern coastal area having a rich, warm temperate mixed mesophytic forest, with numerous conifers. The woodland– grassland vegetation of the Great Plains graded westward into a western montane coniferous forest and mixed mesophytic deciduous forest. The Pyramid flora of Nevada (15.6 Ma; figure 8.3) estimated to have lived at 2.8 km elevation and composed of a deciduous hardwood forest and floodplain association, with an MAT of 13°C (or less) and annual precipitation about 35–40 inches. The approximately coeval Mascall flora of Oregon (same site as John Day, figure 8.3) reflects a swamp cypress–deciduous forest in the lowlands and a hardwood–conifer forest in the upper slopes and probably was sited at lower eleva-



FIGURE 8.7 Early Miocene time scale, mammal ages, and dispersal of mammalian taxa. Time, chrons, polarity, epochs, and ages after Berggren et al. (1995). Mammal ages and dispersal/taxa after chapter 6. Tb2 is time of major sea level fall.

334 Michael O. Woodburne

tion than the Pyramid. The Clarkia flora of Idaho (ca. 16 Ma; figure 8.3) shows a bottomland, swamp, and riparian forest community and a drier slope forest. These and other floras of comparable age in Nevada, Oregon, and Washington typically show abundant proportions of exotic deciduous hardwoods2 that most resemble elements from modern eastern North America and Asia, whereas floras only about 1 m.y. younger either lack these exotic elements (e.g., Stewart Valley, Nevada, ca. 14.5 Ma; figure 8.3) or possess them in reduced numbers and apparently reflect the effects of decline in global temperatures and at least local rainfall that began at about 15 Ma (Graham 1999). Especially in the southern part of western North America, floras younger than 15 Ma apparently lived under regimes with less than 3.5 inches of rainfall in the summer.

The Clarendonian Chronofauna (Janis et al. 1998a-1998c) saw a diversification of the borophagines (Wang et al. 1999), neomustelids, and procyonines. Amphicyonids and hemicyonine ursids declined. Among the ungulates, many lineages were extinct, including anthracotheriids, entelodontids, most merycoidodontid oreodonts (except ticholeptines, which declined in the interval), hypertragulids, and most leptomerycids. Allomyine and promylagauline rodents, stenomyline camels, and all dromomerycini became extinct during the interval. First appearances include scalopin moles, dipodomyine rodents, castorini beavers (Hystricops), Aepycamelus (Lamini), Procamelus (Camelini), Ramoceros, Plioceros (Antilocapridae), tayassuines, and proboscideans. Equines horses begin a major radiation, composed of merychippines (Merychippus), hipparionines (Cormohipparion, Hipparion, Neohipparion, Pseudhipparion, and Nannippus), protohippines (Protohippus and Calippus), and pliohippines (Parapliohippus, Acritohippus, Heteropliohippus, and Pliohippus s.s.; Kelly 1995, 1998; Hulbert and MacFadden 1991; MacFadden 1998). Aceratherine and teloceratine rhinos persist.

The later Hemingfordian immigrant episode (**9**, figure 8.7) is dominated by mustelids (*Dinogale*, *Plionictis*, *Sthenictis*, and *Mionictis*) but also includes cricetid (*Copemys*), eomyid (*Eomys*), and sciurid (*Petauristodon*) rodents, a true felid (*Pseudaelurus*), and aceratherine (*Aphelops* and *Peraceras*) and teloceratine (*Teleoceras*) rhinos.

Climatic cooling at about 15 Ma may be linked to the modernization of global oceanic circulation. An evolutionary turnover of Pacific benthic foraminifera from about 17 to 14 Ma (Flower and Kennett 1995) is considered to reflect circulation changes of the deep oceans caused by a major expansion of the East Antarctic Ice Sheet and the spread of cooler deep ocean waters, and Flower and Kennett (1993) identify 15 Ma as the approximate date of the beginning of modern oceanic circulation, temperature conditions, and influence of the cryosphere.

15 Ma also is the time when the vegetation and climate record of northwestern Canada and Alaska suggest a decline in temperature from a continental global warm peak (White et al. 1997). The early and middle Miocene Seldovian floral stage and correlative intervals in Japan and Siberia (Volkova et al. 1986; Itoigawa and Yamanoi 1990) showed the warmest climate of the last 24 m.y. This flora was rich in tree genera now living in temperate climates of Asia and North America (Wolfe 1966; Wolfe and Tanai 1980; Leopold and Liu 1994; White and Ager 1994). The temperate flora extended northward at 15.2 Ma (White and Ager 1994), but subsequent cooling reduced highlatitude floral diversity (Wolfe et al. 1966), positively correlated with a decrease in available energy (Currie and Paquin 1987).

European evidence of climatic cooling over the continent at about 14 Ma is based on terrestrial mammal records in Spain, correlated to the global increase in δ^{18} O (Krijgsman et al. 1996). This is based on a change in rodent faunas, which show an increase in diversity of immigrant, cool-adapted northeastern taxa; this also results in a peak of new occurrences (Daams et al. 1999).

Hemicyonine bears (*Plithocyon*) and proboscideans are important immigrants at the beginning of the Barstovian (**10**, figure 8.7), with a former Barstovian indicator (*Copemys*) being recognized in the second Hemingfordian pulse (chapter 6). The Proboscidean datum of the early Barstovian apparently represents mammutids, followed by the later appearance of gomphotheriids in the later Barstovian, especially in the Great Plains and adjacent areas. In the later Barstovian (figure 8.7), other immigrants include the ochotonid rabbits *Hesperolagomys* and *Russellagus*, the erinaceids *Lanthanotherium* and *Untermannerix*, the zapodid rodent *Megasminthus*, the mustelid *Pliogale*, and the amphicyonine *Pseudocyon*.

By about 13 Ma, at about the midpoint of the duration of the Clarendonian Chronofauna, the trend toward colder and winter-dry climates resulted in a mosaic of open deciduous forest—woodland and grassland patches in the Great Plains region (Kilgore, Nebraska; figure 8.3), and intervening highlands tended to separate Great Plains floras (with affinities mainly to the east and south) from those of the Columbia Plateau. The latter tended to support a rich broadleaved deciduous forest at low to midelevations to montane woodlands, with summer-wet conditions in contrast to their southern (summer-dry) contemporaries. To the southwest of the Rocky Mountains vegetation was largely piñon pine-juniper woodland and shrubland with evergreen, oak, a depauperate western montane coniferous forest in the higher elevations, and woodland-chaparral associations in southern exposures and drier situations.

Limited immigrations define the subdivisions of the Clarendonian (figure 8.8), with the exit of *Cormohipparion* to the Old World (12, figure 8.8) forming the basis of the *Hippotherium* datum at the base of the Vallesian mammal age in that region (Woodburne 1996). Discussions in chapter 6 illustrate the faunal provincialism that besets the correlation of Arikareean through Barstovian mammal faunas from the Great Plains region to the Great Basin and Mojave Desert and the extension of key elements of the (mostly equid) fauna to the western province at the beginning of the Clarendonian. As summarized in Janis et al. (1998a–1998c), the Gulf Coastal region commonly held a distinct fauna (*Merychyus* the sole oreodont, *Prosynthetoceras* and *Floridatragulus* distinctive, and amphicyonids, canids, and antilocaprids largely absent).

The Miocene-Pliocene Chronofauna (Janis et al. 1998a-1998c) begins with the Hemphillian at ca. 9 Ma and continues through the Blancan (ca. 1.3 Ma; figure 8.9). The interval is distinctive in recording (13–14, figure 8.8) an increased communication with South America before and after the establishment of the Panamanian land bridge at ca. 3.5 Ma (Keigwin 1982). Haug et al. (2001) evaluate restricted surface water exchange between the tropical Atlantic and Pacific oceans to indicate that shoaling occurred in the Central American seaway as a result of Panamanian isthmus evolution by about 4.7 Ma. This is compatible with the increased influx of Neotropical taxa to North America during the Blancan and later, but the mammal record also shows periodic immigration of edentates in the Hemphillian (e.g., figure 8.8, with 13 and 14 generally embracing the edentate and other [boreal] dispersals from 9 to ca. 7 Ma).

The interval also witnesses at about 8–6 Ma a global increase in biomass of plants using C_4 photosynthesis as indicated by changes in carbon isotope ratios of fossil her-



FIGURE 8.8 Middle–Late Miocene time scale, mammal ages, and dispersal of mammalian taxa. Time, chrons, polarity, epochs, and ages after Berggren et al. (1995). Mammal ages and dispersal/taxa after chapter 6. Tb3 is time of major sea level fall.

336 Michael O. Woodburne



FIGURE 8.9 Pliocene–Pleistocene time scale, mammal ages, and dispersal of mammalian taxa. Time, chrons, polarity, epochs, and ages after Berggren et al. (1995). Mammal ages and dispersal/taxa after chapter 7. Cud., Cudahyan; GAI, Great American Interchange; Rex., Rexroadian; S.A., South America; Sap., Sappan; Sen., Senecan; Sher., Sheridanian.

bivore tooth enamel in Asia, Africa, and North and South America (MacFadden et al. 1994, 1996; Quade et al. 1989; Wang et al. 1994; Ojha et al. 2000). This apparently reflects a change in herbivore diet to C_4 grasses, rather than shrubs and leaves, concurrent with a mid-Hemphillian mass extinction of grazing equids and antilocaprids, browsing camelids, and gomphotheres (Webb et al. 1995). The vegetation change may be related to a decrease in atmospheric CO₂ below the threshold favored by plants using the C₂ photosynthetic pathway and concurrent increased seasonality in rainfall and lower temperatures. Raymo (1994) and Raymo and Ruddiman (1992) link atmospheric lowering of atmospheric CO₂ to increased rates of erosion since about 40 Ma, focused on the active Himalayan-Tibetan region. Garzione et al. (2000) suggest that the Tibetan Plateau achieved its current elevation as early as ca. 7 Ma and the beginning of the change to steppe conditions in Northern Hemisphere (Webb et al 1995; Webb and Opdyke 1995). The photosynthetic change is about coeval with a remarkable warming of Pacific Ocean marine climate at about 7.5–6.0 Ma (Climatic Optimum 3; Barron and Baldauf 1990; Ozawa and Tomida 1996) and was followed by the terminal Miocene bioevent in Pacific Ocean (Beu 1973), where 23 molluscan genera in New Zealand become extinct at about 5.5 Ma, probably caused by intensification of oceanic circulation around Antarctica.

As summarized by Graham (1999), overall climatic conditions for North America show increased aridity and a decrease in temperature during the final 10 m.y. of the Cenozoic Period, with a warm pulse at about 3 Ma. Elevation changes leading to the modern topography for the Coast Ranges, Sierra Nevada, Great Basin, Rocky Mountains, and Great Plains transpired during this interval. Modern deserts appear at about 5 Ma, northern boreal forests at about 4 Ma, tundra and permafrost at about 2 Ma.

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The Great Plains floras show increasing influence of grasses and prairie herbs in the interval beginning about 10 Ma, with a sparsely wooded grassland reconstructed for the Oklahoma Panhandle area at ca. 6 Ma, with about coeval sites in Nebraska (Ash Hollow) preserving remains of sedges, grasses, and borages (forget-me-not), including hackberry. Farther north (Jackson Hole, Wyoming) the Teewinot Lake flora (ca. 8 Ma; figure 8.3) is a semiarid shrubland, with riparian elements along streams, giving way to a western montane coniferous forest in higher elevations. Floras in the Great Basin and Idaho-Washington also record the late Miocene through Pliocene change from humid and summer rain conditions to those of a more semiarid dry summer regime, as does the Mt. Eden flora (ca. 5 Ma; figure 8.3) in nearly coastal California, where semiarid conditions prevailed, with rainfall at about 12-18 inches annually (Graham 1999).

In the Columbia Plateau, the late Miocene floras flourished under warm temperate (summer rain) conditions. After the Hemphillian, progressively arid (dry summer) conditions developed on the leeward side of the rising (Reiners et al. 2002) Cascade Range and Sierra Nevada, with sparse pine and conifer forests having only rare hardwoods growing in the Snake River Plain at ca. 3 Ma. Vegetation about this old in northwestern Oregon (Oak Grove; figure 8.3), in northern California (Tulelake; figure 8.3), and in northern Utah suggest temperatures 2-4°C warmer than at present, but more arid conditions, with the Utah sites suggesting a more continental climate. The Palousie Prairie (Idaho, eastern Washington, eastern Oregon) records the occurrence of grasslands here about 10 m.y. later than in the Great Plains. In coastal locations of northern California, redwood forests were maintained, with rainfall estimated at 40 inches annually, with a greater summer component and an MAT ca. 3°C warmer than now at 3-4 Ma, whereas somewhat more interior sites record a pine-Douglas fir forest near sea level with an oak-woodland on the slopes.

Janis et al. (1998a–1998c) indicate that the Miocene– Pliocene Chronofauna began when climatic cooling relative to the medial Miocene thermal maximum was well advanced. The opening of the landscape apparently was amenable to the introduction and success of a variety of bone-cracking carnivores, an increase in canid and feloid diversity, and an acme of mustelid carnivores. A dramatic decrease in the ungulate component occurred in this interval, apparently coincident with the regional effects of increased aridity as summarized earlier in this chapter. The interval saw the demise of protoceratids and oreodonts and a reduction of camelids (to camelines), with specialized diversity in a number of lineages (Alforjas and Megacamelus in the Hemphillian, Titanotylopus and Gigantocamelus in the Blancan) and the persistence of Camelops. Previously diverse antilocaprids dwindled to the extent that merycodontines were extinct and dromomeryids almost extinct by the Pliocene. However, cervids appeared in the early Blancan and persisted. Whereas browsing equids had been extirpated by the mid-Hemphillian mass extinction, browsing rhinos persisted (Aphelops and Teleoceras) at least through the age. In contrast to the survival and persistence (Astrohippus) of the ultimate monodactyl lineage leading to Equus, formerly typical grazing horses became extinct (Protohippus and Hipparion) or limited to a Gulf Coast refugium (Cormohipparion, Neohipparion, Calippus, and Pseudhipparion; Webb et al. 1995; MacFadden et al. 1999). Taxa in which the development of the preorbital fossa (presumptively housing a diverticulum of social significance) had been an important attribute (e.g., Cormohipparion) lost this feature, as also occurred independently at about the same time by various hipparionine groups in the Old World (Woodburne 1989), apparently as a result of increased hypsodonty (Webb et al. 1995). Continuing aridity apparently contributed to the demise of the shovel-tusked proboscideans by at least the Blancan, which witnessed a minor radiation of beak-jawed taxa (Rhynchotherium and derivatives, Stegomastodon, Cuvieronius), which, along with their mammutid cousin (Mammut), survived into the Pleistocene.

Edentates from South America form a major new aspect to North American faunas of Hemphillian and later times, with Pliometanastes, Thinobadistes, and Megalonyx known from Florida in the Hemphillian (chapter 7; figure 8.8). Each of these participates in the definition of subdivision of the age: Pliometanastes appears in the North American record at ca. 9 Ma, at the beginning of the Hemphillian, Thinobadistes at the medial Hemphillian (Hh2, ca. 7.3 Ma), and Megalonyx in the later Hemphillian (Hh3, ca. 6.8 Ma; figure 8.8). For Hh1, Pliometanastes is joined by Crusafontina (soricid), Lemoynea (desmanine mole), Kansasimys (eomyid), and the murids Paramicrotoscoptes and Pliotomodon. In Hh2, immigrants coeval with Thinobadistes include a variety of carnivores (Indarctos, Simocyon, Lutravus, Enhydritherium, Eomellivora, and Machairodus) and the bovid ungulate Neotragocerus. For Hh3, immigrants associated with Megalonyx are a pika (Ochotona), a murid (Prosomys), a zapodid (Pliozapus), a beaver (Castor), and a variety of carnivores (Agriotherium, Plesiogulo, and Felis).

Hh4 immigrants are wholly Holarctic and, except for the flying squirrel *Miopetaurista*, the arvicolines *Protopliophenacomys* and *Ogmodontomys*, and the ungulate *Eocoileus*, continue to favor carnivores (*Mustela*, *Trigonictis*, *Smithosinis*, *Lutra*, and *Megantereon*; chapter 7).

Except for the latter part of Hh4, the Blancan is almost the sole representative of the Pliocene in North America and, as indicated in chapter 7, the interval that continues into the Pleistocene and modern times witnessed episodic and progressive climatic deterioration. These changes were largely of global scale but also were locally driven by tectonism that eventually resulted in the present diversity of landscape and climate setting. The interval was one of frequent immigration of new taxa, apparently mostly from the American polar regions with contribution from and also influence on Holarctic Asia. In fact, it is clear that a coherent discussion of mammal age relationships is enhanced by setting aside, for now, a treatment that includes the Boreal region. Discussion in chapter 7 illuminates the presence of zoogeographic provinces, with focus on those on either side of the Rocky Mountains and those of the Gulf Coastal region. The use of mammal evolution and dispersal in correlation may be more problematic regionally across North America in the Pliocene and Pleistocene than for any other part of the mammalian record, and chapter 7 demonstrates the positive role played by applying independent age information to the mammalian stratigraphic and biochronologic framework. The importance of assessing the relationship of faunal data to independent chronologic systems is a theme on which much of this book is based.

Chapter 7 demonstrates the presence of at least six distinct episodes of immigration from the Blancan through Rancholabrean, most of which are documented by the record of arvicoline rodents. At the same time, the Neotropical influence that began in the Hemphillian culminates in the Great American Interchange (GAI, figure 8.9), with a major overland dispersal attesting to the development of the Panamanian isthmus by about 2.5 Ma. The North American fauna received mostly edentates and rodents from the Neotropics but gave in return a diversity of carnivores and ungulates.

If identifying the source of the immigrants on both sides of the Panamanian isthmus can be said to be straightforward, in that the host taxa are well known or can be readily sought, the opposite is the case for the dispersals recorded from the Late Cretaceous onward that require input from areas north of the main fossilproducing districts of the coterminous United States. This has been alluded to or mentioned directly in many chapters of this book, as has been the generally disappointing record found in the Yukon and other northern territories. Currently limited data from Ellesmere Island in the Wasatchian, from the "Arikareean" Haughton Astrobleme of the Canadian Arctic, and from the arvicoline rodent record of the Pliocene and Pleistocene (and the *Bison* problem) illustrate the tantalizing uniqueness and importance of the Boreal province to the faunal record for more equator-ward districts in North America. Perhaps a future volume will provide further enlightenment.

Another goal is to diversify the geographic coverage of North American fossil mammal sites in parity with that of the paleobotanical record, especially for the Paleogene. This, plus the improved correlation network now in place, will permit a more comprehensive appraisal than reviewed here of the mammalian response to our increasingly sophisticated understanding of the climatic and topographic evolution of the continent during the Age of Mammals. Only then will mammalian paleontologists be in a position to evaluate more precisely the role global (Prothero, 1999), as well as local, change plays in molding mammalian evolution.

ENDNOTES

- 1. Simpson coefficient is calculated as $C/N \ i^{\circ}$ 100, where C = the number of taxa being compared between two faunas and $N \ i$ = number of taxa in the smaller of the two being compared. See Simpson (1960).
- Exotic elements include *Carya* (hickory), *Diospyros* (persimmon), *Eugenia* (myrtle), *Gymnocladus* (Kentucky coffeetree), *Quercus* (oak), *Robinia* (locust), *Sophora* (mescal bean), *Ulmus* (elm), and *Zelkova* (Japanese keaki tree) (after Graham 1999:262).

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Woodburne 08 2/1//04 1:40 PM Page 340

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342 Michael O. Woodburne

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Woodburne_08 2/17/04 1:40 PM Page 344

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Plants

Aquilapollenites 24R, 318R calcareous nannofossils 89R *Celtis* 326R coccoliths 124R Coyote Creek flora 120L *Ephedra* 326R nannoplankton 133R, 134L *Normapolles* 24R, 318R *Nothofagus* 330L *Ocotea* 326R *Wodehousia spinata* 32L

Invertebrates

ammonite(s) 34L, R *Arctica islandica* 237L cephalopods 25L foraminifera(ns) 24L, 89R, 90L, 92L, 94R, 124R, 171R, 206R, 317L, 320L, R, 334L *Hoploscaphites birkelundi* 34R *H.* aff. *nicoletti* 34R *Jeletzkytes nebrascensis* 34L, R mollusca(n) 124R, 269L, 291L, 336R

Non-mammalian vertebrates

chondrichthyian(s) 92R *Glyptosaurus* 131L ray 205L shark 205L

Mammals

Aaptoryctes 55, 79R, 84L *Absarokius* 112R, 113L, 114L, R, 120R Aceratherinae 231L aceratheriine rhino(s) 332L, 333L, 334L *Achaenodon* 117L, 120R, 121L, 127R *Acheronodon* 54, 63R, 64L, 65R, 80L Acidomomys 86L, 87R Aclistomycter 119R, 129R, 329R, 330R Acmeodon 55, 71R, 73R, 75L, 76L, 79R, 81L, R, 82R Acritohippus 174L, 219R A. isonesus 178R, 188L, 189R, 190L, 192R, 199L, 206R, 207L A. quinni 174L A. stylodontus 176L, 190R A. tertius 173L, 175R Acritoparamys 86L, 87L, 88L, R, 324L A. atavus 86L Actiocyon 217R adapid primate 329L adapiform(s) (euprimates) 111R, 112R adapisoricid(s) 82L, 126L Adjidaumo 119R, 164R, 165L, 329L A. craigi 119R A. minutus 164R Adunator 58, 71R, 75L, 76L, 79R, 81L, R, 82R, 83R, 84L, R, 86L, 87L, 88L Aelurodon 172L, 195L, 197R, 215L, 217L A. aphobus 171L A. asthenostylus 171R, 176L, 177R, 190L, R A. ferox 192R, 199R A. saevus 192R A. taxoides 171L, 198L, 200L, 217L A. wheelerianus 199R A. (Strobodon) 199R A. (Strobodon) stirtoni 199R, 215R, 217L Aelurodontina 213R aelurodontine borophagine canid(s) 195L Aepycamelus 172L, 173R, 174L, 175R, 188L, 189R, 195R, 199L, 200L, 208L,

213R, 218R

A. elrodi 190R A. madisonensis 190R Aethomylos 117R, 118L Agnotocastor 188L, 189R, 205L, 211L A. praetereadens 166L A. readingi 164L agriochoerid(s) 117R, 130R, 133R, 328L, R, 329L Agriochoerus 118R, 119R, 129R, 179R, 211L Agriotherium 200R, 218R, 249R, 252L, 259R A. gregoryi 175L, 251R Aguascalientia 201L, R A. wilsoni 201R ailuravine rodent(s) 328R, 329L Alagomys 55, 86L, 87L, 324L Alcidedorbignya 93R Alces 285L, 288L A. latifrons 285R Aletodon 60, 79L, 82R, 83R, 84L, R, 86L, 87L, 88L A. gunnelli 86L, 87R aletomerycine dromomerycid(s) 332R Aletomeryx 213L A. occidentalis 176R Alforjas 218L, R, 337R Alilepus 215R, 250R A. vagus 256R, 260L allomyid, ine rodent(s) 330R, 331L, 334R Allomys 179R, 187L, R, 193L, 195R, 211L, 216L Allophaiomys 246L, 265R, 266L, R, 267L, R, 273L, R, 275L, 278R, 279R, 280L, 281L, R, 282R, 284L, 290R, 294L A. pliocoenicus 250R, 270R, 279L Alostera 28R, 32, 33, 55, 63L, R, 64L, 65R A. saskatchewanensis 28R, 33

Alphadon 30, 54, 64L, R, 64L, R, 65R, 321L A. eatoni 28R A. jasoni 28R A. wilsoni 28R alphadontid(s), alphadontine(s) (marsupial) 321L Alphagaulus 178R, 190L, R, 191L, 196L, 199L A. douglassi 191L A. pristinus 190L Alticonodontinae 23L Alticonus 61, 63R, 67R, 321R *Aluralagus* 235, 250L, 264R Alveugena 56, 63R, 67L, 321R *Alwoodia* 179R, 188R, 189L, 193L, R, 196R, 211L A. cristabrevis 191L A. harkseni 211L A. magna 211L Ambloctonus 112R amblypod(s) 132L Amebelodon 218R Amelotabes 56, 79R, 83R Amphechinus 188R, 196R, 205L, 211L Amphicaenopus 330R Amphictis 213L, 333L amphicynodontine ursid 328R Amphicyon 171R, 192R, 199L, 208L, 213L, 215L, 333L A. ingens 176L, 199R A. sinapius 171R, 175R amphicyonid(s), ine(s) 171R, 179R, 195L, 199R, 211R, 212L, 213L, R, 215L, R, 329L, 330R, 331L, 332R, 333L, 334L, R, 335L Amphicyonidae 217R Ampliconus 61, 63R, 64R, 65R, 67R Amynodon 111R, 116R, 117L, 119R, 120R, 121L, 127R, 129R, 130R amynodontine rhino(s) 328L, 329L, 330R Amynodontopsis 118R, 119L, 124R, 129R, 133R Anacodon 60, 79L, 83L, 84L, R, 86L, 87R, 112R anagalid(s) 90R Anancus 249R Anaptomorphus 113L, 114R, 120R A. westi 115L Anasazia 59, 72L, 76L Anchippodus 132R Anchippus 204L, R, 205L A. texanus 205R Anchitheriinae 217R anchitherine(s) 176L, 200L, 332R Anchitheriomys 192R, 195R, 208L, 213R, 216L Anchitherium 178R, 195R, 199L, 203R, 208L, R, 216L

A. clarencei 175L, 206R Anconodon 54, 71R, 75L, R, 76L, 79R, 80R, 81L, R Angustidens 190R Anemorhysis 112R Anisonchus 61, 62R, 63L, 67R, 70L, 72L, 73R, 75L, 76L, 78R, 79R, 80R A. sectorius 78L Ankalagon 61, 72L, 75L, 76L, 324L Ankylodon 117R Anonymus 119R A. baroni 119R Anouroneomys 218L Antecalomys 217R Antesorex 213L, 333L anthracothere 189L, 211R, 328R, 331L, 332R anthracotheriid, iine 328R, 332R Anthracotheriidae 213L Antiacodon 113L, R, 114R, 115L, 117L, R, 328L Antilocapra 288L, R A. americana 281L antilocaprid(s), artiodactyl 190R, 195L, R, 196L, 199R, 213R, 215L, 263R, 333L, 335L, 336L, 337R Antilocapridae 212L, R, 213R, 334L antilocaprine 200R, 216L, 216R, 218L, R, 219L apatemyid(s) 82L, 323R, 329R Apatemys 56, 78R, 79L, 82R, 83R, 84L, R, 86R, 87L, 88L, 114R, 116R, 119R, 133L, 325R Apatosciuravus 55, 86L, 87L, 88L, 324L Aphelops 172L, 175R, 195L, 199L, 200L, 206R, 207R, 213R, 334L, 337R A. jemezanus 200L A. mutilus 218R Apheliscus 60, 86L, 87L, 88L, 113L A. nitidus 86L, 88L Aphronorus 56, 71R, 73R, 75L, R, 76L, 79R, 81L, R, 82R A. ratatoski 78L Aplodontia 285L A. rufa 285L aplodontid(s) rodents 179L, 187L, R, 188R, 191L, 195R, 211L, 216L Aplodontidae 211L Apriculus 117R Apternodus 119R Archaeocyon 173L A. pavidus 173L Archaeohippus 176L, 192R, 195R, 199L, 203R, 204L, 208L, 212L, 216L, 332L A. blackbergi 208L A. minimus 190L A. mourningi 172L, 174L, 176L A. penultimus 173R A. stenolophus 192L A. ultimus 188L

archaeolagine(s), lagomorph 187R, 198L, 218L Archaeolagus 172R, 179R, 188R, 189L, 192L, 193R, 196R, 198R, 199L, 201L, 330R A. ennisianus 211L A. esmeraldensis 191L Archaeolambda 91R Archaeomeryx 328R Archaeotherium 161R A. coarctatum 163R A. mortoni 165L A. trippensis 197L archaic ungulates 36L, 67L Arctocyonidae 60, 62R arctocyonid(s), arctocyonine(s) 62L, 82L, 321R, 323R, 324R Arctodontomys 58, 86L, 87L, 88L, 113L Arctodus 278L A. pristinus 270L, 283R, 284L, 285L A. simus 270L, 278R, 282R arctoid(s), carnivore 199R Arctomyoides 190L Arctonasua 215L Arctostylops 60, 79L, 84L, R, 86L, 87R, 88L, 91R A. steini 120L Arctostylopida, arctostylopid(s) 91L, R, 92L, 324L Arctostylopidae 94R Ardynomys 119R, 328R, 329R Arfia 112R, 325L Arikareeomys 193R, 205L, R, 211R Armintodelphys 113L Arretotherium 189L, 197L, 204R, 211R A. acridens 189L, 204R A. fricki 189L, 192L A. leptodus 189L, 204R Artiodactyla 85R, 88L, 89R, 106L, 112R, 325L artiodactyl(s) 90L, 120R 122L, 126L, 130R, 134R, 324R, 327R, 328L, R, 329R, 333L Arvicola 246L Arvicolidae 239R Arvicolinae 239R, 245L arvicoline(s), rodent 198R, 218R, 219L, 232L, 239R, 245L, 247L, R, 249R, 250L, 252R, 253L, R, 254L, R, 258R, 261R, 262L, 265R, 276L, R, 278R, 279L, R, 281L, 292R, 293L, R, 294L, 295L, R, 338L, R Asiostylops 91L, R astrapothere(s) 92R Astrohippus 219L, 249R, 337R A. ansae 200R, 218R A. stocki 200R, 252L Atopomys 276L, 282R, 284L A. texensis 268R, 282R Aulolithomys 119R

Auraria 61, 63R, 64R, 65R Australocamelus 199L, 200L, 213L Auxontodon 118L, 133L Avunculus 56, 72L, 75L, 76L Aztlanolagus 282R A. agilis 282R Azygonyx 120L A. ancylion 120L Baioconodon 60, 62R, 63L, R, 64L, R, 65R, 67R, 69R Baiomys 200R, 219L, 261R, B. minimus 261R Baiotomeus 54, 64L, 71R, 75R, 76L, 79R, 81L, R, 82R Barbourofelis 171L, 172R, 216R, 217L, 218R B. lovei 171L, 172R, 217R B. morrisi 217R B. osborni 217L B. whitfordi 217L Barbouromeryx 187L, 196L, 212L, 213R Barylambda 57, 78R, 82R, 83R, 84L, R, 86R, 87L, 88L Bassariscus 260R B. casei 260R Bathygenys 120L, 161R, 162R Bathyopsis 114L, 115L B. fissidens 114R B. middlewsarti 115L Bathyopsoides 78R Batodon 28L, 58, 63L, R, 64L, 65R, 318R B. tenuis 28R Batodontoides 118L beaver 187R, 189L, 193L, 195L, R, 198L, 211L, 212L, 213L, R, 215L, R, 216L, 217L, R, 218L, R, 331R, 333L, 334L, 337R Beckia 217R Bemalambda 91L Bison 236, 245, 247R, 264R, 269R, 272L, 273L, 274R, 281L, 283L, 284R, 285-289, 290L, 293L, 295L B. alaksensis 287R B. alleni 287R B. antiquus 287R B. bison 287R, 288R B. b. antiquus 287R B. b. bison 287R B. b. occidentalis 287R B. latifrons 286L, 287R Bisonalveus 56, 79R, 80R, 82R Blackia 173R Blancocamelus 263L Blarina 250R, 270L, 290R blastomerycine artiodactyl(s) 332R Blastomeryx 188L, 191L, 192L, 200L, 206R, 208L, 212L, 217R B. elegans 190R B. galushai 208L

B. gemmifer 190R Blickomylus 196L, 199L, 213L Bomburia 62R Bootherium 285R B. bombifrons 285R Borophagina 213R borophagine canid(s) 171R, 176L, 177R, 187L, 190R, 195L, 196L, 198L, 199L, R, 207L, 212L, 213L, R, 215L, R, 217L, R, 218L, R, 330R, 331R, 332R, 334L Borophagina 213R Borophagini 213R Borophagus 217L, 249R, 263R, 264L, 267L, 281L, B. diversidens 244, 249R, 250L, R, 259L, 260R, 264L, 265L, 266L, R, 267L B. dudleyi 219L B. hilli 219L, 244, 250R, 256R, 258L, 264L B. littoralis 171L, 172L, R, 177L, 217L B. parvus 218R B. pugnator 218L B. secundus 203R, 218L, 219L B. solus 259R Bothriodon 328R bothriodontine anthracothere 328R Bothriostylops 91R Bouromeryx 172L, 178R, 187L, 196L, 206R, 207L, 213R, 216L B. americanus 190R B. milleri 174L Brachycrus 174L, 188L, 196L, 199R, 203R B. buwaldi 176L B. rusticus 190L brachyericine 211L *Brachyerix* 190R, 192R, 196L Brachyhyops 118R, 119R Brachylagus 236, 270R, 285L *B. idahoensis* 236, 270R, 285L Brachyops 119R, 130R, Brachypotherium 213L, 332R, 333L Brachyprotoma 236, 270R, 285L Brachypsalis 217R Brachyrhynchocyon 161R B. dodgei 161R Bretzia 261R brontothere(s), iid(s) 115L, 124R, 126L, 129R, 130R, 131R, 133L, 133R, 134L, 160L, R, 161L, R, 163R, 164L, 325L, 328L Bubodens 29, 33 B. magnus 28R, 33, 35L Bubogonia 60, 63R, 67R, 69R, 321R Buisnictis 198L, 219L bunodont artiodactyl(s) 120R bunomerycine(s) 328L Bunomeryx 117L, R, 118L Bunophorus 114L, R, 122L

Caenolambda 57, 79R, 81R, 82R Caenopus 133R, 189L Calippus 192R, 195L, 197R, 202R, 203R, 215L, 218R, 251L, 334L, 337R C. cerasinus 217R C. hondurensis 203R C. proplacidus, 207L C. (Grammohippus) martini, 198L Calomys 198R, 200R, 261R, 262L C. (Bensonomys) 198R, 200R, 218R, 261R C. (Bensonomys) arizonae 262L camel(s), artiocactyl, 166L, 172L, 173R, 175L, 187L, 188L, 189R, 190R, 193L, 195L, R, 196L, 197L, 198R, 199L, R, 200L, R, 201L, R, 202L, R, 211L, R, 212L, 213L, 217R, 219L, 260R, 263L, 282L, 331L, R, 334L Camelidae 117R, 213R camelid(s) 117R, 118L, 130R, 173L, 195L, 199L, 201L, 202R, 206L, 207L, 211R, 213R, 215L, 261R, 282R, 328L, 330R, 332R, 336L, 337R Camelops 249R, 265R, 278L, R, 280R, 281L, 282L, R, 284R, 286L, R, 288L, 337R C. hesternus 288L, R C. minidokae 281L Campestrallomys 165L C. annectens 165L canine(s), carnivore 195L, 196R, 199R, 331R Canis 235, 249R, 270R, 290R C. armbrusteri 236, 270L, 278R, 280L, 282L, R, 283L, R, 284L C. dirus 236, 281L, R, 284R, 285L, 288L C. edwardii 250R, 259R, 268L, 270R, C. latrans 236, 270R, 283L, 285L, 288L C. lepophagus 250L, 256R, 258L, 263L, 265L, R, 266L, R, 267L, *C. lupus* 236, 270R, 283R, 285L, 288L Cantius 90L, 112R, 113L, 114R, 115L, 120L, 121L, 132R, 325L Capacikala 211L C. gradatus 211L Capatanka 211L C. cankpeopi 211L Caprini 260R Capromeryx 256R, 278L, R, 282L C. arizonensis 268L Carcinodon 60, 62R, 63R, 67R, 69R, 321R Carnivora 57, 91L, 171L carnivoran 91L, 279L, 284R, 325R carnivore(s) 82L, 92L, 134L, 190L, 196R, 198R, 291R, 202R, 205R, 216R, 218L, 324R, 328L, R, 329L, 331L, R, 337L, R, 338L

canid(s), 118L, 171L, 173L, 176L, 179L, 190R, 195L, 196L, 198L, 199R, 200R, 205L, 211L, 212L, 213L, R, 215L, R, 217L, R, 218L, R, 219L, 252L, 328R, 329R, 330R, 331L, R, 332R, 335L, 337L Canidae 171L, 202R Canini 217R, 218L Carpocristes 59, 79R, 83R, 84L Carpocyon 195L, 199R, 215L, 219L C. compressus 178L, 197R C. robustus 217L Carpodaptes 59, 73L, 79R, 80R, 81R, 82R, 83R, 84L Carpolestes 59, 79L, 84L, R, 85R, 86L, 87L, 88L C. nigridens, 86L carpolestid(s) 59, 75L, 82L, 323R, 324L Carpomegodon 59, 83R Carsioptychus 62R Castor 218R, 261R, 337R C. californicus 258L castorid (ine) beaver(s) 190R, 333L, 334L castorimorph(s) 329L Castoroides 244, 283R C. ohioensis 281R Catopsalis 54, 63L, 64L, 65R, 67R, 70L, 71R, 72L, 73R, 75L, R, 76L, 79R, 81L, R, 82R, 83L, 321R, Cedrocherus 58, 79R, 82R Cedromus 164R, 166L C. wardi 164R C. wilsoni 166L Centetodon 116L, 119R, 129R, 192L, 193R, 205L, R, 211R C. marginalis 165L C. chadronensis 162R Cephalogale 198R Ceratogaulus 215L C. hatcheri 218R Ceratomeryx 249R cervid(s) 175L, 178L, 207R, 251L, 253L, 261R, 332R, 337R Cervus 249R C. canadensis 288L Cete 61, 62R Ceutholestes 58, 86L, 87L, 88L Chaenohyus 211L Chadrolagus 163L C. emryi 163L Chalicomomys 58, 86L, 87L, 88L, R chalicothere(s), oid(s) 195R, 196L, 211R, 328L Chalicotheriidae 216L Chasmaporthetes 235, 251L, 253L C. johnstoni 267L C. ossifragus 268L Chipetaia 117R Chiromyoides 58, 79L, 82R, 83R, 84L, 86L, 87L, R

C. caesor 83R C. major 87R C. minor 82R C. potior 84L Choeroclaenus 60, 63R, 67R, 69R, 321L Chriacus 60, 62R, 63L, 67R, 70L, 71R, 72L, 73R, 75L, 76L, 79R, 81L, R, 82R, 83R, 84L, 86R, 87L, 88L, 321R Chumashius 119R C. balchi 119R *Cimexomys* 23L, 29, 33, 54, 63R, 64L, 65R, 69R C. gregoryi 29 C. judithae 29 C. minor 28R, 29, 33 Cimolestes 31, 33, 56, 63R, 65L, R, 67R, 69R, 92R C. cerberoides 28R, 31, 33 C. incisus 28R, 31, 33 C. magnus 28R, 31, 33 C. propalaeoryctoides 28R, 31, 33 C. stirtoni 28R, 31, 33 cimolestid(s), cimolestan 64L, 92R, 318R, 321L, R, 323R Cimolodon 54, 63R, 64L, R, 65R, 67R, 69R cimolodontid (multituberculate) 318R Cimolomyidae, cimolomyid(s) 23R, 28R, 29, 33 Cimolomys 28R, 29, 54, 63L, R, 64L, R, 65R C. clarki 24R, 29 C. gracilis 28R, 29, 33 C. millensis 29 C. trochuus 28R, 29, 33 Cimolodontidae, cimolodontid(s) 23L, R, 29, 33 Claenodon 60, 71R, 75L, 78R, 79R, 81L, R, 82R, 83R, 84L Clemensodon 28R C. megaloba 28R Clethrionomys 236, 245, 275L, R, 276L, 278R, 279R, 280L, 285L *Colodon* 117R, 118L, 121L, 133L, R *Colpoclaenus* 60, 71R, 75L, R, 76L, 79R, 81L, R, 82R Comancheomys 198L Conacodon 61, 62R, 65R, 66R, 67R, 70L, 72L, 74L, 75L, 76L, 79R, 81L, R, 82R, 321R Conepatus 236, 270R, 285L condylarth(s, -ran) 62L, R, 71L, 86L, R, 92L, R, 132L, 133R, 324L, R, 329L Condylarthra 60, 62L, 85L, 93R *Conoryctella* 56, 73R, 74R, 75L Conoryctes 56, 72L, 75L, 76L Copecion 61, 79R, 82R Copedelphys 165L C. stevensoni 165L Copelemur 112R

Copemys 175R, 192R, 200R, 206R, 207L, 213R, 214R, 215L, 262L, 334L, R C. dentalis 174L C. kelloggae 191R C. lindsavi 198L C. loxodon 199R C. nebrascensis 190R C. russelli 177L Coriphagus 56, 76L, 79R, 80R Cormocyon 212L C. copei 205R Cormohipparion 195L, 203L, 207L, 208L, 334L, 337R C. occidentale 172L, 177R, 203R, 217L C. emsliei, 207R, 219L, 267R C. paniense 197R C. quinni 191R, 203L Coryphodon 57, 85L, R, 86L, 87L, 88L, 90L, R, 91R, 107R, 112R, 113L, R, 114L, R, 120L, 121L, 129L, 130R, 132R, 134L, 324L Coryphodontidae 92L Cosomys 246L, 250L C. primus 246, 255L, 258L, 259R C. sawrockensis 246, 250L, 254L Cosoryx 177R, 197R, 200L, 215L, 217R Cranioceras 172L, R, 197R, 217L, R C. teres 200L cranioceratine dromomerycid, 172L, 174L, 332R Craseops 117R, 118L Craterogale 213L, 333L creodont(s) 82L, 92L, 122L, 324R, 327R, 328R, 329L Creodonta 57, 62L, R, 106L cricetid (s), rodent 187R, 190R, 192L, 198L, R, 214R, 215R, 217R, 218R, 334L Cridetidae 239R cricetine(s), rodent 175L, 211R, 213R, 217R, 218R, 219L cricetodontine murid(s), rodent 218L Cromeromys 246, 275R Crucimys 192L, 211R Crusafontina 218L Crypholestes 117R, 123R, 328L *Cseria* 246, 250L C. parkeri 246, 250L Cuvamalagus 173R Cupidinimus 175L, 188L, 190R, 191R, 198R, 213L C. avawatzensis 177L C. nebrascensis 191R C. tertius 177L C. whitlocki 191R Cuvieronius 260R, 263L, 280L, R, 281R, 282L, 337R cylindrodontid(s), cylindrodontine(s) 324R, 329L, 331L Cynarctina 213R cynarctine borophagine canid(s) 195L

Cynarctoides 176L, 196L, 198R, 199L, R C. lemur 205R *Cynarctus* 176L, 195L, 215L C. crucidens 217L C. marylandica 207R C. saxatilis 215R C. voorhiesi 217L Cynelos 208L, 212L Cynomyoides 190R Cynorca 204R, 205L, R, 206R, 211R, 215L C. occidentale 174L C. proterva 207R C. sociale 208L Cynodesmus 188R, 189R, 211L, 330L C. martini 211L C. thooides 166L *Cynomys* 279R, 281R, 290R C. gunnisoni 236, 270R, 285L C. ludovicianus 236, 270R, 285L, 288L Cyriacotheriuim 57, 82R, 83R, 84L, R, 86L, 88L Daeodon 208R D. leidyanum 208R Daemonelix 212L Daphoenictis 120L D. tedfordi 162R Daphoenocyon 120L, 161R Daphoenodon 198R, 204R, 205R, 206L, 211R, 212L D. notionastes 204L, R, 205R, 206L D. superbus 204R daphoenine amphicyonid(s) 331L Daphoenus 119R, 329L, 330R Dasypus 268R D. bellus 268L, 282R Delahomeryx 201L Deltatherium 57, 70L, 72L, R, 75L, 91R, 324L Deltatheridium 28R, 30, 33 dermopteran 120L, 323R desmanine mole(s), insectivore 218L Desmatippus 178R, 191L, 212L, 215L, 332R D. avus 172L D. crenidens 189R desmatochoerine oreodont(s) 330R Desmatochoerus 197L, 212L D. leidyi 191L D. megalodon 171R, 173L, 179R, 189L, 193R, 196R, 197L Desmatoclaenus 60, 63L, 67R, 70L, 72L, 73R, 75L, 76L, 79R, 81L, R, 321R Desmatolagus 132R, 192L, 196R, 213L, 333L D. schizopetrus 196L Desmocyon 212L, 213L D. thomsoni 199L Deuterogonodon 60, 72L, 75L, 76L

Diacodexis 112R, 113L, 114L, R, 120L, 131R, 325L Diacodon 55, 58, 63L, 69R, 71R, 72L, 74L, 75L, 76L, 79R, 81L, R, 82R, 83R, 84L, R, 86R, 87R, 88L, R, 112R diceratheriine rhino(s) 330R, 331L, 332R Diceratherium 166L, 173L, 179R, 188R, 192L, 193R, 197L, 198R, 203R, 204L, R, 208R, 212L, 330R D. annectens 204L, R D. armatum 204R D. matutinum 208R D. tridactylum 166L dichobunid(s) (artiodatcyl) 327R, 328L, Dicrostonyx 276R, 290R Didelphis 236, 270R, 282R, 285L D. virginiana 283R Didelphodon 25L, 28R, 31, 33, 55, 63L, R, 64L, 65R, 321L D. coyi 31 D. padanicus 31, 33 D. vorax 31, 33 Didelphodus 112R, 119R, 133L, 325R Didymictis 57, 71R, 79L, 84L, R, 86L, R, 87L, 88L, 112R, 114L, R, 325R D. vancleaveae 114R Dillerlemur 59, 79L, 84L, R, 86R, 87L, 88L Dilophodon 114R, 117R, 120R *Dinictis* 166L, 179R, 330R D. felina 163L Dinogale 213R, 334L Dinohippus 171L, 178L, 200L, 217L, 219L, 249R, 251L, 259L, R, 260R D. interpolatus 200R, 218R D. leidyanus 218R D. mexicanus 200R, 219L, 252L D. osborni 175L, 251R Dinohyus 204R, 211L D. hollandi 175L D. minimus 197L Diplacodon 117L, 118L, 130R *Diplobunops* 117R, 118L, 119R, 133R, 134L dipodomyine rodent(s) 334L Dipodomys 235, 244, 250L, 261L, 290R D. gidlevi 260R D. hibbardi 265R Dipoides 218L, 251L D. rexroadensis 235, 244, 250L, 256R, 266L D. stirtoni 218L D. williamsi 200R D. wilsoni 265L Diprionomys 191L Dipsalodon 57, 79L, 84L, 86L, 87R, 88L Dipsaladictides 57, 86L, 87L, 88L Dissacus 61, 71R, 74R, 75L, 76L, 81L, R, 82R, 83R, 84L, R, 86L, 87L, 88L, 131R, 324L D. praenuntius 86L, 88L

Dinocerata 91R, 94R, 117R, 324L, 328R dinoceratan(s) 92L dinosaur (s) 21R, 24R, 26R, 28L, 35R, 36R, 37L, R, 64R, 93R dog 195L Dolichorhinus 116L, R, 117L, R, 127R Dolomys 253R, 255L Domnina 118L, 192R, 193R Domninoides 190R, 198L Dorraletes 60, 79R, 82R, 83R, 84L Downsimus 188R, 192L Draconodus 59, 72L, 73R Dracontolestes 59, 72L, 73R Drepanomeryx 215L dromomerycid(s), artiodactyl 172L, 173R, 174L, 175L, 189R, 190R, 192L, 195L, R, 196L, 199R, 207L, 208L, 212L, 213L, R, 215L, 216L, 218R, 332R Dromomerycidae 212L, 218R Dromomeryx 178R, 191L, 195R, 213R, 216L D. borealis 189R, 190R D. pawniensis 197R Duchesneodus 118R, 119L, 125L, 126L, 129R, 133L, R D. uintensis 124L, 126L D. primitivus 133L Duchesnehippus 118R D. intermedius 118R, 133R dugongid(s) 205L Dyseohyus 201R, 215L Dyseolemur 117L, 118L, 124L, 328R Dyseotylopus 174R Earendil 62R Ecclesimus 165L E. tenuiceps 165L Ectocion 44L, 61, 73L, 77R, 80R, 81R, 82R, 84L, R, 85R, 86L, R, 88L, 112R, 113L, 114R, 122L, 131R E. osbornianus 86L E. parvus 133R Ectoconus 61, 62R, 63R, 65L, R, 66L, R, 67R, 321R Ectoganus 56, 79R, 83R, 84L, R, 86R, 87L, 88L, 112R Ectopocynus 166L E. antiquus 166L Ectypodus 54, 63L, 66R, 67R, 70L, 72L, 74L, 75L, 76L, 78R, 79R, 81R, 82R, 83R, 84L, R, 86L, R, 87L, 88L, 321R E. szalayi 78L Edaphocyon 213L, 215L, 333L Edentata 91R, 218L, 324L *Ekgmowechasala* 211L Elephas 282R Ellipsodon 60, 62R, 63L, 67R, 70L, 72L, 74L, 75L, 321R Elomeryx 192L, 331L E. armatus 173L

Elpidophorus 59, 76L, 79R, 81L, R, 82R, 83L Elphidotarsius 59, 71R, 76L, 79R, 81L, R, 82R Enhydritherium 218L *Enhydrocyon* 197L, 211L, 291L E. pahinsintewakpa 196R, 205L, 211L entelodont(s), artiodactyl 192L, 195L, 197L, 211L, R, 332R, 334L Entelodontidae 213L Entomolestes 58, 79R, 83L, 84L, R, 86R, 87R, 114R entoptychine 205L, 211L, R, 212L, 331L *Entoptychus* 179R, 187L, R, 211R E. basilaris 187R E. fieldsi 187R E. grandiplanus 193R E. sheppardi 187R *Eobasileus* 116R, 117L, R, 127R Eocoileus 219L E. gentryorum, 207R, 251L Eoconodon 61, 62R, 63R, 65L, R, 67R, 70L Eodelphis 23R, 31 E. browni 31 E. cutleri 31 Eoeumys 165L *Eohaplomys* 117L, 118L, 123R, 328R Eomellivora 218L eomoropine chalicothere(s) 328L Eomoropus 117R, 127R *Eomys* 173R, 213R, 330R, 334L eomyid(s), eomyine(s) rodent 118L, 120R, 198L, 205L, 211L, 213R, 215R, 217R, 218L, R, 328L, 329L, 330R, 331R, 334L, 337R Eomyidae 116L Eotitanops 112R, 131R, 134R E. borealis 114R E. minimus 114R Eotitanotherium 118L Eotylopus 124R, 163R, 329R, 330R E. reedi 163R *Epicyon* 172R, 207L, 217L E. aphobus 177L E. haydeni 177L, 200L, R, 218L E. saevus 217L Epihippus 116R, 117R, 118L, 120R, 121L, 130L, 133L, R E. gracilis 129R Epitriplopus 117R, 118L Eporeodon 179R, 212L E. thurstoni 173L equid(s), perissodactyl 191R, 196L, 202R, 203L, 208L, 211R, 212L, 213L, 215L, 216L, 217L, R, 218L, R, 219L, 325L, 329L, 333R, 335L, 336L, 337R Equidae 192R Equinae 213R

equine(s) 178R, 194R, 202L, 332R, 334L Equini 213R Equus, 178L, 219L, 246R, 249R, 252L, 256R, 259L, 262L, 278L, 280L, R, 281L, 282R, 283L, 284R, 286L, 337R E. bautistensis 278R E. calobatus 262R, 280L, 281L E. conversidens 264R, 282R, 288L E. cumminsii 262L, R E. francescana 246L E. giganteus 260L, 288L E. idahoensis 246R, 260L, 263R E. niobrarensis 288L E. phlegon 246R E. scotti 262R, 263L, 271L, 279R, 280L, 281L, R, 282L E. simplicidens 246R, 249R, 258L, 260L, R, 262L, 263L, R, 264L, 266L, 267L E. (Asinus) 261R E. (Dolichohippus) 261R, 263R, 264L E. (Dolichohippus) simplicidens 249R, 256R, 263L, 267L, 282L E. (Equus) 259L, 264L, 278L E. (Hemionus) 260R Eremotherium 267R E. eomigrans 267R Erethizon 259R, 269L E. cascoensis 259R E. dorsatum 283R, 288L E. stirtoni 259L erinaceid(s), insectivore 120R, 189R, 196L, 211L, 216L, 217R, 331R, 334R erinaceomorph 323R, 325R Erinaceidae 217R Ernanodon 91R Ernanodontidae (?Edentata) 91R, 324L Escatepos 62R Escavadodon 56, 72L, 76L Essonodon 28L, R, 29, 33, 36R, 54, 63L, R, 64L, 65R E. browni 29, 33 Esteslestes 131R E. ensis 131R esthonychid 133R Esthonyx 57, 79R, 84R, 85R, 86R, 87L, 88L, 112R, 114L, R, 131R, 324L E. ancylion 86L, R, 87R, 88L E. grangeri 86R, 88L E. xenicus 86L, R, 87R Eubelodon 217L Eucastor 195L, 215R, 217R E. dividerus 217L E. planus 198L, 217L E. tortus 199R, 215R Euceratherium 236, 245, 259L, 260L, 270R, 278L, 285L E. collinum 260L

Eucosmodon 54, 62L, 67R, 70L, 71R, 72L, 73R, 75L, 76L, 79R, 80R eucosmodontid(s) (multituberculate) 318R, 321L, 323L Eucyon 217R *E. davisi* 200R, 218L Eudaemonema 59, 71R, 75L, 76L, 81L, R, 82R Euhapsis 189L, 212L E. platyceps 194L eumyid rodent(s) 330R Eumys 166R, 189R, 211L, 330R E. brachyodus 166L E. elegans 164R, 331L E. parvidens 164R *Euoplocyon* 176L, 213L, 215L euprimate(s) 111R, 112R, 122L Euroxenomys 190R, 333L Eusmilus 211L E. cerebralis 166L, 173L Eutheria, eutherian(s) 23L, 24R, 28L, 31, 33, 37R eutypomyid rodent(s) 329L Eutypomyidae 211R Eutypomys 119R, 165L, 188R, 192L, 196R, 329L, 330R, 331L E. acares 119R E. obliquidens 119R E. magnus 163L E. thomsoni 164R Fanimus 211R felid(s), feloid (s), carnivore 195L, 199L, 202L, 217R, 218L, R, 334L, 337L Felidae 202R, 213R Felis 218R, 249R, 260R, 338L *F. concolor* 236, 285L F. lacustris 267L F. rexroadensis 251L florentiamyid 211L, R, 212L florentiamyine 213L Florentiamys 211R Floresomys 131R F. guanajuatoensis 131R Floridaceras 213L, 332R, 333L Floridachoerus 213L floridatragulid(s), artiodactyl 201R Floridatragulus 213L, 335L Fossodontia 188R Fossorcastor 196R, 197L, 212L F. brachyceps 211L F. fossor 211L, 212L fox 198L Fractinus 54, 80R Franimys 55, 86L, 87R, 88R Frictops 163L F. emryi 163L

Galbreathia 190R, 196L, 215L

Gallolestes 32, 37R G. agujaensis 32 G. pachymandibularis 32 Galushamvs 218R Gelastops 56, 71L, 75L, 76L, 79R, 81L, R, 82R G. joni 78L gelocid(s), artiodactyl 200L, 207R, 216L, R Gelocidae 219L Gentilicamelus 187L, 205L, 211R G. sternbergi 211R geolabidid(s) 126L Geolabididae 211R Geolabis 196R geomyid rodent 190R, 191L, 217R, 218L, R geomyoid rodent (s) 179L, 196L, 198L, 203R, 215R, 328R, 330R Geomys 262L, 262R, 265L, R, 279R, 281R, G. bursarius 283L G. minor 252L G. pinetis 283L, R G. tobinensis 266R, 281R, 282L, R G. (Nerterogeomys) minor 262L G. (Nerterogeomys) persimilis 261R, 262L G. (Nerterogeomys) paenebursarius 262R Geringia 192L, 211R Germanomys 254R Gigantocamelus 263L, R, 267L, 337R G. spatula 260L, 266L Gillisonchus 62R glasbiid(s) (marsupial) 321L Glasbius 28L, R, 30, 33, 37L, 55, 63L, R, 64L, 65R, 318R, 321L G. intricatus 28R, 30, 33 G. twitchelli 28R. 30, 33 Glossotherium 249R, 261R, 264L, 268R G. chapadmalense 235, 244, 246R, 247L, 250L, 262L, 267R G. garbanii 264L glyptodont(s) (edentate) 249R, 267L Glyptotherium 235, 244, 250R, 253L, 261R, 263L, R, 264L, 268R, 285L G. arizonae 261L, 267R, 271L *G. texanum* 263R, 266R gomphothere 202R, 203L, 207L, 218R gomphotheriid(s) 176L, 195L, 197R, 200L, 202R, 203L, 214L, R, 215L, R, 217L, R Gomphotheriidae 215R Gomphotherium 174L, 197R, 202R, 203L, 214R, 219L G. calvertensis 207L, R, 208L G. obscurum 200L G. productum 200L gondwanathere(s) 92R

Goniacodon 61, 62R, 63L, 69R, 72L, 73R, 76L, 323R Goniodontomys 218L Grangeria 117R Grangerimus 173L Gregorymys 173L, 189L, 193R, 196R, 197L, 211R G. montanensis 189L Gripholagomys 189L, 196R, 211L, 212L, 331R *Griphomys* 117R, 118L, 119R Guanajuatomys 132L G. hibbardi 132L Guildayomys 250L, 267L, 290R gypsonictopid(s) 318R Gypsonictops 31, 33 G. clemensi 31 G. hypoconus 28R, 33 G. illuminatus 28R, 33 G. lewisi 31 Hadroleptauchenia 330R Hapalodectes 114R Haplaletes 60, 63L, 69R, 72L, 74L, 75L, 76L, 79R, 81L, R, 82R, 83R, 84L, 323R Haploconus, 61, 62R, 63L, 67R, 70L, 71R, 72L, 75L, 76L, 321R Haplohippus 119L, 133R Haplolambda 57, 79R, 83L, 84L, R, 86L, 87L Haplomylus 60, 85L, 86L, 87L, 88L, 90L, 113L, 121L, 122L, 132R H. simpsoni 86R, 88L H. speirianus 120R, 133R Harpagolestes 114R, 119R, 129R Harrymys 189R, 196L hedgehog 190R, 198L, 215R Helaletes 113R, 114R, 120R, 134R helaletid(s) 325L, 327R Heliscomys 119R, 165L, 192L, 196R, 205L, 328R, 330R H. mcgrewi 165L H. vetus 165L helohyid artiodactyl(s) 328R *Helohyus* 114L, 116L, 117R, 122R, 129R Hemiacodon 114R, 116L, R, 117L, R, 127R, 128R Hemiauchenia 178L, 198L, 200L, R, 249R, 252L, 256R, 260L, R, 278L, R, 280R H. blancoensis 260L, 262L, 263L, R, 267L, R H. macrocephala 268L, 288L Hemicyon 192R, 199R, 208L, 217R H. ursinus 199R Hemicyon (Plithocyon) 176L H. (P). barstowensis 176L Hemicyon (Phoberocyon), 208L, 213L, 333L

Hemicyonidae 213L hemicyonine 214R, 215L, 333L, 334L, R Hemipsalodon 119R, 133R, 328R H. grandis 130R Hemithlaeus 61, 62L, 63R, 65R, 66R, 67R, 69L, 321R Hendryomeryx 119R, 120R, 129R, 328R, 329R Heptacodon 120L, 133L, 328R, 329R H. pellionis 119R Heptodon 113L, 114R, 122L, 128L, 326L herpetotheriine(s) 324R Herpetotherium 116L, R, 165L H. fugax 165L Hesperhys, 187L, 208L, 212L H. antiquus 208R Hesperocamelus 174L, 176R H. alexandrae 174L Hesperocyon 119R, 133L, 166R, 211L, 328R, 329R, 330R H. coloradensis 165L Hesperocyoninae 215L hesperocyonine canid(s) 195L, 199R, 211L, 330R, 331L Hesperogaulus 215L Hesperolagomys 192R, 199R, 215R, 217R, 334R Hesperolemur 115L, 117L Hesperoscalops 198L, 218R H. mcgrewi 251L Hessolestes 119R Heteromeryx 119R, 329R, 330R heteromyid(s) 190R, 198R, 201R, 215L, 218R heteromyine(s), rodent 189R Heteropliohippus 334L heterosoricine(s), shrew 188R, 192R, 331L Hexameryx 219L Hexobelomeryx 200R, 252L Hexacodus 113L Hibbardomys 250L, 290R H. marthae 267L Hidrosotherium 119L, R Hitonkala 211R Hipparion 192R, 215L, 218R, 334L, 337R H. forcei 172R, 177L, 217R H. plicatile 203R H. sanfondensis 199R H. shirleyi 202R H. tehonense 172L, 177L, 198L, 217L hipparionine(s), perissodactyl 191R, 202L, R, 219L, 334R, 337R Hipparionini 213R Hippidion 218L Hippotherium 335L H. peninsulatum 246R H. speciosum 199R Holmesina 235, 250R, 264R, 268R, 270R, 290R

Holmesina (continued) H. floridanus 267R, 268L, R H. septentrionalis 282R, 283R Homacodon 114L H. vagans 115L homacodontine dichobunid(s) 328L, R Homo 236, 285L H. sapiens 236, 285L Homogalax 112R, 122L, 130L, 132R, 325R H. protapirinus 113L, 132L Homotherium 235, 250R, 270R, 278R, 282L H. serum 278R, 283L Hoplictis 217R Hoplophoneus 163L, R, 164R, 166L H. dakotensis 166L H. mentalis 163L, R H. occidentalis 164R horse(s) 166L, 171L, R, 173R, 174L, R, 175L, 176L, 177L, 178L, R, 187R, 188L, 189R, 190L, R, 193L, 194R, 195L, R, 197L, R, 198L, 199L, R, 200L, 201R, 202L, R, 205L, 207L, 208L, 212L, 213R, 215R, 218L, R, 219L, 246L, 252L, 258L, 260R, 262R, 264L, 265L, 281L, R Huerfanodon 56, 72L, 75L Hyaenodon 118R, 129R, 130R, 162R, 163L, 165L, 166L, 174R, 211L, 328R, 329L, 330R H. brevirostris 166L H. crucians 165L H. horridus 166L H. megalodon 163L H. microdon 163L H. montanus 162R hyaenid 263R hyaenodontid(s) ine(s) 74R, 90L, 106L, 122L, 325L, 327R, 328R Hyaenodontidae 89R, 112R Hylomeryx 117, 118L hyopsodontid(s) 132L, 133R, 321R, 323L, R, 324L, R, 329L Hyopsodus 60, 86L, 88L, 112R, 113L, 114R, 120L, 121L, 122R, 129R, 131R, 325R, 328R *H. lepidus* 115L, 128R H. lovei 120R H. paulus 120R H. powellianus 130R hypertragulid(s) 211L, 212L, 328L, R, 330R, 331L, 332R, 334L Hypertragulus 129R, 162L, 164L, R, 179R, 211L, 212L, 330R H. calcaratus 162L, 164L, R, 173L H. hesperus 172L H. (Allomeryx) planiceps 211L Hypisodus 120L, 211L, 330R hypocarnivore (ous), 187L Hypohippus 178R, 192L, 196L, 199L, 200L, 213L, 217R

H. affinus 207L H. equinus 189R H. osborni 172L, 188L, 190R, 192R, 197R H. pertinax 197R Hypolagus 173R, 190R, 191L, 199R, 213R, 235, 244, 250R, 256R, 258R, 259R, 266R, 281L H. edensis 252L, 256R, 260R H. furlongi 256R, 260L, 265R H. gidleyi 178L, 256R, 258R, 262R H. limnetus 258L H. mexicanus 264L H. regalis 267L H. ringoldensis 252L, 260R H. tedfordi 252L, 260R H. vetus 198L, 218L, 258L, 264L, 256L Hypsiops 179R, 211R, 212L H. brachymelis 211R H. erythroceps 197L H. latidens 197L hyrachyine rhino(s) 328R Hyrachyus 112L, 113R, 114L, R, 116L, 117L, R, 120R, 122R, 129R, 133R, 134R H. eximius 127R Hyracodon 118R, 119R, 211L, 329L H. leidyanus 166L H. primus 119R hyracodontid, ine, rhino(s) 130R, 325L, 327R, 328L, 329L, 330R Hyracotherium 112R, 113L, R, 114R, 121L, 129L, 130R, 131R, 132R, 325L Hystricops 217R, 218R, 334L hystricomorph(s), rodent 249R Ibarus 117R, 118L, 120L Icaronycteris 58, 86L, 88L *Ictidopappus* 57, 70L, 74L, 75L Ignacius 59, 71R, 75L, 76L, 79R, 81L, R, 82R, 83R, 84L, R, 86R, 87L, 88L, R *Ignatiolambda* 57, 79R, 83L, 84L Ilingoceros 218R Indarctos 218L insectivoran(s) 133R insectivore(s) 23R, 126L, 189R, 196L, 218L Ischnognathus 119L, R ischvromvid(s) 128R Ischyrocyon 176L, 177R, 217R Ischyrognathus 328R ischyromyid, ine rodent(s) 329L, 330R Ischyromys 119R, 163L, 329L, 330R I. parvidens 164R, 165L I. typus 165L I. veterior 162R *Ischyrosmilus* 249R, 268L Ischyrotomus 117R isectolophid(s) 133R, 325L, 328L

Janimus 117R, 118L, 119R, 133L

Jaywilsonomys 119R Jepsenella 56, 71R, 75L, 76L, 79R, 80R *Kalobatippus* 212L, 213L Kansasimys 218L K. dubius 198L Kimbetohia 28R, 30, 33, 54, 63R, 65R, 67R, 70L, 321R K. campi 28R, 30, 33 kyptocerine protceratid(s), artiodactyl 212L Kirkkomys 211L K. schlaikjeri 211L Knightomys 114R Kollpaniinae 93R Kraglievichia 268R Krauseia 54, 71R, 76L, 79R, 80R K. clemensi 78L *Kyptoceras* 219L K. amatorum 207R kyptoceratine protoceratid(s), artiodactyl 202L, 212L Labidolemur 78R lagomorph(s) 117R, 187R, 190R, 328L Lambdoceras 231L Lambdotherium 107R, 112R, 113L, R, 121R, 122L, 127L, 129L, 131L, 132L Lambertocyon 60, 79R, 82R, 83R, 84L, R, 86L, 87L Lanthanotherium 174L, 206R, 215R, 334R Laredochoerus 118L Laredomys 118L Lasiopodomys 246L, 275L, R, 276R L. deceitensis 246, 284L Leidymys 166R, 174R, 175L, 188R, 205L L. blacki 166R L. nematodon 172R, 179R Leipsanolestes 58, 86L, 88L, R Lemmiscus 276L, 280L L. curtatus 236, 245, 246, 270R, 276L, 279L, R, 280L Lemmus 235, 244, 276R Lemoynea 218L Lepoides 219L, 252L L. lepoides 178L, 252L leporid(s), lagomorph 178L, 191L, 198R, 211L leporine 198L Leptacodon 58, 63L, 69R, 72L, 75L, 76L, 78R, 79R, 81L, R, 82R, 83R, 84L, R, 86R, 88L, R leptictid(s) (placental) 92R, 321L, 323R, 329L *Leptictis* 83L, 165L, 329L L. haydeni 165L Leptictida 55, 93R leptictoid(s) 24R Leptarctinae 213L

Leptarctus 195L, 202L, 213L, 218R, 333L L. primus 190R, 197R Leptauchenia 165R, 166L, 189R, 193R, 196R, 330R L. decora 165R L. major 165R leptauchenine(s) 173L, 187L, 189R, 197L, 211R, 330R, 332R leptochoerid(s), ine(s) 114R, 327R Leptochoerus 166R, 211L L. emilyae 165L *Leptocyon* 195L, 196R, 199R Leptodontomys 173R, 192L, R, 218L, 215R, 218R leptomerycid(s), artiodactyl 188R, 195R, 200L, 212L, 216L, 329R, 330R, 331L, 334L Leptomerycidae 216L Leptomeryx 119R, 162R, 163L, 164L, R, 192L, 211L, 330R "L." (?Hendryomeryx) defordi 119R L. evansi 164L, R L. mammifer 163L L. speciosus 163L L. yoderi 162R Leptonysson 55, 72L, 75L Leptoreodon 116L, R, 119R, 124L, 129R, 130L, 133L L. edwardsi 129R L. major 129R L. pusillus 129R Leptotomus 129R leptotraguline(s) 133R, 330R Leptotragulus 117L, 119R, 132R Lepus 235, 245, 250R, 259L, 261L, 265R, 270R, 272R, 278L, 283L Lignimus 191L, R, 192R, 215R L. montis 191R L. transversus 191R Limaconyssus 58, 79R, 81R, 82R, 83R, 84L, R, 87L, 88L *Limnocyon* 114R, 117R, 118L, 131R limnocyonid(s), limnocyonine(s) 118L, 328R Limnoecus 190R Liodontia 178R L. alexandrae 178R Liotomus 54, 79R, 80R Lipotyphla, lipotyphlan 23R, 37R, 321L, 325R Litaletes 60, 63L, 69R, 72L, 73R, 74L, 75L, 76L, 79R, 80R L. disjunctus 78L Litocherus 58, 71R, 76L, 79R, 81L, R, 82R, 83R, 84L Litolestes 58, 79R, 82R, 83R, 84L Litomylus 60, 63L, 67R, 70L, 72L, 74L, 75L, 76L, 79R, 81R, 82R, 83L, 321R litoptern(s) 92R

Litoyoderimys 162R *L. lustrorum* 162R llama, lamini 178L, 198L, 334L *Longirostromeryx* 200L, 216L, 217R *Lophiohyus* 328L *Loupomys* 275R *L. monahani* 246, 253L, 275R *Loveina* 112R, 113L *Loxolophus* 60, 62R, 63L, 66R, 67R, 70L, 71R, 72L, 74L, 75L, 76L, 321R *L. pentacus* 67L, 68L *L. priscus* 68L *Lutra* 219L, 235, 250R, 270R *L. canadensis* 235, 250R, 270R *Lutravus* 218L, R, 249R

Machaeromeryx 175L, 212L machairodont(s) 171L Machairodus 200R, 218L, R, 219L, 249R, 251R Macrocranion 112R, 117R, 118L, 325L Macrognathomys 198L Macrotarsius 116L, R, 117R, 121L M. siegerti 121L Mahgarita 119L, 129R Maiorana 61, 63R, 65L, R Malaquiferus 117R, 118L, 129R, 330R Mammacyon 196R, 211R, 212L M. obtusidens 205R M. (Temnocyon) 206L Mammut 253L, 284L, R, 286L, R, 337R M. americanum 236, 260L, 270L, 278L, 284L, 285L mammutid(s) 172L, 176L, 177R, 178L, R, 189R, 197R, 214L, R Mammutidae 189R Mammuthus 236, 245, 250R, 252R, 259R, 261L, 263L, 264L, R, 267R, 269R, 270L, R, 271L, R, 273L, R, 276R, 278L, 280L, 281L, R, 282L, R, 283L, R, 284L, R, 286R, 290L, R, 293L, 295L M. columbi 278R M. hayi 283R M. imperator 280R, 282L, 288R M. jeffersonii 288L M. primigenius 288R Manitsha 130L Manteoceras 114R, 115L Marfilomys 132L M. aewoodi 132L Marmota 217R, 236, 270R, 285L M. flaviventris 236, 270R, 285L M. monax 236, 270R, 285L M. vetus 219L marmotine(s), rodent 189R, 198L, 331L marsupial(s) 23L, R, 24R, 28L, 35L, 45R, 64L, 92R, 93R, 126L, 131R, 318R, 321L, 324R

Marsupialia 30, 33, 54 Martes 190R, 215L Martinogale 260R mastodon(t)(s), proboscideans 190L, 206R Matthomervx 215L Mediochoerus 213L M. mohavensis 176L Megabelodon 217L Megacamelus 175L, 219L, 337R M. merriami 251R Megadelphus 113L, 114L, R M. lundeliusi 114R Megahippus 172L, 176L, 197R, 199L, 207L, 215L, 217R M. matthewi 177R, 200L, 217L M. mckennai 176L, 200L Megalagus 165L, 188R, 189R, 192L, 205L, 330R M. brachyodon 163L Megalictis 205R, 212L Megalesthonyx 112R, 113L megalonychid sloths 175L, 251L Megalonychidae 218L Megalonyx 218R, 249R, 250L, 251L, 263R, 278L, R, 281R, 290L, 337R M. jeffersonii 236, 245, 284R M. leptostomus 235, 244, 256R, 258L, 260L, 265R, 266R, 267R M. rohrmanni 256L M. wheatleyi 245, 280R, 281R, 283R, 284L Megantereon 219L, 235, 244, 250R, 252L, 253L, 265L, 338L M. hesperus 251L Megasminthus 192R, 215R, 216L, 334R Megatylopus 200L, R, 249R, 252L, 256R, 260R M. gigas 218L M. matthewi 200R Megoreodon 187R, 188R, 211L M. grandis 197L, 211L Melaniella 56, 79R, 82R Meliakrounomys 163L Meniscoessus 25L, 29, 33, 54, 63L, R, 64L, R, 65R M. collomensis 29, 33 M. conquistus 29, 33 M. intermedius 24R, 29 M. major 24R, 29 M. robustus 28R, 29, 33, 35L M. seminoensis 28R, 29, 33 Meniscomys, 174R, 179R, 187R, 211L Meniscotherium 61, 86L, 88L, 109R, 112R, 113L, R, 131R Menoceras 176R, 195L, 199L, 201R, 206L, 208R, 211R, 213L M. arikarense 206L, 208R M. barbouri 175L, 176R Menops 119R

Mentoclaenodon 60, 79R, 81R mephitine(s), carnivore 215R Merriamoceros 176L, 213R, 215L Meryceros 175R, 200L, 213R M. joraki 176L merychippine equid(s) 334L Merychippus 171R, 202L, 213R, 217R, 334L *M. brevidontus* 172L, 174L, 178R, 207L M. calamarius 178L, 200L *M. insignis* 188L, 197R "Merychippus" 191L, 199L, 202R, 202L, 208L, 213L "M." californicus 172L, 178L *"M." goorisi* 207L *"M." gunteri* 206R, 213L "M." intermontanus 176L, 178L, 190R, 199L "M." primus 196L, 206R "M." sumani 176L Merychyus 192L, 195R, 197L, 199R, 211R, 212L, 215L, 335L M. arenarum 175L, 188L, 191R, 198R, 212L M. calaminthus 201L M. elegans 175R, 201L, R, 213L M. minimus 202L M. relictus fletcheri 175R M. (Metoreodon) 188L Merycobunodon 117L, R merycochoerine oreodont(s) 331R Merycochoerus 187L, 212L, 213L *M. magnus* 191R, 194R M. matthewi 194R M. proprius 192L 194R merycodont(s), antilocaprid 177R, 195R, 200L, 202R, 333L Merycodontinae 217R merycodontine(s) 195R, 213R, 215L, 216L, 333R, 337L Merycodus 173R, 188L, 191L, 196L, 199L, R, 213R M. agilis 190R M. cerroensis 174L M. necatus 190R, 192R M. nevadensis 178R M. sabulonis 192R Mervcoides 179R, 189R, 211R Merycoidodon 119R, 120L, 166R, 330R M. bullatus 165L M. culbertsoni 163R M. dunagani 161R M. major 166L M. presidioensis 162R Merycoidodontidae 217R merycoidontontid, ine 328L, 334L Mesatirhinus 114R, 115L, 127R Mesocyon 173L, 174R, 330R M. brachyops 173L M. coryphaeus 174R

Mesodma 23R, 29, 33, 54, 63R, 64L, 65L, R, 67R, 70L, 72L, 74L, 75L, 76L, 79R, 81L, R, 82R, 83L M. formosa 28R, 29, 33 M. hensleighi 28R, 29, 33 M. primaeva 24R, 29 M. senecta 29 M. thompsoni 29, 33 Mesogaulus 189R, 213L Mesohippus 119R, 160R, 211R, 329L, 330R *M. bairdi* 163R, 165L M. barbouri 164R, 165L *M. exoletus* 163R, 165L M. planidens 192L *M. westoni* 163L, R, 165L Mesomeryx 117L, R Mesonychia 91L, 324L mesonychid(s) 61, 74R, 90R, 325R, 329L Mesonyx 114R, 117R, 118L, 120R Mesoreodon 166L, 174R, 187R, 189R, 205L, 211L M. minor 166L 196R, 211L Mesoscalops 189R, 191L, 196L Metadjidaumo 166L M. hendryi 166L Metamynodon 129R, 330R Metanoiamys 117R M. korthi 119R M. lacus 119R Metarhinus 116R, 117L, R metatherian 318R Metatomarctus 175L, 196L, 199L, 208L, 213L, R M. canavus 176R, 199L, 208L Metechinus 211L, 217R miacid, miacoid 133R, 134L, 324R, 325R, 328L Miacis 112R, 114R, 325R Michenia 175R, 192L, 199L, 200L, 211R, 212L, 218R M. agatense 175L, 188L, 198R Microclaenodon 61, 72L, 75L, 76L Microcosmodon 54, 63L, 67R, 79L, 72L, 73L, 74L, 75L, 76L, 79R, 81L, R, 82R, 83R, 84L, R, 86L, 87L, R, 321R Microeutypomys 118L, 119R, 133L M. tilliei 119R Micromomys 58, 79R, 82R, 84L, R, 86R, 88L, R Microparamys 55, 86L, 87R, 88R, 116L, 119R, 124L, 129R M. nimius 1194 Microsus 113L, 114L microsyopid primate(s) 328R, 329L Microsyops 112R, 113L, 114R, 117R, 118L, 120R, 129R, 130R M. annectens 115L, 116L, R M. elegans 115L Microsyopoidea 82L

Microtinae 239R microtine(s), rodent 239R Microtus 235, 245, 246, 250R, 259L, R, 271R, 272L, 273L, 274R, 278L, R, 279L, R, 280L, 281L, 282L, R, 290R M. aratai 246, 283R M. californicus 274R, 278L M. deceitensis 246, 275R M. guildayi 246, 282L, R M. llanensis 236, 246, 270L, 273R, 274L, 281R, 282L, R, 284L, R M. meadensis 236, 245, 246, 259R, 270L, 273R, 275L, R, 276R, 278R, 279L, R, 281L, R, 282R, 289L M. mexicanus 276L M. montanus 276L M. ochrogaster 274L M. paroperarius 236, 245, 250R, 270L, 273R, 274L, 275R, 276R, 278R, 279L, R, 280L, 281L, R, 282L, R, 284L, R, 294L M. pennsylvanicus 274L, 276L, 290L, 290R M. pliocoenicus 246, 266L Microtomarctus 197R, 199R, 213L *M. conferta* 176L, 178L, 199L Mictomys 253L, 255R, 261R, 273R, 290L M. borealis 278R M. kansasensis 235, 244, 246, 250R, 259R, 266L, R, 267R, 273R, 275L, 276L, 278R, 279R, 280L, 281L M. landesi 256R, 265R M. meltoni 235, 244, 246, 250R, 273R, 276L, 278R, 279L, R, 280L, 281L, R, 282L, R M. vetus 235, 244, 250L, 256R, 258R, 261R, 266L Mimatuta 61, 62R, 63L, R, 64L, R, 65L, R, 67R, 321L, R Mimetodon 54, 71R, 75R, 76L, 79R, 81L, R, 82R, 83R, 84L Mimomys 246L, 250L, 253R, 254L, 275L, R, 280L, 295L M. dakotaensis 246, 267L, 276L, 280L M. monahani 246, 253L, 275R M. panacaensis 250L, 252L, 254L, 260R M. virginianus 246, 267R, 275L, R, 276L, 279L, 284L M. (Cosomys) primus 246 M. (Cosomys) sawrockensis 246, 250L, 254L M. (Cromeromys) dakotensis 246 M. (Cromeromys) virginianus 246 M. (Ogmodontomys) poaphagus 246 M. (Ophiomys) 246 M. (Ophiomys) mcknighti 250L Mimoperadectes 54, 86L, 88L

Mimotricentes 60, 63L, 67R, 70L, 74L, 75L, R, 76L, 78L, 79R, 81R, 82R, 83R, 84L, R, 321R M. subtrigonus 78L miniochoerine oreodont(s) 330R, 331L Miniochoerus 163L, R, 164L, R, 165L, 166L, 330R M. affinis 164R M. chadronensis 163R, 164L M. douglasensis 164L M. forsythae 163L M. gracilis 164R M. starkensis 165L, 166L Mingotherium 55, 79R, 83R mioclaenid(s) 62R, 93R, 321R, 323L Mioclaenidae 60, 62R Mioclaenus 60, 72L, 73R, 76L Miocyon 119R, 133L Mioheteromys 217R miohippine equid(s) 329L, 330R Miohippus 163L, 164L, 166L, 173L, 179R, 187L, R, 197L, 204L, 205L, 212L, 330R M. annectens 166L M. equinanus 166L, 197L M. gidleyi 166L M. grandis 163L, R, 164L M. intermedius 166L miolabine camel(s), artiodactyl 212L, 217R, 332R Miolabis 172L, 200L, 202R, 212L M. fricki 174L M. montanus 190R Miomastodon 172L Miomustela 213L, 333L M. madisonae 190L Mionictis 213R, 217R, 334L Miopetaurista 207R, 219L Miospermophilus 173R, 192L, 196L, 19L Miotapirus 204R, 212L Miotylopus 173L, 174R, 197L, 211L, 212L M. gibbi 173L Miracinonyx, 282L M. inexpectatus 235, 244, 250R, 267L, 270L, 284L *M. trumani* 236, 284R Mithrandir 61, 62R, 63R, 66R, 67R, 70L, 321R Mixodectes 59, 72L, 75L, R, 76L, 324L M. pungens 72R, 74L, 75L mixodectid(s) 59, 75R Mojavemys 191L, 215L mole(s), insectivore 196L, 198L, 218R Molinodus 93R Monosaulax 171R, 193R, 195R, 215L, 216L M. pansus 171R, 199R M. skinneri 171R monotreme(s) 92R Montanatylopus 120L, 330R Mookomys 173R, 189L, 190R

Moropus 179R, 187L, 204R, 205R, 206L, 211R, 216L M. elatus 204R M. merriami 178R M. oregonensis 204R, 205R moschid(s), artiodactyl 188L, 190R, 199R, 200L, 212L, 215L, 216L Moschidae 212R, 217R Multituberculata, multituberculates 23L, R, 24R, 25L, 29, 33, 35L, 36R, 37R, 54, 64L, 66L, 75L, 92R, 318R, 321L, R, 323L, 324L murid(s), muroid(s) rodent 211L, 218R, 218L, 337R Muridae 239R Mustela 219L M. erminea 236, 270R, 285L M. rexroadensis 258L mustelid(s), carnivore 190R, 195L, 207L, 211L, 212L, 213L, 215L, 217R, 218L, R, 219L, 331R, 332R, 333L, 334L, R, 337L Mustelinae 213L musteline(s) 213R musteloid(s) 205L mylagaulid(s), rodent 189R, 190R, 196L, 212L, 213L, 251L, 331L Mylagaulidae 211L, 218R mylagauline(s), rodent 190R, 194R, 211R, 215L, 216L Mylagaulodon 187L, 192L, 212L Mylagaulus 199R, 206R, 215R Mylodon 282R mylodont sloth 246R, 249R Mylodontidae 218K Mylohyus 219L, 251L, 284L M. elmorei 251L M. nasutus 284L Myrmecoboides 55, 71R, 75L, 79R, 81L, R, 82R, 83R, 84L, Myrmecophaga 280R tridactyla 280R Mysops 113R, 114R, 116L, 117R, 129R Mytonomeryx 117L, R, 118L *Mytonomys* 119R, 129R, 134R Mytonolagus 117R, 118L

Nannasfiber 212L Nannippus 218L, 249R, 252L, 261L, R, 262L, 263L, 267L, 268L, 334L N. aztecus 198L, 218R, 219L N. lenticularis 218R N. minor 251L N. montezuma 263R N. peninsulatus 235, 244, 246R, 249R, 261R, 262L, 263L, R, 264L, 265L, 266L, 267L, R N. phlegon 246R Nannodectes 59, 79R, 80R, 81R, 82R, 83R, 84L

N. gazini 81R N. gidleyi 83R N. intermedius 77R, 78L, 80R N. simpsoni 82R Nanodelphys 165L N. hunti 165L Nanotragulus 166R, 171R, 174R, 197L, 204R, 211R, 212L, 330R N. loomisi 166R, 205L, R, 211R N. ordinatus 205L, R, 211R Navahoceros 259L, 278L Navajovius 58, 80R, 81R, 82R, 83R, 84L Neatocastor 204R, 205L, R, 208L N. hesperus 189L *Nebraskomys* 250L, 253L, 254R, 255L, 262L, 265L N. mcgrewi 253R, 265R, 266L N. rexroadensis 253R nectogaline shrew(s), insectivore 218L Nekrolagus 235, 249R, 250R, 256R, 260R N. progressus 252L Neochoerus 261R, 268R N. cordobai 264L N. dichroplax 267R N. holmesi 264L Neoclaenodon 60, 72R, 76L, 79R, 81L *Neofiber* 235, 250R, 270R N. alleni 283R N. leonardi 274L, 276L, 283L, R Neohipparion 195L, 215R, 217R, 219L, 249R, 252L, 334L, 337R N. affine 217L N. coloradense 199R, 215R N. eurystyle 200R, 218R, 219L N. leptode 218L N. phosphorum 251L N. repulicanus 191R N. trampasense 217R Neoliotomus 54, 81R, 84L, R, 86R, 87L, 88L, R, 113L neomustelid carnivore 334L Neoplagiaulacidae, neoplagialacid(s)23L, R, 29, 33, 318R Neoplagiaulax 30, 33, 54, 63R, 65R, 67R, 70L, 72L, 74L, 75L, R, 76L, 81L, R, 82R, 83R, 84L, 321R N. burgessi 28R, 33 *Neotoma* 198R, 259R, 278L, 290R N. fuscipes 278L N. quadriplicata 262L N. taylori 265R N. (Hodomys) 289R N. (Paraneotoma) 198R, 259R, 261R N. (Paraneotoma) fossilis 259R, 261R Neotragocerus 218L *Nexuotapirus* 196R, 204L, 211R, 213L N. marslandensis 204R N. robustus 179R

Niglarodon 187R, 188R, 211L N. blacki 191L nimravid(s) 173L, 196R, 205R, 216R, 217R, 330R Nimravidae 120L, 211R, 217L, 218R, 325, 328R, 329R Nimravides 218R N. catocopis 218L N. galiani 171L, 217R N. thinobates 171L, 172R, 217R Nimravus 166L, 179R, 196R, 211R, 330R *N. brachyops* 166L, 173L Niptomomys 58, 86L, 87R, 88R, 112R nontherian (mammal) 92R notharctine(s) 324R, 327R, 328R Notharctus 113L, 114R, 115L, R, 116L, R, 117L, R, 122R, 127R, 128R, 129R, 131L N. pugnax 115L, R N. robinsioni 114R N. robustior 127R N. tenebrosus 115L, 132R Nothokemas 204R, 205L N. waldropi 205L, R Nothotylopus 199L, 213R, 217R Nothrotheriops, 235, 244, 250R, 259L, 270R, 278R, 280R, 281L, 285L, 286R N. shastensis 282L N. texanus 283R Notiotitanops 134L N. mississippiensis 134L Notolagus 200R, 252L Notoparamys 112R Notoungulata 93R, 94R notoungulate(s) 92R nyctitheriid(s) 58, 82L, 126L, 133R, 324L Nyctitherium 83L, 114R, 116R, 119R, 129R, 133L Ocajila 118R, 193L, 211L Ochotona 218R, 284R ochotonid(s) 173R, 176R, 190R, 192R, 196L, 198L, 211L, 213L, 215R, 216L, 217R, 331R, 334R Ochotonidae 211L Odocoileus 249R, 260L, 261R, 265L, 280R, 288L, 290R Ogmodontomys 235, 244, 246L, 250L, 253R, 254L, R, 255R, 262R, 265R, 290L, R O. poaphagus 244, 246, 253R, 255L, 262L, R, 265L, 266L, 267L O. sawrockensis 244, 246, 250L, 251R, 254L, 265L Oklahomalagus 198L Oligoryctes 116R, 117R Oligospermophilus 165L omomyid(s), omomyine(s), omomyoid(s) 92L, 324R, 327R, 328L, 328R, 329L

Omomys 112R, 114L, 116L, R, 119R, 120R, 128R, 129R O. carteri 114R Ondatra 253L, 255R, 260R, 279L, 282R, 290L, R O. annectens 235, 245, 246, 250R, 266R, 267R, 270R, 273R, 274L, 275L, 279R, 281R, 282L, R, 284L, R O. hiatidens 282R O. idahoensis 235, 244, 246, 250L, 256L, 258R, 259R, 260L, 261L, R, 265R, 266L, 268L O. nebracensis 246, 274L O. zibethicus 236, 245, 246, 255R, 270R, 274L, 285L, 288L Onohippidion 218R O. galushai 218R Onychodectes 56, 63R, 67R, 70L, 321R Onychomys 218L Ophiomys 235, 244, 246L, 249R, 250L, 253L, R, 254L, R, 255R, 256R, 258R, 259R, 290L, R, 295L O. fricki 266L O. magilli 255L, R, 260R, 266L O. mcknighti 250L, 254L, 255L, 256R, 260R *O. meadensis* 253R, 255R, 265R O. parvus 256L, 258R, 266L, 275L, 278R O. taylori 253R, 255L, R, 256R, 258L, 261R Oreamnos 236, 270R, 285L O. harringtoni 270R oreodont(s), artiodactyl 162L, 164L, R, 165L, 166L, 171L, 176L, 178R, 187L, R, 188L, 189L, R, 190L, 191R, 193L, 195L, R, 196L, R, 197L, 199L, R, 200L, 201R, 203R, 205L, 206L, 211L, R, 212L, 213R, 215L, 216L, 217L, 328R, 329L, R, 330R, 331L, 332R, 334L, 335L oreodotine oreodont 329R Oreodontoides 196R, 212L O. oregonensis 179R, 197L, 211L, R Oregonomys 191R O. agrarius 191R Oreolagus 190R, 191L, 192L, 199L, 213L, 333L O. nebrascensis 196L O. nevadensis 178R, 190R Orientolophus 91R Orohippus 113L, R, 114R, 115L, 120R, 122R, 128R, 133R O. major 115L O. sylvaticus 115L oromerycid(s) 328L, 329R, 330R Oromeryx 116R, 117L, R, 118L, 130L Oropyctis 166L O. pediasius 166L

Orthogeomys 268L O. propinetis 268L Osbornoceras 218L, R, 249R Osbornodon 199R, 205L, 215L Osteoborus 249R, 251L, 265L O. diabloensis 171L, 177L Otarocyon 330R Otionohyus 330R Ourayia 116L, R, 117L, R, 118L, 127R, 129R Ovis 285L O. canadensis 236, 285L, 288L Oxetocyon 166L O. cuspidatus 166L Oxyacodon 61, 62R, 63R, 66R, 67R, 70L, 321R O. priscilla 67L Oxyaena 57, 79R, 84L, R, 85R, R, 86R, 87L, 88L, R, 90R, 112R, 113R, 131R oxyaenid(s) 117R, 324L, 327R, 328R, 329L Oxvaenodon 117L, 118L oxyclaenid 321R, 323L, 324R Oxyclaenidae 60, 62R Oxyclaenus 60, 62L, R, 63L, 65R, 67L, 70L, 72L, 73R, 321R O. antiquus 68L oxydactyline camel(s), artiodactyl 212L Oxydactylus 198R, 202R, 205L, 212L, 213R O. longipes 188L, 195R Oxyprimus 60, 63L, R, 64L, R, 65L, 80L, R, 321L, R Oxytomodon 60, 72L, 73R Pachyaena 112R, 325R Paciculus 173L, 187R, 188R, 211R P. woodi 211L Palaeanodon 56, 86L, 87L, 88L, R palaeanodont(s) 132L Palaechthon 59, 72L, 73R, 75L, R, 76L, 78L, 79R, 81L, R, 82R P. alticuspis 78L P. nacimienti 78L Palaeictops 55, 63L, 69R, 72L, 74L, 75L, 76, 79R, 81L, R, 82R, 83R, 84L, R, 86R, 87R, 88L, R, 112R, 122R, 133L, 323R, 328L Palaeolama 286R P. mirifica 268L Paenemarmota 200R, 218R, 235, 244, 250R, 252L, 264L, 265L P. barbouri 263R P. sawrockensis 219L Palaeoarctomys 190L Palaeocastor 187R, 196R, 204L, 211L, R, 212R P. nebrascensis 166R, 211L Palaeogale 205L, R Palaeolaginae 211R

Palaeolagus 120L, 173L, 179R, 187R, 188R, 193R, 196R, 204L, 211R P. burkei 165L, 166L P. hypsodus 166R, 189R, 211L P. intermedius 164L, R, 165L P. primus 162R P. temnodon 163L, R Palaeolama 286R P. mirificus 268L Palaeonictis 57, 86R, 88L, 325R Palaeoryctes 55, 72L, 76L, 79R, 81L, R, 82R, 83R, 84L, R, 86L, 87L, 88L, 92R palaeoryctid(s) 92L, R Palaeosinopa 56, 78L, R, 79R, 81R, 82R, 83R, 84L, 86R, 87L, 88L, R, 114L, 325R Palaeosyops 112R, 113L, R, 114L, R, 120R, 121R, 122R, 134R P. fontinalis 114L Palenochtha 59, 72L, 75L, 76L, 79R, 80R P. minor 78L paleomustelid(s) 332R Paleotomus 56, 72L, 75L, 76L, 78L, 79R, 81L, R, 82R, 84L P. milleri 78L Pandemonium 58, 63R, 67R, 70L, 321R Panolax 199R P. santaefidei 199R Panthera 278R, 290R P. atrox 236, 284R, 288L *P. onca* 236, 270R, 283R, 284L, 285L pantodont(s) 82L, 83L, 89L, 90R, 92L, R, 93R, 131R, 323R, 324R, 327R Pantodonta 57, 85L, 91L, 93R, 94L, 324L Pantolambda 57, 70L, 72L, R, 75L, 76L, 324L P. intermedium 93R pantolambdid(s) 131R Pantolestes 113L, 114L, R, 117R, 134L, 328L pantolestid, pantolestan 133R, 318R, 323R, 324R Pappogeomys 264R Parablastomeryx 192L, 212L, 217R P. mollis 178R Paracimexomys 23L, 29, 33 P. priscus 28R, 29, 33 P. magnus, 29 Paracosoryx 177L, R, 196L, 212L P. alticornis 192R P. furcatus 190R P. furlongi 172L, 174L, 177L P. loxoceras 178L Paractyptotis 256R, 258L P. gidleyi 258L *P. rex* 256R Paracynarctus 196L, 199L, R P. kelloggi 171R, 178L, R, 208L

Paradjidaumo 132R, 165L, 166R, 330R P. validus 164R parahippine 207L Parahippus 173R, 178R, 188L, 191L, 192L, 197L, 212L, 215L, 332R P. leonensis 208L P. pawniensis 175L, 187L P. tyleri 191R, 199L Parahyus 129R Parailurus 256R Paralabis 166R, 330R P. cedrensis 166L Parallomys 192L, 193R, 211L Paramerycoidodon 330R Paramerychyus 197L, 212L P. harrisonensis 197L Paramicrotoscoptes 218L Paramiolabis 174L, 199L, 200L, 213R, 215L P. singularis 175R, 188L P. taylori 164L P. tenuis 175R Paramoceros 176L, 200L paramyid(s) 130R Paramylodon 249R, 263L, R, 250R, 267L, 286R, 278R P. harlani 235, 245, 246R, 247L, 250R, 268L, 270R, 278L, R, 280L, 282L, R, 285L Paramys 55, 86L, 87L, 88L, R, 112R, 114R, 117R, 324L P. delicatior 115L P. delicatus 115L Paranasua 217R Paraneotoma 256R, 259R, 261R Paranotolagus 264L P. complicatus 264L Paranyctoides 23R, 28R, 32, 33, 37R P. maleficus 32 P. megakeros 32 P. sternbergi 32 Parapliohippus 173R, 213R, 334L P. carrizoensis 173R, 175R Parapliosaccomys 176L Paratomarctus 176L, 192R, 195L, 199R, 215L, 217R P. euthos 217L P. temerarius 177R, 190R Paratylopus 166R, 330R P. labiatus 165L P. primaevus 166L Pararyctes 55, 72L, 75R, 76L, 79R, 81L, R, 82R, 83L Paratoceras 203R, 217R Parectypodus 28R, 30, 33, 54, 65R, 67R, 72L, 74L, 75L, R, 76L, 79R, 81R, 82R, 83R, 84L, R, 86R, 87L, 88L, R, 321R P. foxi 28R, 30, 33 Parenhydrocyon 197L, 330R P. wallovianus 201L

Pareumys 117R, 119R Parictis 325, 328R Parisectolophus 114R Paroligobunis 205R P. frazieri 205R paromomyid 111L, 323R Paromomys 59, 72L, 73L, R, 75L, R, 76L, 79R, 81L, R, 82R P. depressidens 78L Paronychomys 177L, 218L Paroreodon 179R, 211R, 212L Parvericius 188R, 192L, 205L, R, 211L, 216L Parvitragulus 162R P. priscus 162R Patriofelis 114L, R, 133R Patriolestes 117L Patriomanis 162R, 325, 329R P. americanus 325, 329R pauromomyid(s) 324L Pauromys 113L, R, 114R, 117R, 129R, 328L P. lillegraveni 123R peccary, 187L, 201R, 208L, 211R, 213L, 215L, 291R Pediomeryx 175L, 218R P. hemphillensis 251R, 259R Pediomyidae, pediomyid(s) 23L, 24R, 31, 33, 318R, 321L "Pediomys" 31, 33, 321L "P." clemensi 31 "P." cooki 28R, 31, 33 "P." elegans 28R, 31, 33, 35L "P." fassetti 31 "P." florencae 28R, 31, 33 "P." hatcheri 28R, 31, 33 "P." krejcii 28R, 31, 33 "P." prokrejcii 31 Pediomys 55, 63L, R, 64R, 65R Pedomys 246, 273R, 274L, 282R, 284R P. llanensis 276L, 284R Pelvcodus 112R Pelycomys 165L, 330R P. brulanus 164R P. placidus 165L Penetrigonias 120L Pentacemylus 117R, 118L Pentacodon 56, 72L, 75L, 76R, 79R, 80R Pentacosmodon 54, 79R, 84L Peraceras 195R, 199R, 200L, 207L, 213R, 217R, 334L P. hessei 207L P. superciliosum 178L, 190L, R peraceratheriine rhino(s) 328L Peradectes 45R, 53L, R, 54, 63L, 64L, 65L, R, 67R, 70L, 74L, 75L, 76L, 79R, 81L, R, 82R, 83R, 84L, R, 86R, 88R, 321L

Peratheriuim 114R, 129R, 132R Perchoerus 179R, 188R, 211L Peridiomys 188L, 190R, R, 191L, 196L, 215L periptychid 62L, 71L, R, 321R, 323R Periptychidae 61, 62R Periptychus 61, 62R, 63L, 65R, 66R, 67R, 70L, R, 71R, 72L, 73R, 74L, 75L, 76L, 79R, 81L, R, 83L, 321R, 324L P. carinidens 62L, 63R, 67R, 71L, R, 72L, R, 73L P. gilmorei 71L Perissodactyla 89R, 91R, 112R, 325L perissodactyl(s) 90L, 122L, 127R, 132L, 133R, 324R Perognathus 190R, 198L, R, 215L P. furlongi 174L P. gidleyi 261R, 265R P. mclaughlini 252L Peromyscus 198R, 218R, 260R, 280L P. cragini 265R, 282R P. hagermanensis 261R P. polionotus 268L P. valensis 269R Petauristodon 213R, 217R, 334L P. uphami 174L Pewelagus 259L P. dawsonae 235, 250L, 252L, 260R Phaiomys 246L Phelosaccomys 190R, 217R phenacocoeline(s) 332R Phenacocoelus 179R, 205L, R, 212L P. typus 194L, 206L P. luskensis 206L phenacodontid(s) 60, 82L, 86L, R, 323R Phenacodus 44L, 60, 72L, 73L, 76L, 78R, 79R, 81L, R, 82R, 83R, 84L, R, 86L, R, 87R, 88L, R, 112L, 113L, R, 114R, 121R, 122R, 128R, 129L, 131R, 132R P. grangeri 78, 83R P. primaevus 86L P. vortmani 86L Phenacodaptes 60, 79R, 83L, R, 84L, R, 86L Phenacolemur 59, 83L, 84L, R, 86R, 87L, R, 88L, R, 113L, 129L P. pagei 86R, 87L P. praecox 86R, 88L phenacolemurine(s) 324R Phenacolophidae 91R, 324L Phenacomys 235, 245, 250R, 258R, 270R, 272R, 273L, R, 275L, 276L, R, 278R, 279L P. gryci 258R, 278R, 279L, 280L P. intermedius 281R Pithecistes 330R Phlaocyon 205L, 213R P. achoros 205R P. annectens 201L P. leucosteus 205R

P. minor 204L Phlaocyonini 213R Phoberocyon 208L, 213L, 333L Phosphatherium 92R Picrodus 59, 72L, 75L, 76L, 79R, 81L, R, 82R, 83R, 84L Pipestoneomys 156L, 331L pitymyine species 246L Pitymys 246, 266L, 273R, 275L, R, 282R, 283R, 289L placental(s) 94L plagiaulacidan(s) 23L, R Plagioctenodon 58, 86L, 87L, 88R Plagiomene 59, 86L, 87R, 88R Planetetherium 59, 86R, 87L, R Planisorex 266L P. dixonensis 266L Platybelodon 217R, 218R Platygonus 218R, 249R, 259R, 260R, 264R, 285L, 290L P. alemanii, 285L P. bicalcaratus 235, 250L, 262L, 263L, R, 265L, 266R, 267L, R, 268L, P. compressus 236, 245, 284R P. cumberlandensis 283R P. pearcei 235, 244, 250L, 256R, 258L, 260L P. vetus 235, 245, 250R, 268L, 270L, 281R, 282L, R, 283L, R, 284L Platymastus 60, 63R, 66R, 67R, 321R plesiadapid(s) 58, 71L, 75R, 77R, 78L, 82L, 89L, 323R, 324L Plesiadapis 59, 71L, 73L, 76L, 78L, R, 79R, 80R, 81R, 82R, 83R, 84L, R, 85R, 86R, 87R, 88L, 90L, 113L P. anceps 44L, 80L, 81L, R P. churchilli 80L, 82L, 82R, 83R P. cookei 80L, 84L, 85R, 86L, R, 87L, R, 88L, 120L P. dubius 84R, 85R, 120L P. fodinatus 84L P. gingerichi 8oL, 83R, 84L, R, 86R, 87L P. praecursor 44L, 72L, 73L, 75L, 77R, 78L, 80L, R P. rex 80L, 81L, 82L, R P. simonsi 80L, 82R, 83R, 84L P. tricuspidens 89R Plesictis 196R Plesippus 246R, 249R, 258L, R, 260L P. francescana 246R, 259R, 278L P. idahoensis 246R, 259R P. shoshoniensis 258L P. simplicidens 246R Plesiogulo 200R, 218R, 249R, 251L Plesiosorex 213L, 333L Plesiosoricidae 213L Plesiolestes 59, 72L, 73R, 75L, 76L, 79R, 80R Plesiosminthus 193L, 196L, 209R

pleurolicine 187L Pleurolicus 179R, 188R, 189L, 196R, 199L, 211R P. sulcifrons 211L Plioceros 200L, R, 127R, 218R, 334L P. floblairi 216L Plioctomys 253L, 255R P. rinkeri 255R Pliocyon 213R, 215L P. ossifragus 190L *Pliogale* 215R, 218R, 334R Pliogeomys 198L, 200R, 218R, 265L P. parvus 252L, 260R pliohippine equid(s) 334L Pliohippus 200L, 215R, 218R, 249R, 252L, 264L, 334L P. leardi 171L, R, 172R, 177L P. mirabilis 215R P. nobilis 218L P. pernix 200L, 217L P. spectans 218R P. tantalus 177L P. tehonensis 172L, 177L Pliolemmus 235, 244, 250L, 253L, R, 255R, 266L *P. antiquus* 253R, 255L Pliometanastes 200R, 218L, 337R Plionarctos 218R P. edensis 218R Plionictis 190R, 213R, 334L P. oaxacaensis 202R Pliophenacomys 250L, R, 254R, 265R, 266L, 267L, 290R P. finneyi 253R, 255L, 265L P. osborni 250R, 256L, 266L, 281L P. parkeri 246, 251L P. primaevus 253R, 255L P. wilsoni 252L Pliopotamys 235, 244, 250L, 253L, R, 255L, R, 260R, 261R, 266L P. meadensis 246, 253R, 255L, 266L P. minor 253R, 255L, 256R, 258L Pliosaccomys 198L, 218L Pliotaxidea 218L Pliotomodon 218L Pliozapus 218R Plithocyon 175R, 176L, 214R, 215L, 334R Poabromylus 118R, 130R, 329L, 330R Poebrodon 117R, 118L poebrodontine camelid(s) 330R Poebrotherium 120L, 330R P. eximium 163R, 164L P. franki 163R Pontifactor 58, 86L, 87R, 88R, 114R Potamotherium 213L, 333L Praeovibos 285R P. priscus 285R P. recticornis 285R Pratilepus 235, 250L, 258L, 264L

P. kansasensis 235, 250L, 264L P. vagus 258L Premnoides 59, 72L, 76L Preptoceras 282R Presbymys 119L Princetonia 60, 79R, 84L, R, 86R, 87R, 88L, R primate(s) 58, 64L, 71L, 75R, 78R, 79R, 82R, 90L, 106L, 111R, 112R, 116R, 126L, 133L, 321R, 323L, R, 324L, R, 325L, 237R, 328L, R, 329L Priscocamelus 201L, 212L Pristinictis 57, 79R, 80R Proantilocapra 217R Probarbouromeryx 213L Probassariscus 213L Probathyopsis 78R Problastomeryx 212L, 215L Proboscidea 171R, 172L, 175L, 176L, 177R, 190L, 195L, 197R, 214R, 215L proboscidean(s) 92L, 189R, 195L, 200L, 203L, 206R, 214L, R, 215L, R, 219L, 252L, 334R, 337R Procadurcodon 133R Procamelus 176L, 195R, 200L, 215L, 218R, 334L P. grandis 203R P. lacustris 190R Procaprolagus 117R, 118L, 133L Procastoroides 244, 249R, 250L, 253L, 256R, 258L, 265R, 266L P. idahoensis 253L, 266L P. sweeti 253L Procerberus 56, 63L, R, 64L, 65R, 67R, 70L Prochetodon 54, 79R, 82R, 83R, 84L, R, 86L, 87R, 88L Procranioceras 192R, 216L P. pawniensis 197R P. skinneri 192R, 207L Procreodi 327R Procoelius 175L Procynodictis 117L, 118L, 121L Procyon 218R procyonid(s), ine(s), carnivora 215L, 331R, 333L, 334L Procyonidae 213L Prodaphoenus 117L, 118L Prodesmatochoerus 330R Prodiacodon 55, 63L, 69R, 72L, 74L, 75L, 76L, 79R, 81L, R, 82R, 83R, 84L, R, 86R, 87R, 88L, R, 321L, R, 323R P. puercensis 78L Prodinoceras 59, 78R, 84L, R, 86L, R, 87R, 88L, R, 90R Prodipodomys 198L R, 200R, 218R, 235, 244, 250R, 252L, 259R, 265R P. centralis 266L, R P. minor 252L P. tiheni 252L

P. tineni 252L Progeomys 198R Prohesperocyon 330R Proheteromys 174L 192L, 196L, 198R, 204R, 205L, R, 206R, 330R P. sulcatus 173R P. magnus 173R, 205R, 208L P. maximus 174L Prolapsus 117R, 129R Prolimnocyon 74R, 112R, 114R, 131R Promartes 196R, 198R, 199L, 211L Promerycochoerus 171R, 179R, 187L, 189R, 192L, 211R, 212L P. carrikeri 194L, 197L P. hesperus 173L *P. superbus* 191L, 197L P. (Parapromerycochoerus) barbouri 189L Promesoreodon 330R prometheomyine murid(s), rodent 218L Promioclaenus 60, 63R, 66R, 67R, 70L, 72L, 74L, 75L, R, 79R, 81L, R, 82R, 321R Promylagaulinae 211L, 215L promylagauline(s), rodent 187R, 190R, 211R, 334L Promylagaulus 211L Proneofiber 275L, 282L P. guildayi 275L, 282L Pronodens 188R, 212L Pronothodectes 58, 75L, 76L, 79R, 80R Pronotolagus 198L, 215R Propalaeanodon 56, 79R, 84L Propalaeosinopa 72L, 75L, R, 76L, 79R, 81R, 82R, 83R, 84L Proscalopidae 189R, 211R Proscalops 196R, 211R Prosciurus 165L, 330R P. magnus 165L P. vestustus 163L Prosigmodon 198R, 200R, 218R Prosomys 218R Prosthennops 200R, 215L, 249R, 252L P. niobrarensis 208L P. serus 203R, 218R P. xiphodonticus 207R Prosynthetoceras 195R, 204L, 206L, 208R, 211R, 216L, 335L P. orthrionanus 204R P. texanus 204R Protadjidaumo 117R, 118L, 132R P. pauli 119R Protalphadon 28R, 321L P. foxi 28R P. lulli 28R Protapirus 133R, 166R, 211L P. obliquidens 166L Protentomodon 56, 83L, 86R, 87L Protepicyon 215L P. raki 176L Proterixoides 117R, 118L, 119R, 123R, 124L

proteutherian 328L Prothryptacodon 60, 72L, 75L, 79R, 80R Protictis 57, 72L, 75L, 76L, 79R, 81L, 82R, 83R, 84L Protictops 119L Protitanotherium 117L, 118L Protoceras 165R, 166R, 330R P. celer 166L protoceratid(s) ine(s) 130R, 187L, 195R, 202L, R, 207L, R, 212L, 213L, 217L, R, 328L, 329R, 330R, 331L, 332R, 337R Protoceratidae 218R protohippine(s), perissodactyl 202R, 334L Protohippus 190L, 195L, 199L, 213R, 218R, 334L, 337R P. gidleyi 217R P. perditus 207L P. supremus 207L, 217L Protolabinae 218R protolabine camel(s), artiodactyl 212L, 332R Protolabis 173R, 175R, 176R, 188L, 195R, 196L, 199L, 200L, 202L, R, 212L, 218R P. barstowensis 199L P. heterodontus 203R Protomarctus 178R, 196L P. optatus 171R, 173R, 175R, 199L Propliophenacomys 219L, 250R P. parkeri 246, 251L Protoprocyon 217R Protoptychus 117L, R Protoreodon 116R, 117R, 119R, 127R, 129R, 130R, 133R P. pacificus 119R P. petersoni 129R P. pumilus 121L, 129R Protosciurus 165l, 171R, 205, 231L, 331L Protoselene 60, 62R, 63L, 68L, 69R, 71R, 72L, 74L, 75L, 76L, 79R, 81L, R, 82R *P. opisthacus* 71R, 72R, 73L, 74L Protospermophilus 189R, 192L, 196L, 204R, 206R, 217R Prototomarctus 172L, 196L, 213L, R Prototomus 112R, 325 Protungulatum 31, 35R, 36L, 44L, 53L, R, 59, 61R, 62L, 63L, R, 64L, R, 65L, 67R, 321L, R P. donnae 21R, 28L, 36L Protylopus 116R, 117R, 119R, 124L, 1 27R P. pearsonensis 119R Proviverra 118L Psalidocyon 199R, 215L Pseudadjidaumo 191L Pseudaelurus 199L, 202L, 213R, 252L, 334L

Pseudhipparion 215R, 334L, 337R P. gratum 198L, 200L, 217L P. retrusum 217L P. simpsoni 207R, 219L P. skinneri 217R Pseudoblastomeryx 192L, 202L P. advena 175L Pseudoceras 200L, 203R, 207R, 216R, 217L, 219L Pseudocyclopideus 330R Pseudocylindrodon 117R, 132R, 163R, 329L Pseudocyon 215R, 217R, 334R Pseudodesmatochoerus 212L pseudolabine camelid(s) 330R Pseudolabis 212L, 330R P. dakotensis 166L Pseudopalaeocastor 197L, 204L, 212L P. barbouri 204L, 212L Pseudoparablastomeryx 192L, 202L, 216L Pseudoprotoceras 119R, 120L, 133L P. longinaris 163L P. semicinctus 162R P. taylori 163R Pseudotomus 130L P. timmys 119R Pseudotheridomys 173R, 175L, 192L, 193R, 196R, 211L, 217R Pseudotrimylus 188R Psittacotherium 56, 72L, 75L, 76L, 79R, 81L, R, 82R, 83R, 84L Pterodon 328R Pterogaulus 215L ptilodontid(s) (multituberculate), 318R, 321L Ptilodus 54, 63L, 66R, 67R, 70L, 71R, 72L, 73R, 74L, 75R, 76L, 79R, 81L, R, 82L, R, 83R, 84L, 321R Purgatorius 58, 63L, R,64L, 65R, 67R, 70L, 83L, 321R rabbit(s), lagomorph 198L, 211L, 213R, 328R, 330R, 333L, 334R Ragnarok 62R Rakomeryx 174L, 176L, 199R, 206R, 213R, 215L R. kinseyi 188L, 189R, 190R R. raki 174L Rakomylus 199L, R, 215L Ramoceros 174L, 176R, 195R, 200L, 215L, 216L, 334L Rangifer 270R R. tarrandus 236, 270R, 285L, 299L Rapamys 118L, 119R *Raphictis* 57, 79R, 82R, 83L Ravenictis 55, 63R, 70L, 323R R. krausei 91L Reithrodontomys 279R R. humulis 268L

R. rexroadensis 261R R. wetmorei 268L Reithroparamys 55, 86L, 87R, 88R, 117R *Repomys* 175L, 219L, 252L R. gustelyi 219L, 251R R. maxumi 175L R. panacaensis 252L, 260R, 263L rhino, rhinoceros 172L, 175L, 176L, 178L, 189L, 190L, R, 192R, 193L, 195L, 198L, 199L, R, 200L, 201R, 202L, 203L, 207L, 212L, 213R, 217R, 218L, R, 250L, 251L, 252L, 260R, 267L, 325L, 327R, 328L, R, 329L, 330R, 331L, 332R, 333L, 334L, 337R rhinoceratid 211R Rhynchotherium 203R, 218L, 235, 250R, 263R, 264L, 337R R. blicki 203R R. falconeri 263R, 264L R. praecursor 266R rodent 44L, 85R, 87L, 113L, 120R, 126L, 128R, 130R, 131R, 133R, 134R, 171L, 174L, 179L, 187L, R, 190L, R, 191L, R, 192L, 193L, 194R, 198L, 199L, 201R, 203R, 205R, 209L, R, 211L, R, 212L, 213L, 215L, 218L, 232L, 239R, 246, 247L, 248, 251R, 252L, 253L, R, 254L, 261R, 263L, R, 265L, 267R, 273R, 274L, 276L, 278R, 279L, R, 281L, 282R, 284R, 290R, 293L, 295R, 324R, 327R, 328L, R, 329L, R, 330R, 331L, 332R, 334L, R, 338L Rodentia 44L, 55, 78R, 80L, 84L, R, 85L, R, 87L, 89L, 90L, 91R, 92L, 324L Rooneyia 119L Russellagus 192R, 199R, 215R, 217R, 334R Saiga 285R S. tatarica 285R Sanctimus 211R Satherium 235, 250R, 253L S. ingens 260L S. piscinaria 256R, 258L Saxonella 58, 79R Scalopoides 211L Scalopus 218R, 262R S. (Hesperoscalopus) 218R, 262R Scapanus 278R Scenopagus 114R, 116L, 117R, 129R, 129R, 328L Schaubeumys 191L, 192L Schizodontomys 175L, 179R, 187L, 192L, 196L Schochia 56, 63R, 66R, 67R, 321R Sciuravidae 112R sciuravid(s) 131R, 327R, 328R, 331L Sciuravus 113L, 114R, 116R, 117R, 118L,

120R

Scottimus 166R, 192L S. lophatus 166L S. viduus 163R selenodont artiodactyls 120R, 328L, R Semantorinae 213L Sespedectes 117R, 118L, 119R, 123R, 124L, 133L S. singularis 124R sespedectine(s) 328L Sespemys 173L S. thurstoni 173L Sespia 173L, 174R, 189R, 192L, 196R, 211L S. nitida 211L Shoshonius 113L, 114L Shunkahetanka 211L S. geringensis 211L Sigmodon 259L, 262L, 282R S. bakeri 283R S. curtisi 235, 250L, 267L, 268L, 280R, 282L, R S. hudspethensis 263R S. libitinus 283R S. medius 249R, 261R, 266L, R, 267L, R S. minor 235, 249R, 250L, 259R, 261R, 262L, 265R, 266L, R, 267L, R sigmodontine(s), rodent 201R, 217R, 218R Simiacritomys 119R S. whistleri 119R Simidectes 118L, 119R, 129R S. merriami 119R Similosciurus 201L Simimeryx 117R, 118R, 119R S. hudsoni 119R simimyid rodent 328R Simimys 117R, 118L, 119R, 123R, 124L, R, 328R S. landeri 119R Simocyon 218L Simpsonictis 57, 72L, 75L, R, 76L, 79R, 81R Sinclairella 119R, 133L S. dakotensis 162R Sinclairomeryx 213R Sinopa 114L S. rapax 115L Sinostylops 91R skunk(s), carnivore 198L, 219L sloth(s), edentate 175L, 200R, 201R, 218L, R Smilodectes 113L, 114L, R, 115R S. gracilis 115L S. mcgrewi 115L Smilodon 259L, 263L, 272R, 278L, R, 280L, 284L, 286R, 290R

sciurid(s), ine(s) 177L, 190L, R, 191L,

217R, 330R, 334L

Sciuridae 120L, 328R

Sciurus 325, 250R, 270R

Teilhardina 112R, 113L

S. californicus 288L S. fatalis 274L S. gracilis 235, 244, 267R, 268L, 270L, 274L, 283R, 284L S. populator 236, 245, 270R, 274L, 284L, 285L, 288L Sminthosinus 219L Soergelia 272R, 282R S. mayfieldi 272R Sorex 260R, 278L, 290R S. meltoni 260R S. powersi 256R soricid(s) 117R, 190R, 328L, 331L, 333L, 337R Soricinae 213L soricomorph, 32, 33, 37R, 318R, 323R spalacotheriid(s) 23L, R Sparactolambda 78R Spermophilus 190R, 191L, 198L, 252L, 279R howelli 260L tridecemlineatus 279R wellingtonensis 260L S. (Buiscitellus) dotti 198L S. (Otospermophilus) primitivus 190L Sphenocoelus 117L Sphenophalos 218R, 251L squirrel(s), rodent 173R, 196L, 198L, 207R, 213R, 219L Stagodontidae, stagodontid(s) 23L, R, 24R, 25L, 28R, 31, 33, 318R, 321L Stegomastodon 236, 244, 249R, 250R, 253L, 258R, 262L, 265L, R, 266L, R, 267L, 273R, 280L, 281R, 282L, 337R S. mirificus 258R, 262L, R stegomastodont 267L Stelocyon 61, 72L, 76L Stenoechinus 189L Stenomylinae 215L stenomyline(s), artiodactyl 199L, 211L, 331R, 334L Stenomylus 198R, 199L, 201L, 211R, 213L Stenopsoschoerus 330R Sthenodectes 129R Sthenictis 213R, 218R, 334L Stibarus 120L S. obtusilobus 166L S. quadricuspis 165L Stilpnodon 55, 72L, 75L, 76L, 79R, 81L, R, 82R Stockia 117L, R, 328L Stygimys 29, 54, 63R, 64L, 65R, 67R, 70L, 72L, 74L, 75L, 321R S. cupressus 29 S. kuszmauli 37R Stylinodon 116L, 122R, 129R Subantilocapra 219L Subdesmatochoerus 330R Subdromomeryx 213R, 215L S. antelopinus 189R

Subhyracodon 119R, 174R, 330R S. occidentalis 165L, 173L Submeryceros 195R, 213R Submerycochoerus, 212L Swaindelphys 54, 72L, 76L Sylvilagus 235, 244, 250R, 259L, 261L, 270L, 272R, 282R, 285L S. hibbardi 282R S. palustris 236, 270R, 283R S. webbi 250L, 268L symmetrodonts 23R Synaptomys 235, 245, 250R, 268R, 270R, 283R, 284L S. cooperi 276L S. kansasensis 246 S. meltoni 246 S. (Plioctomys) 253L Syndyoceras 194R, 212L S. cooki 202L Synthetoceras 207L, 217L synthetocerine protoceratid(s) 331R, 332R Tachylagus 119R T. gawneae 119R taeniodont 74R, 117R, 321R, 324R, 328R Taeniodonta, 56, 62R taeniolabidid 68R Taeniolabis 54, 62R, 63R, 65R, 66L, 67L, 68L, R, 69L, R, 70L, 323L T. lamberti 68R, 69L T. taoensis 65L, R, 67L, 68L, 69L Taligrada 62L, R Talpavus 119R, 133L talpid(s), (insectivore) 190R, 198L, 211L Talpinae 193L Tamias 190R Tanupolama 249R, 263R, 267L, 278L T. stevensi 288L Tanymykter 212L, 213L T. brevidontus 175L tapir 211R, 212L, 263R tapirid 331L tapiroid(s) 117R, 132L, 325L, 327R, 328L Tapiravus 208L, R T. validus 208L, R Tapirus 261R, 280R, 284L, 286R T. copei 267L, 282L T. haysii 267R, 268L, 282L, 283R, 284L T. veroensis 283R Tapochoerus 117R, 118L *Tapocyon* 117R, 118L, 129R Tapomys 117R, 118L Tardontia 191L, R Tarka 120R *Taxidea* 200R, 218R, 252L, 260R T. taxus 278R Taxymys 1145

tayassuid, ine 207R, 212L, 219L, 328R

Tayassuidae 120L, 328R

Telacodon 28R, 31, 33 T. laevis 28R, 31, 33 Teleobunomastodon 281R Teleoceras 175L, 178L, 195L, R, 198R, 199R, 200L, 200R, 203L, 207L, 213R, 250L, 252L, 334L, 337R T. fossiger 218L Teleoceratinae 213L, 332L, 333L Telmatherium 115L, 131L, 133R *Temnocyon* 173L, 206L, 212L T. altigenis 173L Tenudomys 165L, 330R T. basilaris 165L Tephrocyon 215L *Terricola* 246L, 259R, 273R, 275R, 289L T. meadensis 246, 259R *Tethyopsis* 115L, 125L, 127R Tetonius 112R, 132R Tetraclaenodon 60, 72L, R, 73R, 75L, R, 76L, 78L, R, 80R, 324L T. puercensis 78L Tetrameryx 282L T. irvingtonensis 236, 270L, 278L, R T. schuleri 283L Texoceros 218R Texodon 117R Texomys 204R, 205R, 206L T. stewarti 203R Thangorodrim 62R Thelysia 56, 86R, 87R theria (ian) 36R, 66R Thinobadistes 218L, 337R Thinocyon 114L Thinohyus 165L T. lentus 165L Thisbemys 116L, 117R, 129R Thomomys 219L, 251R, 259R T. carsonensis 260L T. (Plesiothomomys) 219L Thryptacodon 60, 72L, 75L, 77R, 78R, 79R, 79R, 80R, 81R, 82R, 83R, 84L, R, 86L, R, 87R, 88L, R, 114R Thylacaelurus 59L, 79R, 80R, 81R, 82R, 83R, 84R, 86R, 87R, 88L, R, 117R, 118L, 132R ticholeptine oreodont(s) 332R, 334L *Ticholeptus* 178R, 192R, 195R, 197R, 206R, 213R, 216L T. zygomaticus 173R, 188L, 189R, 190R tillodont(s) 66R, 67R, 85L, R, 90L, 132R, 133R, 327R Tillodontia 57, 91L, R, 324L, 327R Tillodon 115L Tillomys 113R, 114R, 120R *Tinimomys* 58, 86L, 87L, 88L, R Tinuviel 61, 63R, 65R, 67R, 70L, 321R *Titanoides* 57, 78R, 79R, 80R, 81R, 82R, 83R, 84L, R, 86L, 87L titanothere 160R

Titanotheriomys 330R *Titanotherium* 160R Titanotylopus 281R, 337R Tiuclaenus 93R Tiznatzinia 60, 63R, 67R, 70R, 321R todralestid(s) 92L Tomarctus 192R, 199R, 215L T. brevirostris 199R T. hippophaga 174L, 176L, 199R *Toromeryx* 117R, 118L, 130L Toxotherium 119R, 129R, 163R, 329L tragulid(s), artiodactyl 200L *Tregomys* 198L, 215R, 217R Tribosphenomys 91R Tricentes 60, 62R Trigenicus 119R, 133L T. profectus 162R Trigonias 119R Trigonictis 219L, 235, 249R, 250R, 253L, 265L T. cookii 256R, 258L T. macrodon 258L, 267R, 268L trigonostylopoids 92R Triisodon 61, 73R, 75L triisodontid 323R Triisodontidae 61, 62R Triconodontidae 23L, R Trilaccogaulus 187R, 193R, 211L triplopodine rhinos 328L *Triplopus* 116L, R, 119R, 127R, 129R trogonotheriine beaver(s) 213L Trogolemur 119R T. leonardi 119R Trogomys 175L, 176R *Trogosus* 112R, 114L, R, 115L, 120R, 122R, 132R Turgidodon 24R, 30, 33, 54, 63L, R, 64L, 65R, 321L T. lillegraveni 30 T. madseni 30 T. parapraesagus 30 T. petaminis 28R, 30, 33 T. praesagus 30 T. rhiaster 28R, 30 T. russelli 30, 33 *Tylocephalonyx* 196L, 208L tylopod 328L *Tytthaena* 57, 79R, 82R

Uintaceras 116R, 117R, 121L Uintacyon 57, 86L, 87R, 88R, 129R U. scotti 129R Uintanius 114L, R uintathere(s) 89L, 328L, 329L Uintatherium 114R, 115L, 116L, 123L, 127R Uintasorex 114R, 116L, 119R, 128R, 129R, 133L Umbogaulus 215L, 216L ungulate(s) 36L, 53L, R, 62L, 63R, 64L, R, 66R, 67L, R, 68L, 69L, 321L, R, 332L, 337L, R, 338L ungulatomorph(s) 28L, 318R, 324L Untermannerix 198L, 215L, 217R, 334L Unuchinia 56, 72L, 75L, 76L, 79R, 81L, R, 82R, 83R, 84L Urocyon 265R Ursavus 192R, 213L, 215R, 333L U. pawniensis 215R ursid(s) 175L, 212L, 213L, 215R, 217R, 218R, 328R, 333L, 334L Ursidae 213L, 328R Ursus 244, 252L, 253L, 270L, 285L U. abstrusus 178L, 235, 250L, 252L, 258L, 260L Ustatochoerus 172L, 195R, 197R, 211R, 212L, 217R U. californics 172R, 217L U. leptoscelos 201L U. major 200L, 217L U. medius 177R, 197R, 200L, 216L U. profectus 177L Utahia 114L, R Utemylus 60, 79R, 83R Viejadjidaumo 119L Viridomys 54, 63R, 65R, 67R, 70L, 72L, 73R viverravid carnivore(s) 328R, 329L Viverravus 57, 70R, 84L, R, 86R, 87R, 88L, R, 112R, 117R, 120R, 132L *Vulpavus* 112R, 114R, 134L V. australis 125R Vulpes 198L V. stenognathus 200R, 218L *V. velox* 236, 285L

Vulpini 218L

Wallia 117R Wasatchia 112R washakiine omomyid primate(s) 328L Washakius 113, 114L, 116R, 117L, R, 120R, 122R, 328L W. insignis 115L Wilsoneumys 165L W. planidens 165L Worlandia 59, 86L, 87R, 88R Wortmania 56, 62R, 63R, 67R, 70L, 321R Wyolestes 131R Wyonycteris 58, 86R, 87L, 88L

Xanoclomys 54, 72L, 75L Xenacodon 55, 79R, 83 xenarthrans 92R Xenicohippus 111L, 112R Xenocranium 163R Xenocyon 285R X. lycaenoides 285R xenungulates 92R Xyronomys 54, 63L, 67R, 72L, 75L, 321R

Yatkolamys 175L Yoderimys 119R, 162R, 329L Y. stewarti 162R Yoderomyinae 211R yoderomyine(s), rodent 193R Yumaceras 218R

Zanycteris 59, 79R, 82R, 83L zapodid(s), rodent 191L, 193L, 198L, 209R, 215R, 216L, 218R, 337R Zapus 290R Z. sandersi 266L, 281R Zemiodontomys 163L Z. burkei 163L Ziamys 198R Zodiolestes 212L Zygolophodon 172L, 178R, 190L, 197R, 207L, 214R, R, 215L Z. brevidens 189R, 190L Z. merriami 178R, 214R Z. proavus 192R zygolophodont 178L

- A. ferox-Pantolambda cavirictum Interval Zone 17L
- AB Tuff, John Day Formation, Oregon 211L, 220L
- Abundance (Acme) Zone xiR, 2, 5, 6L, R, 17L, 44L
- accumulation (rate) xviiiL, 8R, 10L, R, 11L, 12L
- accurate, accuracy 8L, 9L, 14L, 18L, 45L, 78L, 93L, 94L, 114L, 171R, 176R, 238L, 247R
- Acme Zones xiR, 17L, 44L, 86R, 87R, 88L
- Cf3 acme zone 78R, 86R, 87L, 88L
- Across the River Tuff, Oregon 220R Adobe Town Member, Washakie Formation, Wyoming 108R, 109L, 115L, 116R, 117L, R, 127R
- lowest part equivalent to Washakie A of Granger 127R
- Africa 92L, R, 336L
- Aftonian interglacial stage (Pleistocene) 237R
- Agate Ash, Nebraska 194L, 220R
- Agate Bone Bed, Nebraska 194L
- Agate National Monument, Nebraska 194L
- Age or age viiR, xiiL, xiiiL, R, xivL, R, xviiiL, R, xviiiL, 1L, R, 2L, 3L, 4, 7, 8L, R, 9L, R, 10L, R, 11L, R, 12R, 13R, 14L, R, 15L, 16L, R, 17L, R, 18L, 21–28L, R, 32L, R, 34L, R, 35L, R, 36L, R, 37R, 43–45L, R, 47, 53L, R, 61R, 62–66L, R, 67L, 68L, R, 69R, 70–73L, R, 74R, 75R, 76L, R, 77R, 78–79L, R, 80L, 81L, R, 83R, 84R, 85–87L, R, 88R, 89–94L, R, 95L, 96L, 106–107L, R, 111L, R, 113L,

115R, 116L, 118R, 119L, 120–121L, R, 122R. 123L, 123L, 124-138L, R, 158L, 159, 161L, R, 162R, 164R, 167L, 171R, 172R, 173L, R, 174R, 175L, R, 176R, 177-178L, R, 187-189L, R, 190R, 191L, R, 192R, 194L, 195R, 197R, 198L, R, 200–203L, R, 204R, 205-206L, R, 207L, 210L, R, 211L, 216L, R, 233L, R, 236-238L, R, 240, 241, 244, 246R, 247R, 249L, 250R, 251-252L, R, 255L, R, 256R, 257, 258L, R, 259L, 260-269L, R, 271-273L, R, 274L, 275-277L, R, 278L, 279L, R, 285L, R, 286L, 287L, R, 288R, 289, 291L, 292–293L, R, 294R, 295L, R, 315R, 321R, 324L, R, 327L, 331L, R, 332R, 334R, 335L, 337R, 338L age boundary not synchronous with lithologic boundary 107L, 115R, 116L, 159L–162L, 163R–164L, 165R, 213L Agua Fria area, Trans-Pecos, Brewster County, Texas 108, 116L, R, 129L, R Aguja Formation, Texas 24L Ahearn Member, Chadron Formation, South Dakota 158L, 162L, R Alamo Wash, San Juan Basin, New Mexico 45L, 65R, 66L, R, 67R Alamosa Formation, Colorado 279L Alaska 26R, 27, 95R, 111L, 132L, 239L, 249L, 255R, 256L, 270R, 272R, 275R, 280L, 285L, R, 292L, 318R, 230L, 326R, 327L, 334R Albian Stage/Age, faunas, rocks 22R, 23L, 317R Albuquerque Basin, New Mexico 196L, 198R, 199L, R, 257, 262R alien faunal elements 28L, 321R

Allerød pollen zone 238R allochthonous 13R, 209L, 210, 211L, 212R, 214L, 318R Almagre beds, New Mexico 109R, 130L, R Almy Formation, Wyoming 107R American Falls Formation, Idaho (early Bison) 245, 286L, 289, 295 Amynodon sandstone, Utah 111R analog vs nonanalog faunas 290R, 291L, R Andean Basin, northwest Argentina, southern Bolivia 92R, 93L, R, 94R Animas Formation, Colorado 76L Antarctic(a) 317R, 318L, 320L, 324R, 326L, R, 329R, 330L, 334L, 3336R Antelope Valley, Nevada 260L Anxiety Butte, Saskatchewan, Canada 192L Anza-Borrego Desert, California 232R, 256L, 257, 259L, 271L, R, 272L, R, 371L, 275R, 277 Anza-Borrego Desert State Park, California 258R, 259R, 271L, 277L Appalachian (region) 318R, 332L A-P Zone (= part of *Deltatherium* Zone, To2) 72R, 74L APTS (Astronomical Polarity Time Scale) xiL Aptian Stage/Age, faunas, rocks 23L Aquilan mammal age, faunas, rocks 21L, R definition and characterization 23L, R Arcadia Formation, Florida 204R, 207L Archaeolambda Interval Zone 91L Archusa Marl Member, Cook Mountain Formation, Mississippi 134L

Ardath Shale, California 123L, 124R Arenazzolo Formation, Messinian Stage, Italy 233R Argile Plastique, Sparnacian, France 89L Arikareean mammal age, faunas, rocks 156R, 166L, R, 171R, 173L, 174R, 176R, 179L, 187L, R, 188–189L, R, 191–192L, R, 193L, 196L, 201L, 204L, R, 205L, R, 206L, 208R, 209R, 211-212L, R, 331-332L, R, 333L, 338R definition and characterization 209R-211L zonation 209R-212R Arikaree Group, Great Plains, North America 173L, 179R, 188R, 189L, R, 192L, 193–194L, R, 196L, R, 197L, 209R, 211L, 212R, 213L Arroyo Chijuillita Member, Nacimiento Formation, New Mexico 45R, 66R, 67R, 72R, 75L arvicoline rodent biochronology, faunal zones 232L, 247L, R, 248, 250L, 253R, 254L, R, 258R, 274-276L, R, 278R, 279L, R, 281L, 292R, 293L, R, 294L Ash Hollow Formation, Nebraska 177R, 195R, 216L, R, 220R, 337L Asia 23R, 37R, 78R, 85R, 89R, 90-91L, R, 92L, 93R, 94R, 173R, 207R, 209L, 218L, 238L, 250L, 254-255L, R, 274R, 275R, 284R, 323, 324–326L, R, 328L, R, 329R, 330L, 334L, R, 336L, 338L Asian origins for: pantodonts 91L, 93R, 94R rodents 85R tillodonts 85R Asiostylops Interval Zone 91R Assemblage Chron xiL, R, 5, 15L Assemblage Fossizone or Fossilzone xiR, xiiR, 4, 5, 6L, R, 15L Assemblage Zone xiL, R, xivR, 5, 6L, R, 15L, 32L, 113L, 121R, 170L, 177L, 181, 191L Australian Creek beds, British Columbia, Canada 133L astronomical precession cycles 233R Australia 324R, 326L, 329R autochthone, autochthonous 209L, 211L, 212L, 215L, 217R, 218R Axel Heiberg Island, Nunavut Territory, Canada 108R, 109R, 111L, R, 133L, R Aycross Formation, Bighorn Basin, Wyoming 108L, R, 114L, R, 120L, 122L Baca Formation, New Mexico 109R, 115R, 130R, 131L Badwater Creek, Wind River Basin, Wyoming 115L, R, 118R, 120L, R, 121R, 160L

Baja California del Norte, Mexico 25L, 37R, 108L, 111L, 131R, 138L, 321R Baja California Sur 257, 264L Bajo de la Palangana, Bolivia 94R Bald Peak Volcanics, California 219R Balm Creek, John Day region, Oregon 187L Banco Negro Inferior, Argentina 94R Bandelier Tuff, Jemez Mountains, New Mexico 234, 262R, 271L Barstow Formation, California 9L, 171R, 173R, 174L, 175R, 177R, 178L, 191L, 213R, 214L, 215R Barstovian mammal age, faunas, rocks 171R, 172L, 173R, 174L, R, 175R, 176L, 177R, 178L, R, 188L, R, 189R, 190R, 191R, 192L, R, 195L, 196L, 197R, 199L, 200L, 202L, R, 203L, R, 204R, 206R, 207L, 208L, 209L, 213R, 214–215L, R, 216L, 217L, 260R, 332R, 334R, 335L definition and characterization 215-216L zonation 215L-216L Peridiomys-Parahippus Zone (Ba1) 191L Lignimus-Tardontia Zone (Ba2) 191L Barstovian-Clarendonian boundary 217L Bashi Formation, Mississippi 108L, 111L, 134L Bathygenys Interval Zone (earliest Chadronian) 162R Bayfield, San Juan Basin, Colorado 83R Bear Creek, Montana 50, 76R, 85R, 87L Bear Formation, Montana 62L, 69R Bearpaw Shale, Montana 24R Beaver Divide, Wind River Basin, Wyoming 108R, 115L, R, 121R, 158R Beaverhead Mountains, Idaho 187R *Bemalambda*, Interval Zone 91L Bena Formation, California 172L bentonite (itic) 63L, 123R, 134L Beringia(n) (dispersals) 91R, 254L, 274L faunal region 249L, 274R, 276R, 280L, 292R, 293R Bermont Formation, Florida 270R, 283R Betonnie-Tsosie wash, San Juan Basin, New Mexico 45R, 48, 66L, R, 71L, 72R, 73R BFE (benthic foraminiferal extinction) 320L Big Badlands, South Dakota 160L, 162L, 164R, 165L, R, 166L Big Basin Member, John Day Formation, Oregon 179L Big Bend area (National Park), Texas 69R, 77L, 80L, 82L, 83R, 85L, 108L, R, 129L, R, 134R, 201L, R, 211R

- Big Cottonwood Creek Member, Chadron Formation, Nebraska 158L, 161L
- Bighorn Basin, Wyoming 11R, 12L, 16L, 17L, R, 24L, 25R, 47, 50, 63R, 64L, 70R, 74R, 75R, 76R, 77L, R, 78R, 79L, 80L, R, 81L, 82–83L, R, 85L, 86L, 87L, R, 88L, 90L, 107R, 108L, R, 111R, 114L, 121, 122L, R, 122L, 125L, R, 132R,
- 135, 138L, 139L, 231L, 324R "Big Horn Wasatch," (= Willwood Formation) 107R

biocorrelation 14R

- biochron xiL, R, xiiL, 4, 5, 7, 16R, 17L, 43R, 113R, 114R, 115L, 116L, R, 117L, R, 125R, 131L, 135, 136, 137, 176R, 217L
- biochronologic (unit) xiL, xiiR, xiiiR, xivL, R, xviiiL, 1L, 2, 4, 5, 7, 9R, 10L, 13R, 14L, R, 15L, R, 16L, 17L, 18L, 43R, 45L, 46, 47, 53R, 63L, 64R, 66L, R, 68L, 69L, 70L, 75R, 76L, 79R, 90R, 95L, 106R, 109L, 111R, 112R, 131R, 138R, 139L, 171L, 175L, 179R, 193R, 194L, 195L, 197L, 198L, 204R, 205L, 209R, 239R, 252R, 254R, 268R, 270L, 279L, R, 281L, 292L
- biochronology xiR, xviiR, 1L, R, 3R, 6L, 12R, 14L, R, 15L, 16L, 21L, 23L, 24R, 35R, 44R, 46, 68L, 106L, R, 112L, 160R, 169L, R, 173R, 192R, 198R, 208R, 213L, 232L, R, 239R, 247R, 249L, 253R, 274R, 276L, R, 279R, 292L, 293R, 295L
- biogeographic (-graphy) 25L, 28L, 36R, 37L, 38L, 69R, 95L, 290R, 292L, R, 293R
- *Biorbia* seed assemblage, Ogallala Formation, Oklahoma 198L
- biostratigraphic (unit) xiL, R, xiiiL, R, xivL, R, xviiL, xviiiL, 2, 3L, R, 4, 5, 6L, 9R, 13R, 14L, R, 15L, R, 16L, 17L, 18L, 25L, 36R, 53R, 65L, 66L, 74L, 75R, 79R, 89L, 95L, 112L, R, 116R, 122R, 127L, 156L, 161R, 162L, R, 163R, 164L, R, 165L, R, 166R, 169R, 170L, 177L, 179L, 188L, 192R, 193L, 197R, 207R, 208R, 214L, 217R, 233R, 239R, 247L, 259L, 263L, 264R, 268R, 291L
- biostratigraphy viiL, xiR, 1L, 3L, R, 6L, 10L, 14R, 17R, 46, 53R, 90L, 158L, 162L, 164L, 173R, 176R, 177L, 179L, 187R, 191L, 193L, 196R, 197L, 200L, 207R, 232L, R, 239R, 268R, 270R, 283R, 295L
- biotic/abiotic 232R, 293L
- Biotite Tuff, Oregon 220R
- biozone xiR, xiiL, xiiiR, 2, 3R, 4, 7, 10R, 16R, 17R

Bishop Ash, Long Valley Caldera, California 234, 265R, 279R Bison Basin, Wyoming 77L, 81L, 82L, 83R Bitter Creek, Wyoming 126R, 127L Black's Fork Member, Bridger Formation 108R, 111L, 115R Blacksforkian subage (Br 1b, Br-2), Bridgerian mammal age 115L, R Black Peaks Member, Tornillo Formation, Texas 74R, 77L, 79L Blackwater Draw Formation, Texas 266R Blaine County, Montana 23R Blancan mammal age, faunas, rocks 175L, 178L, 200R, 201R, 207R, 218L, 232L, 233L, 235, 236, 239L, 246L, R, 247R, 248, 249–270, 271R, 272L, 273R, 274L, R, 276R, 277L, 278R, 280R, 281L, 282R, 283L, R, 289, 292L, R, 293R, 294–295L, R, 335R, 337R, 338L definition and characterization 250L, R geographic distribution 256L, R Pacific Northwest 256L, R Snake River Plain 256R-258R California 258R-260L Great Basin 260L–261L Southwestern U.S. 261L-263R Mexico 264R-264R Great Plains 264R-276R Florida 267R-268R historical treatment 249L-250L zonation 252L, 252R-256L Blancan I subage 253R, 254L, R, 256L Blancan II subage 253R, 254R–255L, 256L Blancan III subage 253R, 255L, R, 256L Blancan IV subage 253R, 254R-255R, 256L Blancan V subage 253R, 255R-256L Arvicoline Zones II and III 253R-254L Rexroadian subage 253L, R Senecan subage 253L, R Blancan-Irvingtonian boundary 263L, 269R, 277L, 283L Blanco Ash, Blanco Formation, Texas 266R Blanco Formation, Texas 253R, 266R Bonanza, Utah 126L boundary stratotype 233L, R, 237L, 238L, R, 239L, 295R bolide impact 320R Bølling pollen zone 238R Box Butte Formation, Nebraska 194R

Bracks Rhyolite, Texas 120L, 137, 138R Bramblett Formation, Texas 263R Branch Canyon Formation, Cuyama Valley, California 173R Brandon flora, Maine 332L Brennan Basin Member, Duchesne River Formation, Utah 109L, 112L, 117R, 118L, R, 126R, 136 Bridge Creek flora, Oregon 330L Bridger A-D (Bridgerian) 111L, R, 114R–115R, 128L, R Bridger E (early Uintan) 108R, 111L, 116L, R, 117L, 128L, 129R, 136 Bridger Formation 107L, 108R, 111L, R, 128L, R, 135, 136 "Bridger Group" 111L Bridgerian mammal age, faunas, rocks 106R, 107L–109R, 111L, 112R–117L, 120R, 121R, 122L, R, 123L, 124R, 126L, R, 127L, R, 128L, R, 129R, 130R, 131L, R, 132L, R, 133R, 134L, R, 135, 138L, R, 139L, 326L, R, 327L, R, 328L definition and characterization 113L-114R zonation 114R-115R Blacksforkian subage, (Br1b, Br2) 114R-115R Gardnerbuttean subage 107R, 113L, 114R, 115L, 121R, 126L, 135 Twinbuttean subage 115L, R Bridger A 108R, 111L, R, 115L, R, 128L, R, 135 Bridger B 108R, 111R, 115L, R, 128L, 135 Bridger C 111L, 115L, R, 128L, 135 Bridger D 115R, 116L, 128R Bridger E (early Uintan) 108R, 111L, 116L, R, 117L, 128L, 129R, 136 Bro, Gardnerbutean 107L, 108L, R, 113L, R, 114L, R, 115L, 121L, R, 126L, 127L, 131L, 134R Br1a, Gardnerbuttean 108L, R, 113R, 114L, R, 115L, 121L, 127L, 128R, 131L, R, 134L, 135R Brıb, Blacksforkian 108R, 114R, 115L, R, 128R, 135 Br2, Blacksforkian 108L, R, 114R, 115L, R, 120R, 122R, 123L, 126L, 127R, 135 Br3, Twinbuttean 107L, 108R, 114R, 115L, R, 116L, 117L, 120R, 125L, 127R, 131L, 135 Bridgerian-Uintan boundary 115R, 116L, R, 117L, 129L, 131R, 138L British Columbia 108R, 109R, 132R, 326R, 327L, 330L Brougher Dacite, Nevada 220L Brown Siltstone Member (Bed), White River Group, Nebraska 158L, 166R, 193L, 196L, 209R

Brule Formation, Nebraska, South Dakota 158L, 160L, R, 161L, 163R, 164L, 165R, 173L, 193L, 196L, 200L Bruneau Formation, Idaho 271L, 276R, 277 Brunhes magnetic polarity chron 233L, 238L, 259R, 261L, 263L, 274L, 278L, 279L, R, 280L, 281L, 285R, 287L Buckshot Ignimbrite, Texas 120L, 130L, 137, 138R Buffalo Canyon flora, Nevada 332L Bug Creek, Montana 35L, 36L, 51, 53L, 63R, 64L, R "Bugcreekian" (mammal age) 35L, 43L, 53L Bull Draw fauna (Irvingtonian, Cudahyan), Texas 273R, 277, 282R Bullhead Member, Fox Hills Formation, South Dakota 34L Bumbanian mammal age, Asia (approx. corresponds to Wasatchian) 89R, 92L Bunophorus Interval Zone 17R Burge Member, Valentine Formation, Nebraska 177R, 195R, 216L, R, 217L Burnt Fork Limestone, Bridger Formation, Wyoming 115R C_3/C_4 photosynthesis 335R Cabbage Patch beds, Montana 187R, 188R, 189L Cabrillo Formation, California 122R Cady Mountains, California 176R Calabrian Stage, Italy 236R Calcaires de Rona, Transylvania, Romania, ?Clarkforkian equivalent 89L calibration viiR, xviiiL, 1R, 8R, 10L, 11L, 14L, 93L, 95R, 134R, 135, 136, 137, 138L, 156L, 162L, 166L, R, 167L, 169L, 171R, 172L, R, 175L, R, 176L, 177L, 178L, 187L, R, 191L, 195R, 196L, 200R, 206L, 207L, 210, 211R, 212L, 233L, 238L, 254L, 258R, 259L, 261L, 267L, 275L, 290L Calico Mountains, California 214R Caliente Formation, California 173L, R, 174L, R, 214L, 219R Caliente Range, California 173L, R California Coast Ranges 171L, 203L, 214L, R Calvert Formation, Maryland 207R, 208L Campanian Stage/Age, faunas, rocks 22R, 23L, R, 24L, R, 25L, 37R, 92R, 317R, 318L, 321R Camp Rice Formation, New Mexico, Texas 257, 263L, R

Canada 23R, 26R, 37L, 45R, 46, 52, 62L, 63R, 68R, 69R, 71L, 81L, 83L, 95R, 106L, 108R, 109R, 111L, R, 132R, 191R, 192L, 239L, 249L, 257, 270R, 277, 280R, 289, 318R, 334R Cañon Rhyolite, Nevada 178R, 220L Canyada Pilares Member, Zia Formation, New Mexico 196L, 199L Cape Deceit, Alaska 257, 270R, 275R, 280L, 285L Capo Rossello, Sicily 233R Capote Mountain Tuff, Texas 160L Carbon Basin, Wyoming 77L, R, 80R, 82L carbon isotope (excursion) 32L, 36R, 43R, 89R, 90L, R, 92L, 106L, 138L, 316, 317L, 318L, 320L, R, 335R Caribbean (area, plate) 317L Carson Valley, Nevada 260L Carter, Wyoming 107R Carter County, Montana 26L Carter Mountain, Wyoming 122R Carthage-La-Joya Basin, New Mexico 131L Cascade Range, Oregon 187L, 327L, 330R, 331L, 332L, 337L Cathedral Bluffs Tongue of Wasatch Formation 107L, 108R, 112R, 113R, 114L, R, 115L, 126R, 127L, 128L, R Cedar Butte Basalt, Idaho 286L Cedar Creek Member, Orella Formation, Colorado 160L, 165L Cedar Mountain Formation, Utah 22R, 111L Cedar Mountain Member, Bridger Formation, Wyoming 111L Cedar Mountain, Wyoming 50, 51, 62L, 63R, 64L, 77R cement-bearing, hypsodontd (equid) cheek teeth 199L Cenomanian Stage/Age, faunas, rocks 22L, R, 23L, 317R, 318L Cenozoic System/Period, faunas, rocks 43L, 90R, 93L, 122R, 194R, 202L, 209L, 232L, R, 233R, 234, 247R, 252R, 260R, 292L, 316, 317L, 318L, 336R Cernasian mammal age, France 89L, R, 90L Cernay Conglomerate, France 89L, R Cerro Conejo Fm., New Mexico 221L Cerro Redondo, Argentina 94R Cerro Toledo B Ash, Kansas 234, 240, 266L Cerro Toledo X Ash, Texas 234, 240, 271L Cerro Toledo Rhyolite, New Mexico 234, 266L, 280R Cerrotejonian Stage 171L, R, 172L, R, 174R, 177L, R Cf1-Cf3 see Clarkforkian

Chappo Member, Wasatch Formation, Wyoming 49, 77L, 82L, 85L Chadron A, Nebraska (informal subdivision of formation) 158L Chadron B, Nebraska (informal subdivision of formation) 158L Chadron C, Nebraska (informal subdivision of formation) 158L Chadron Formation, Nebraska, South Dakota 156R, 158L, 160R, 161L, R, 162L, 163R, 164L purplish-white layers 159, 160R, 161L "Chadronian-aspect" taxa 119L, R Chadronian mammal age, faunas, rocks 106L, 109, 119L, R, 120L, 123R, 129R, 130L, R, 131L, 133L, R, 134L, R, 137, 138R, 156L, R, 158L, 159, 160–163L, R, 164L, 166R, 167L, 192L, 325, 328R, 329R, 331L definition and characterization 120L, 160L-162L zonation 162L-163R Earliest Chadronian 162R Late early Chadronian 162R Bathygenys Interval Zone (earliest Chadronian) 162R Leptomeryx yoderi Interval Zone (late early Chadronian) 162R Leptomeryx mammifer Interval Zone (middle Chadronian) 163L Miniochoerus chadronensis Inverval Zone (late Chadronian) 163R Chadronian-Orellan boundary 160L, R, 161L, 162L, 163R, 164L Chalk Cliffs (Hepburn's Mesa), Montana 190R, 191L Challis volcanics, Idaho 326R Chamberlain Pass Formation, South Dakota 158L Chambers Tuff, Texas 160L Chamisa Mesa Member, Zia Formation, New Mexico 198R Chamita Formation, New Mexico 200L, R Chanac Formation, California 172R characterize, characterization xiL, R, xiiL, 1L, 3L, R, 5, 6L, 11, 12, 13L, R, 16L, R, 17R, 21R, 28L, 36R, 43R, 44L, 62L, 65R, 66R, 71L, R, 78R, 79L, 83L, 85R, 86L, 93L, 95L, 111R, 113L, 115L, 116R, 117L, 118L, 119L, 120L, 121R, 134R, 138L, R, 161R, 162R, 164R, 165L, 166L, 170L, 171L, 176L, 177L, 191L, 192R, 193L, R, 194L, 206L, 209L, R, 211L, 212L, R, 213L, R, 214L, R, 215L, R, 217L, R, 218R, 219L, 249R, 250L, 253L, R, 254L, R, 255L, R, 256L, 263L, 269R, 270L, 271R, 273R, 274L, 275L, 276L, R, 283R, 284R, 290L, 291R, 293L, 294L, 318R, 324R, 328L, 330R, 332R

chemostratigraphy (ic) 10L, 32L, 36R Cheswold Sand, Calvert Formation, Maryland 208L Chiapas, Mexico 202R, 203L, 214R Chickaloon Formation, Alaska 132L Chimney Rock Ash, Nebraska 220R China 85R, 90R, 91R Chisos Formation, Texas 109L, 129R, 130L Choptank Formation, Maryland 207R, 208L Choteau County, Montana 23R Cripple Creek Sump, Alaska 285R chron xiL, R, xiiL, xiiiL, R, xivL, R, 2L, 4, 5, 7, 12R, 15L chronocline(s) 290L chronocorrelation 14R chronofauna xiiL, 166R, 173L, 193L, 194L, R, 195L, 197R, 205L, 206L, 209L, R, 214L, 215R, 216R, 217L, 218L, 328R, 329L, 330L, R, 331L, R, 332R, 333R, 334L, R, 335R, 337L chronology viiR, xiiiL, xviiR, 1L, R, 2R, 3L, R, 6L, 7, 8L, R, 9R, 10L, 12R, 14L, R, 15L, 16L, 24L, 171L, 175L, 179L, 209L, 210, 213L, 249L, 255R, 265R, 269R, 274R, 287L, R, 288L, R chronologic(al) viiL, R, xiiiL, xviiL, xviiiL, 1L, R, 5, 7, 8R, 9R, 13R, 14L, R, 16L, 17L, 169L, 171L, 172R, 175L, R, 176R, 180, 187L, 194L, 197L, 198L, 204L, 210, 213R, 215L, 218R, 239L, R, 247L, 253R, 257, 258L, 267R, 268R, 277, 279L, 285R, 287L, R, 289, 290L, 295L, 338L chronometric 239L chronostratigraphic (unit) xiR, xiiL, R, xivL, xviiL, xviiiL, 1L, R, 2L, R, 3L, R, 5, 6L, R, 7, 8L, R, 13L, R, 14L, R, 15L, R, 18L, 21L, 43R, 47, 95L, R, 161R, 238L, 239L chronostratigraphy viiL, xiiL, 1L, 2R, 3L, 5, 6L, R, 8L, 10L, 14R, 138R, 161R, 167L, 177L chronozone xiR, xiiL, xivL, 2L, 5, 6L, 7, 8L, R, 14R, 71R, 72L CIE (carbon isotope excursion, at LPTM) 106L, 316, 320L, R, 324R Cita Canyon, Texas 244, 255L, R, 257, 266R, 267L, 268R cladogenesis 213R, 232L Clarendonian Chronofauna 333R, 334L, R Clarendonian mammal age, faunas, rocks 174L, 176L, 177R, 178L, 195R, 197R, 198L, 200L, 207L, R, 216L, R, 217L, R, 218L, R, 260R, 332R, 333R, 334L, R, 335L definition and characterization 216L, R, 217L, R

zonation 217L, R Ustatochoerus profectus-Copemys russelli Assemblage Zone (Cl1) 177L Cupidinimus avawatzensis-Paracosoryx furlongi Assemblage Zone (Cl2) 177L Epicyon haydeni-Hipparion forcei Assemblage Zone (Cl2/3) 177L Clarendonian-Hemphillian boundary 195R, 217R Clarkforkian mammal age, faunas, rocks 43R, R, 44L, R, 45L, 46, 49, 61, 76R, 78R, 83R, 84R, 84R-88L, 89L, R, 90L, 91R, 92L, R, 95R, 112R, 120L, 122L, 125L, R, 126R, 127L, 128L, 129L, 131R, 134L, R, 138L, 321L, 324L, R definition and characterization 84R-86L zonation 86R-88R Rodentia/Plesiadapis cookei Interval Subzone (Cf1) 87L, R Plesiadapis cookei Lineage Zone (Cf2) 87R, 88L Phenacodus-Ectocion Acme Zone (Cf3) 88L, R Clarkforkian Stage/Age 16L Clarkforkian-Wasatchian boundary 134R, 138L, 324R Clark Fork faunal zone, Wyoming 84R Clark Fork Member, Polecat Bench Formation, Wyoming 84R Clarkia flora, Idaho 334L Clarks Fork Basin, Wyoming 16L, 17R, 46, 71R, 75R, 76R, 77L, 78R, 79L, 80L, R, 81R, 82R, 83L, R, 84L, R, 85L, R, 86L, R, 87L, R, 88L, 90L Clarkston Basin, Montana 160L Clarno flora, Oregon 327L, R, 330L Clarno Formation, Oregon 108R, 109R, 133R, 327L, R, 332L climate (atic) 232R, 237L, 238L, R, 266L, 280R, 286R, 287L, 290L, 291R, 292R, 293L, 294R, 315L, R, 316, 318L, R, 319, 320L, R, 321L, R, 324R, 326R, 327L, 328L, R, 329L, 330L, R, 331R, 332L, 333L, R, 334L, R, 336R, 337L, 338L in correlation 232R, 237L, 238L, R, 247R, 266L, 280R, 287L, 290L, 291L, 292L, 320L, 324R, 333R Climbing Arrow Formation, Montana 160L Coalspur Formation, Alberta, Canada 71L, 75L Coal Valley Formation, Nevada 220L Cobb Mountain magnetic polarity subchron of Matuyama Chron 240, 263L Cochiti magnetic polarity subchron of Gilbert Chron 240, 256R, 258R, 259L

Coldwater Formation/Sandstone, California 124R, 138R Coffee Ranch Ash, Texas 221L Colgate Member, Fox Hills Formation, South Dakota 34L Colter Formation, Montana 191L, R Colton Formation, Uinta Basin, Utah 108L, 114L, R, 125R Colmena Formation, Texas 109L, 188R, 130L Columbia Plateau, Nevada, Oregon 171R, 178L, R, 212R, 214R, 215L, 334R, 337L concurrent-range chron xiiL, 4, 15L concurrent-range zone xiR, xiiL, 4, 6L, 15L Coniacian Stage/Age, faunas, rocks 23L, R, 317 Continental Divide, North America 187R, 188L, R, 189L, R, 326L, R Copper Basin flora, Nevada 327R Cupidinimus avawatzensis-Paracosoryx furlongi Assemblage Zone, Clarendonian (Cl2), California 177L Cook Mountain Formation, Texas 134L Cornell Dam Member, Valentine Formation, Nebraska 195L correlation viiL, R, xiL, xiiL, R, xiiiR, xviiL, xviiiL, 1L, R, 2R, 3R, 5, 7, 8L, R, 9R, 12R, 13L, R, 14L, R, 15L, R, 16L, R, 17L, 18L, 21R, 23R, 24L, R, 25L, R, 26R, 32L, R, 34L, R, 36L, R, 43L, R, 44R, 45L, R, 46, 47, 63L, 65L, R, 66R, 67L, R, 68L, 69L, R, 71L, R, 72L, R, 73L, R, 74L, R, 75R, 76L, 77L, 78L, 79L, 80R, 81R, 82L, R, 84L, 87L, R, 88L, R, 89L, R, 90R, 91L, R, 92L, 93L, R, 94L, R, 95L, R, 106L, 109L, 113R, 119L, 120R, 121, 122L, R, 123L, R, 124L, 125L, R, 127L, R, 129L, 130L, 131R, 133L, R, 134L, R, 136, 138L, R, 156L, R, 158L, R, 159, 160L, 162L, R, 164R, 165L, 166L, R, 169L, 170, 171R, 172R, 173L, R, 174L, R, 175L, 176R, 177L, R, 178L, 179L, R, 180R, 188L, R, 189L, 191R, 192L, R, 193R, 194L, R, 197R, 198R, 199R, 201L, 204L, 205L, 206R, 207L, R, 209L, 214R, 216L, R, 219L, 233L, R, 234, 237L, 238L, 239L, R, 240, 247R, 251R, 252R, 255L, R, 256L, R, 258L, 260L, 261R, 263L, 265L, 266L, R, 267L, 268L, R, 270L, 278R, 281R, 283L, 285R, 287L, 291L, 294R, 295L, 315R, 317R, 318L, 320R, 324L, 330L, 334R, 335L, 338L Coryphodon zone 107R Coso Formation, California 257, 259R Cougar Point Tuff V, California 177L, 220L

Cougar Point Tuff XIII, California 220L Coyote Creek flora, Aycross Formation, Wyoming 120L Cozy Dell Shale, California 124R Crater Tuff-Breccia Member, Colter Formation, Wyoming 191R Crazy Johnson Member, Chadron Formation, South Dakota 158L, 162L, 163L Crazy Mountains (area, basin, field) 51, 69R, 70R, 71R, 73R, 74L, 76R, 77L, 80L, R, 81L, R, 82L Creede flora, Colorado 330L Cretaceous System/Period, rocks, faunas 21L, R, 22, 23L, R, 24L, 25R, 26R, 32L, R, 34, 35L, R, 36L, R, 37L, R, 43R, 53L, 62L, 64R, 89L, R, 92R, 93R, 95R, 111L, 116L, 122R, 130L, 315R, 317L, R, 318L, R, 319, 320L, R, 321L, R, 324L, 326L, R Cretaceous-Paleocene boundary 43R Cretaceous-Tertiary boundary 21R, 32L, R, 35R, 36L, R, 37L, 43R, 62L, 64R, 320L Cronese Tuff, California 220L Crooked Creek Formation, Kansas 265R Crookston Bridge Member, Valentine Formation, Nebraska 191R, 195R CTS (Classical Time Scale) xiiL, 9L, R Cuba Mesa Sandstone Member, San Jose Formation, New Mexico 45L, 48, 71R, 72R, 73R, 76L 130R Cub Creek, Montana 50, 75R, 77L, 80R Cub Mountain Formation, New Mexico 109R, 131L Cucaracha Formation, Panama 203R Cuchara Formation, Colorado 108L, 131L Cudahyan subage, Irvingtonian mammal age 273L, R, 274L Cudahy Ash 281R Cuisian Stage/Age, Europe 89R Cuyama Badlands, Cuyama Valley, California 173R, 174L, R Cuyama Valley, California 172R cyclostratigraphy viiR, xiiR, 10L Cypress Hills Formation, Saskatchewan, Canada 109L, 118R, 119R, 160L, 192L Cypress Hills Plateau, Saskatchewan, Canada 133L, 191R, 192L, R Cypress Hills, Saskatchewan, Canada 26R, 329L Dababiya section (Paleocene-Eocene boundary), Egypt 106R

Dakota Formation, Utah 22R Dano-Montian Stage/Age 94R

Dated Tuff, California 219R datum xiiR, xiiiL, R, xivL, xviiiR, 5, 13R, 14L, R, 15L, R, 17L, 23R, 44L, 203L, 215L, 258R, 269L, 334R, 335L Davis Ash, Ash Hollow Formation, Nebraska 195R, 220R δ¹³C excursion 11R, 18L, 32L, 43R, 89R, 90L, R, 92L, 316, 317R, 320L Debeque Formation, Colorado 85L, 108L, 125L, R deciduous (forest) 318R, 319, 320R, 321L, 324L, 326R, 327L, R, 328L, 330L, R, 332L, 333R, 334L, R Deep Creek Tuff, John Day Formation, Oregon 172R, 179R, 187R, 189R, 211L, R. 220R Deep River Formation, Montana 188L, 189R, 190R, 191L, 213R, 214R Deer Gulch lava, Idaho 240, 258L define (ing), definition viiL, xiL, R, xiiL, R, xiiiL, R, xivL, R, xviiR, xv-iiR, 2, 3L, R, 4, 5, 6L, R, 7, 8L, R, 13L, R, 14L, R, 15L, R, 16R, 17L, R, 18L, 21R, 22, 24R, 25L, 26R, 28L, R, 36L, R, 43R, 44L, 45R, 53L, R, 62L, 63L, R, 64R, 65L, R, 66L, R, 67R, 70L, R, 71L, 72L, R, 73L, 74L, R, 75L, 76L, 78L, R, 80L, 81L, 82L, R, 83R, 84L, 85L, R, 86R, 87R, 88, 89L, 90R, 91L, R, 93L, 95L, 106L, 111R, 112L, R, 114L, 115R, 117L, R, 118R, 120R, 121R, 122L, 130R, 131L, 132R, 158L, 160L, R, 161L, R, 162L, 164L, R, 165R, 166L, 175R, 177L, 191L, 192L, 193L, 194R, 195L, 203L, 205L, 209L, R, 211L, R, 212L, R, 312L, R, 214L, R, 215L, R, 216R, 217L, R, 218L, R, 219L, 233L, R, 237L, R, 238L, 239L, 247R, 248, 249L, R, 250L, 251L, 252R, 253R, 254L, R, 255L, R, 256L, 258R, 260R, 261R, 263L, 264R, 265R, 267R, 269L, R, 270L, 271R, 272L, R, 273L, 274R, 275L, R, 276L, R, 277R, 278L, 281R, 283L, 284R, 286L, 288L, 290L, 291R, 292L, 293L, R, 294L, R, 29RL, R, 335L, 337R base defines boundary 3R, 6L, 8R, 13L, 17R, 177L Delaho Formation, Big Bend area, Texas 201L Delmar Formation, California 108R, 122R, 123L, 124R Deltatherium Chronozone 72L Deltatherium zone 70L, 72L, R De-na-zin wash (Barrel Springs), San Juan Basin, New Mexico 45R, 48, 65R, 66L, R, 67R, 71L, 72R, 73R dentine tracts 247L Denver Basin, Colorado 49, 63R, 66R Denver Formation, Colorado 64R, 66R

117L, R, 118R, 129L, R Devil's Gulch Member, Valentine Formation, Nebraska 195R diachroneity, diachronous, diachrony xiiR, xiiiL, xivR, xviiiR, 10R, 36L, 138L, 239L, 249L, 256L, 272R, 292R, 293L Dinohippus HSD₁, 259L dinosaur (s) 21R, 24L, R, 26R, 28L, 35R, 36R, 37L, R, 64R, 93R Dinosaur Park, Alberta, Canada 24L disjunctive overlap fossilzone 5 disperse, dispersal(s) 13R, 14L, 23R, 78R, 88R, 89L, 90R, 91L, R, 92R, 93R, 94L, R, 95L, 106L, 209L, 239L, 247L, 249L, 254L, 292L, 293L, 315L, R, 316, 317L, 320L, 323, 324L, R, 325, 326L, 327R, 328L, R, 329R, 331L, 333, 335R, 336, 338L Dogtown Member, Torreya Formation, Florida 206R Domingo Basin, New Mexico 257, 262R Douglas, Wyoming 158R, 161L, R, 163L, 164L, R Dove Spring Fauna, California 177L, R Dove Spring Formation, California 175R, 176R, 177L, R Dragonian Mammal Age (= To1) 43L, 49, 62R, 70L, R, 71L, R, 72L, R, 73L, R Drake Passage 326L, 329R Drewsey Fm., Oregon 220R Drinkwater Basalt, Oregon 220R Dry Canyon Tuff, California 219R Dry Gulch Creek Member, Duchesne River Formation, Utah 109R, 112L, 118R, 126R Duchesnean-Chadronian boundary 120L, 161R Duchesnean mammal age, faunas, rocks 106R, 107L, 112L, 118L, R, 119L, R, 120L, 121, 122R, 123, 124L, R, 125L, R, 126L, R, 127, 129L, R, 130L, R, 133L, R, 134R, 136, 137, 138R, 139L, 161R, 328L, R, 329L, R definition and characterization 119L, R faunas restricted to those from Dry Gulch Creek and lower LaPoint members 112L time of faunal revolution and replacement 119L time of provinciality 119L Duchesne River Formation, Utah 107L, 109R, 111R, 112L, 116L, 117R, 118L, R, 126L, 136R

Devil's Graveyard Formation, Trans-

Pecos, Texas 198R, 109L, R, 116L,

160L Dunbar Creek Member, Renova Formation, Montana 160L Duncan Basin, Arizona 257, 261R, 262L Eagle Crag Ash, Nebraska 194L, 220R Early Eocene Climatic Optimum 320L early Wasatchian; see Sandcouleean Eastern Idaho, North America 187R Eastern Oregon, North America 178R East Fork Basin, Wyoming 115R, 117L, 120R, 135 Eastgate flora, Nevada 332L E-A Zone (= part of *Deltatherium* Zone, To2) 72R, 74L E. grangeri-Arctocyon ferox Interval Zone, 17L Ectoconus-Taeniolabis taoensis (Pu2) biochron 16R Ectoconus/Taeniolabis taoensis Interval Zone (Pu2) 63R, L, 65R, 66R EDE (Eolian Dust Event, at LPTM) 320L, R Eden Hot Springs, California 259R "Edmontonian" mammal age, faunas, rocks 21L, 24R, 25L, 26R, 28L, 32 definition and characterization 24R, 25L Edwards Plateau, Texas 280R egg shells (dinosaurs, birds) 93R Egypt 106R El Cameron Formation, Oaxaca, Mexico 202R El Casco, California 259R "El Gallo" Formation, Baja California del Norte 25L Elk Creek facies, Willwood Formation 107R El Kef, Tunisia 21R Ellesmere Island, Canada 108R, 111L, R, 133L, 138L El Molino Formation, Bolivia 94L El Salvador 203L Elsinore Fault zone, California 260L endemic (endemism) 13R, 18L, 23L, 35L, 37L, 88R, 90L, R, 91L, R, 92R, 93R, 94R, 117L, R, 120R, 131R, 178R, 187L, 188R, 198L, 199L, 201L, 203R, 204L, R, 205L, R, 206L, 214L, 215R, 233R, 246L, 274R, 294L, 318R, 321R, 323L, 324L, 328R, 331L environmental zone (zonation) 232R Eocene-Oligocene boundary 133L, 160R, 164L Eocene Series/Epoch, faunas, rocks 11L, R, 16L, 17L, R, 43L, R, 76R, 79L, 89L, R, 90L, R, 92L, R, 93L, 95R, 106L, R, 107R, 112L, 119L, 122L, R, 124L, R,

Dunbar Creek Formation, Montana

Woodburne IUSublinx 2/1//04 1:42 PM Page 369

Subject Index 369

125R, 126L, 129L, 130R, 131L, R, 132L, 133L, 134L, R, 135, 156R, 160L, R, 161R, 164L, 172R, 192L, 317L, R, 318L, 320L, R, 321L, 322, 324L, R, 325, 326L, R, 327L, R, 328R, 330L, 332L Eotitanops borealis Range Zone (Bro; lowest Gardnerbuttean) 113L, 114R Epicyon haydeni-Hipparion forcei Assemblage Zone (Cl2/3) 177L Equus (Equus) LSD₁ 259L Equus sp. LSD_k 259L Erethizon stirtoni LSD_k 259L Escavada Member, Nacimiento Formation, New Mexico 45R Escavada Wash, New Mexico 48, 74L, 75L Esmeralda Formation, Nevada 220L Española Basin, New Mexico 198R, 199L, R Etchegoin Formation, Kettleman Hills, California 255L Etla Member, Suchilquitongo Formation, Oaxaca, Mexico 202L Etla Tuff, Suchilqitongo Formation, Oaxaca, Mexico 202L, R, 221L Europe (an) 16L, 21L, 24L, 88R, 89L, R, 90L, R, 92R, 94R, 233L, 238L, R, 254R, 255R, 274R, 317R, 324R, 325L, R, 328R, 334R Evanston Formation, Wyoming 77L Evanston, Wyoming 127R, 128R evolutionary first occurrence xiiiR, 88L Euceratherium LSD_k 259L Eurasia(n) 173R, 207R, 209L, 247R, 250L, 254L, 255L, R, 284R, 331L Eureka Sound Group, Canada 108R, 109R, 133R, 138L extant 232L, 246L, 255R, 272L, 284R, 290L, 291L, 293L, 294R extinction(s) 37L, 38L, 89R, 90L, 92R, 160L, 179R, 193L, 194R, 195R, 209L, 212R, 213R, 218L, R, 238R, 244, 252R, 255R, 284R, 286L, R, 291R, 293L, 295L, 320L, R, 334L, 336L, R, 337R FAD (First Appearance Datum) xiiR, xiiiL, R, xivL, 13R, 14L, R, 15L, R, 23R, 28L, 35L, 36R, 37R, 44L, 65L, 77R Fairpoint Member, Fox Hills Formation, South Dakota 34L Fallon County, Montana 26L Farisita Formation, Colorado 108L, 131L Farrand Channel, Tullock Formation, Montana 51, 70R, 73L Fauna, faunal viiL, R, xiiR, xiiR, xivR, xviiL, R, 15L, 16L, R, 17R, 21L, R, 22L,

R, 23L, R, 24L, R, 25L, R, 26L, R, 27,

28L, R, 32L, R, 34L, R, 35L, R, 36L, R, 37L, R, 38L, 43R, 44L, 45L, R, 46, 49, 50, 51, 53L, R, 61, 62–95L, 106–107L, R, 109L, R, 111L, R, 112L, 113L, R, 115-134L, R, 138L, 157, 158L, R, 160L, R, 161R, 162L, R, 163L, 164L, 166L, R, 167L, 169–219L, R, 232–234L, R, 236, 237R, 238-242L, R, 244, 246-294L, R, 295L, 317L, 318R, 230R, 321R, 324L, R, 325L, 327L, R, 328-329L, R, 330R, 332L, R, 333R, 334-335L, R, 337L, 338R faunal facies xiL, 35L, 66L, 173L, 194L, 197L, 318R, 321R, 324L, 328L, R faunal turnover 44R, 89R, 90L, 114L, 174R, 176R, 177R, 178L, 193L, 194L, R, 195L, 200R, 209L, R, 211R, 212R, 213L, R, 217L, 218L, 328R, 329L, 334L FAUNMAP 288L, 291R, 292L, R, 293R, 294L faunule xiiR, 22L, 23L, R, 24L, 25R, 26L, 27R, 36R, 250R, 263L, 280L fern spike 320R Ferris (=No. 1) Coal Seam, Saskatchewan, Canada 35R Ferris Formation, Hanna Basin, Wyoming 16R, 27L, 36L, 50, 53R, 61R, 62L, 65L, 66L, R, 68L first appearance(s) 21R, 23L, R, 24R, 28L, 34L, 36R, 44L, 45R, 53L, R, 62-63L, R, 64R, 65R, 67R, 71L, R, 73L, 74L, 75L, 78L, R, 80L, 81L, 82L, R, 83R, 84L, R, 85L, R, 86L, 86R, 87L, R, 88L, 91L, R, 9RL, 112R, 113L, 114L, R, 116R, 117L, R, 118L, R, 119L, R, 120L, 122L, 133L, 161R, 162L, R, 163L, R, 164L, R, 165L, 166L, R, 174L, 176L, 179R, 187L, R, 188R, 189L, 193L, 194R, 195L, 196L, R, 200L, R, 204L, 209R, 211L, R, 212L, 214R, 215L, R, 216R, 217L, R, 218L, R, 247L, 250L, 252R, 253L, R, 254R, 255L, 258R, 261R, 268L, 269R, 270R, 271R, 272R, 273L, 274R, 275L, R, 276L, 280L, 283R, 284R, 285L, R, 286L, 288L, R, 295L, 323R, 324L, 325L, 327R, 328L, R, 331L, 332L, R, 324L First Division, Barstow succession 176L Flagstaff Limestone, Utah 125R Flagstaff Peak Formation, Utah 67L Flagstaff Rim, Bates Hole, Wyoming 158R, 161R, 162L, R, 163L, R Florissant flora, Colorado 327R Fly Tuff, Nevada 220L FOD (First Occurrence Datum) xiiR, xiiiL, R, xivL, 15R Foremost Formation, Alberta, Canada 24L

Fort Hancock Formation, Texas 263R

Fort Logan Formation 187R, 188R, 189R Fort Peck Reservoir, Montana 25R, 27, 28R, 32L, 34 Fort Union Formation, Montana, Wyoming 11R, 17L, 45R, 50, 51, 62L, 63L, R, 64L, 67L, 70R, 71R, 73R, 76R, 77L, R, 80R, 85L, R, 107R, 122L, 126R, 132L Fort Union Group, Montana, Wyoming 70R, 71R, 77L Fossil Basin, Wyoming 77L, 107L, R, 108L, R, 127R, 128R Fossil Butte National Monument, Wyoming 128R Fowkes Formation, Wyoming 107R, 108R, 128R Fox Hills Formation, South Dakota 26R, 27, 32R, 34L, R, 35R Frick Laboratory (collections, American Museum of Natural History) New York 164R, 165R, 166R, 188L, 198R, 199L, 285R Fraction Tuff, Nevada 220L Fraser River, British Columbia, Canada 133L Frenchman Formation, Saskatchewan, Canada 26R, 27, 35R, 52, 53L, R, 64R Frenchman River, Saskatchewan, Canada 26L Friars Formation, San Diego area, California 10L, 9L, 115R, 117L, 118L, 123R, 124L Fruitland Formation, New Mexico 24L, 25L Galisteo Formation, New Mexico 108L, 109R, 115R, 130R Garbani Channel, Tullock Formation, Montana 51, 68R, 73L Gardnerbuttean subage (Bro, Br1a), Bridgerian mammal age 107R, 113L, R, 114L, R, 115L, 121R, 126L, 135 Garfield County, Montana 64L Gashatan, Asian mammal age (approx. correlative with Clarkforkian) 90R, 91R, 92L Gauss magnetic polarity chron 233L, 253L, 255L, R, 256R, 258L, 259L, 261L, R, 262L, 283L, R, 265L, 267L, 268L, 269L, 279L geochron 7R, 160R geochronologic (unit) viiL, xiR, xiiL, xivL, 1-2L, R, 5, 7, 8L, R, 14L, 15L, 24L, 25R, 43R, 46, 47, 93L, 94R, 95L, 134R, 161R, 169L, 189R, 192R, 208R, 209R, 215R, 217L, 232R, 238L, 292L geochronology xiR, xiiL, xiiiL, 1L, 2R, 3L, 7, 8L, 43L, 106L, 134R, 135, 138L, 216R, 232R

geologic time 1R, 2L, R, 3L, R, 6R, 7L, 8R, 9R, 127L, 209L, 233L, 293L Gering Formation, Nebraska 158L, 179R, 187R, 188R, 189L, R, 193L, 209R, 211L Germer flora, Idaho 326L, R Gila River Valley, Arizona, New Mexico 232R Gilbert magnetic polarity chron 233L, 256R, 258L, 259R, 261L glacial, glacial stages, glaciation 191R, 232R, 236L, 237R, 238L, 252R, 280R, 283L, 285R, 287L, R, 288L, R, 290R, 291L, R, 315L, R, 317L, R, 318L, 326L, R, 327L, 329R, 330L glacial till 237R, 288L, R glacio-eustatic (sea level) changes 315R, 317R, 318L Glendive, Montana 67L Glenn's Ferry Formation, Idaho 256R, 258L, R, 271L global xiiL, R, xiiiL, R, xviiR, 5, 7, 8L, R, 9R, 13R, 18L, 21R, 35R, 36R, 37L, 88R, 89R, 90L, 106R, 134R, 138L, 156L, R, 160L, 166R, 209L, 233L, R, 237L, 315L, R, 316, 317R, 320L, R, 324R, 326L, 327L, 330L, 334L, R, 335R, 338L Golden County, Montana 24L Golden Valley Formation, North Dakota 108L, 111L, 132L golden spike 7, 8L Goler Formation, California 53, 62R, 70R, 77L, 81L Gondwanan "Stage," Argentina 92R Gosport Sand, Claiborne Group, Alabama 108R, 134L GPTS (Geomagnetic Polarity Time Scale) xiiiL, 9L, R, 10L, 11L, R, 12R, 22L, 32R, 34L, 65L, 93R, 94L, 138L, 169L, 173L, 209L, 233L, R, 237L, 239L, 254R grass, grassland 326R, 327L, 332L, 333R, 334R, 336L, 337L Gray Bull beds 107R, 108L Graybullian subage (Wa3-Wa5) of Wasatchian mammal age 107L, 111L, 113L, 122L, 130R, 132L, 135 characterized 113L Great American Interchange (GAI), (biotic, faunal) 253L, 268R, 269L, 316, 317L, 336, 338L Great Basin 176L, 178L, 199R, 212R, 214L, 215R, 218L, 328R, 331L, 332R, 335R, 336R, 337L northern 175L-178L, 214L southern 169L, 198R-202L, 214L Great Divide Basin, Wyoming 107R, 126R, 127L, R, 158R Great Plains, North America 169L, 172L, 173L, R, 174R, 176R, 177R, 178L,

R, 179R, 187L, R, 188L, R, 189L, R, 190R, 191L, R, 192L, R, 193L, R, 194L, 195L, R, 196R, 197R, 199R, 200L, R, 201L, 202R, 203R, 204L, R, 205L, R, 206L, R, 207L, R, 209L, 211L, R, 212L, R, 214L, 215L, R, 217L, R, 218L, 219L, 237R, 247R, 252R, 253L, 255L, R, 256L, 258R, 264R, 265L, R, 266L, 272L, 273R, 274L, R, 280R, 285R, 287R, 290R, 291L, 331L, 332L, R, 333R, 334R, 335L, 336R, 337L greenhouse, icehouse conditions 156R, 315L, 317R, 318L, 320R, 326R, 329R Greenland (dispersal) 90R, 239L Green River Basin, Wyoming 82L, 85L, 87R, 106R, 107L, 108L, R, 109L, 111R, 113L, R, 114L, R, 115R, 116L, 125R, 126L, 127L, R, 128L, R, 131L, 132L, 135, 136, 138L, 139L Green River flora 326L, R Green River, Formation, Wyoming 108L, R, 109R, 113R, 114L, R, 115L, 125L, R, 126L, R, 127L, 128L, R Green Valley Formation, California 171R Grey Tuff, Wilkins Peak Member, Green River Formation 113R, 114L, 128L GSSP (Global Boundary Stratotype Section and Point) 7, 8L, 90L, 106R, 134R, 237L Guaje ash, Mt. Blanco, Texas 234, 240, 253L, 266R Guaje Pumice, Otowi Member, Bandelier Tuff, Jemez Mountains, New Mexico 234, 266R, 271L Guanajuato, Mexico 108R, 131R, 201R, 218R, 257 Hackberry Wash, California 176R Hagerman Fossil Beds National Monument 255L, 256R Halfway horizon, Duchesne River Formation 112L Hand Hills, Alberta, Canada 191R Hanna Basin, Wyoming 1L, 16R, 17R, 27L, 50, 61L, 63R, 65L, 66R, 70R, 73L, 75R, 77L, R, 78L, R, 80R, 81R, 82L, 107R Hanna Formation, Wyoming 70R, 77L, R Hannold Hill Formation, Texas 108L, 111L, 129L Haplomylus-Ectocion Range Zone 17R harmonious (vs disharmonious) faunas 290R Harrison Formation, Nebraska 191L, R, 193R, 194L, R, 196R, 197L, 198R, 201L, 204L, 205R, 208R, 209R, 211R, 212L, R Hartford Ash 234, 237R, 240, 281R

Hart Mine Formation, New Mexico 108R, 130R, 131L Hatchetigbee Formation, Alabama 108L, 134L Haughton Astrobleme, Devon Island, Canadian Arctic Islands 192R, 338R Hawthorn Formation, Florida 206L Hawthorn Group, Florida 206L, 207L Haystack Mountain, Wyoming 127R Haystack Valley, John Day region, Oregon 187L Haystack Valley Member, John Day Formation, Oregon 179L, R, 187L Hector Formation, California 176R, 219R Hell Creek Formation, Montana, North Dakota, South Dakota 24R, 25R, 26L, R, 27, 28R, 32L, R, 34L, R, 36L, R, 53L, R, 62L, 63L, R, 64L, 95R Hell Creek, Montana 32L Hemicyon Tuff, Barstow Formation, California 215R, 219R Hemingfordian mammal age, faunas, rocks 172L, 173R, 174R, 175L, R, 176R, 178L, R, 187L, R, 188R, 189L, 191R, 192L, R, 195L, R, 196L, 198R, 199L, 201L, R, 202L, 204R, 206R, 208L, 209L, 211R, 212R, 213L, R, 214L, R, 332R, 333L, 334L, R definition and characterization 212R, 213L, R zonation 213L, R Hemingford Group, Nebraska 212R Hemithlaeus kowalevskianus-Taeniolabis taoensis Zone 16R Hemphill beds, Texas 200R Hemphillian mammal age, faunas, rocks 175L, 177R, 178L, R, 195R, 198L, 200R, 201L, R, 203R, 207R, 216L, 217L, R, 218L, R, 219L, 232L, 244, 247R, 248, 249R, 250R, 251L, R, 252L, 253L, 256L, 257, 259R, 260L, R, 262L, 263L, 264L, R, 265L, 267R, 332R, 333R, 335R, 336L, 337L, R, 338L definition and characterization 217R-219L zonation 217L-219L Paronychomys-Borophagus littoralis Assemblage Zone (Hh1) 177L Hemphillian-Blancan boundary 178L, 251L-252L, 260R, 263R, 264R Hemphill Member, Ogallala Formation 217R Hendry Ranch Member, Wagon Bed Formation, Wyoming 109L, R, 121R Henry Mountains, Utah 23R Hepburn's Mesa, Montana 188L Hepburn's Mesa Formation, Montana 190R, 191L, R Heptodon Range Zone 17R

hiatus 2, 10R, 23R, 89R, 126R, 172R, 174L, 177L, 194L, 197L, R, 199R, 211R, 215R, 216R, 326L Hidalgo, Mexico 251R Hickey Mountain Limestone, Bridger Formation, Wyoming 115R Hickey Mountains, Wyoming 128L high latitudes; independent chronology needed 249R High resolution chronology, chronostratigraphy viiL, 1R, 8L, 156L, 165R, 167L Himalayan-Tibetan plateau 331R, 336L Hippotherium Datum 13R, 335L HO (Highest Stratigraphic Occurrence) xiiiL, R, xivR, 71L, 74R, 174L Hoback Basin, Wyoming 49, 77L, 82L, 83R, 85L, R, 87R, 108L, 111L, 127R, 128R Hoback Formation, Wyoming 47, 77L Holarctic 90L, 292R, 293R, 323L, 324R, 325R, 326L, 338L Holocene 233L, 238L, R, 247R, 269R, 286R, 288R, 290L, R, 291L, 292R, 293R, 294L, R, 295R Honduras 203L, 217L Hoploscaphites birkelundi Range Zone 34R Horseshoe Canyon Formation, Alberta, Canada 259L HSD (Highest Stratigraphic Datum) xiiiL, 259L HSD_k, highest known stratigraphic occurrence 259L Huckleberry Ridge Ash, Yellowstone, Wyoming, western U.S. 234, 240, 261L, 263R, 265R, 266L, 273R, 279R, 280R, 44 Heuco Bolson, Texas 257, 263L Huerfano A 131L Huerfano B 121R, 131L Huerfano Formation, Colorado 108L, R, 112R, 114R, 131L, R Huerfano Park, Colorado 113L, 114L Hurlbut Ash, Valentine Formation Nebraska 195L, 200L, 215R, 220R Hypertragulus calcaratus Interval Zone (earliest Orellan) 164R hypsodont(y) 247L Icehouse World see greenhouse ICS (International Commission on Stratigraphy xiiiL, 233R IGCP 90R Illinoian glacial stage (Pleistocene) 237R, 238L, 285R IMBS (Integrated magnetobiostratigraphic scale) xiiiL, 9L, R, 10R, 11R immigrant, immigrate, immigration xivL, xviiR, 7, 13R, 17R, 18L, 37R,

194R, 195L, 196R, 199L, 204R, 206L, 207R, 209L, R, 210, 211R, 212L, 213L, R, 214L, R, 216R, 218L, R, 253L, 254L, R, 255R, 268L, R, 269L, 274R, 275L, R, 276L, 284R, 321R, 323L, R, 324L, R, 325, 327R, 328R, 331R, 332R, 333L, 334L, R, 335L, R, 337R, 338L Imperial Formation, California 258R index fossils (taxa) 16R, 44L, 62R, 63L, R, 64L, 65R, 67R, 68L, 70L, 71R, 72L, 73R, 75L, 76L, 78L, R, 79R, 80R, 81R, 82R, 83R, 84L, R, 85R, 86L, 87L, R, 88L, 112R, 117L, 118R, 119L, 133L, 162L, R, 163L, R, 165R, 167L, 209R, 249R intercontinental (correlation, dispersal) 44R, 88R, 138L, 139L, 209L, 254L, 324R interglacial(s), times 317L Interior Paleosol, South Dakota 158L International Geological Congress 236R, 237L International Geological Correlation Project 237L International Stratigraphic Guide (ISG) 43R, 44L International Union for Quaternary Research (INQUA) 237L, 238R Interval Chron xiiiL, xivL, 4, 15L Interval Subzone 79L, R, 80L, 84L, R, 85R, 87L Ti6 interval subzone 79L, R, 80L, 84L, R, 85R, 86R Cfi interval subzone 84L, R, 86R, 87L Interval Zone xiL, R, xiiiL, R, 4, 5, 6L, R, 15L, 16L, R, 17L, R, 35L, 44L, 45R, 53R, 61L, 63L, R, 64L, R, 65L, R, 66L, R, 67L, R, 68L, R, 69L, R, 70R, 71L, R, 72L, R, 73L, R, 74L, R, 75L, R, 76L, 79L, 80R, 87R, 91L, 93R, 95R, 162R, 163L, R, 164R, 165L, R, 166L Archaeolambda Interval Zone 91L Asiostylops Interval Zone 91R Bemalambda Interval Zone 91L Puo interval zone 53R, 61L Pu1 interval zone 44L, 45R, 49-52, 53R, 54-60, 61L, 63-65L, R, 66R, 68L, 80L Pu2 interval zone 45R, 48-52, 54-60, 61L, 63–69L, R, 71L, 93R, 95R Pu3 interval zone 45R, 48-52, 54-60, 61L, 63L, R, 64R, 65L-69L, R, 70L, 71L, 73L, 95R Sinostylops Interval Zone 91R T-P interval zone 67R To1 interval zone 71L, R, 72L, R, 73L, R To2 interval zone 72L, R, 73R, 74L, R, 91L To3 interval zone 72L, R, 73L, 74L, 75L, R, 76L, 79L, 80R

iridium (anomaly) 9L, 21R, 28R, 32L, 35R, 43R Iron Lightning Member, Fox Hills Formation, South Dakota 27, 32R, 34L, R Iron Springs Formation, Utah 23L Irvington, Alameda County, California 269L Irvingtonian mammal age, faunas, rocks 233L, 235, 236, 239L, 246L, R, 247R, 248, 249L, 250L, R, 252R, 256L, 257, 258R, 259R, 260L, 261L, 262R, 263L, 264L, R, 265R, 266R, 267L, R, 268L, 269L, R, 270L, R, 271R, 272L, R, 273L, R, 274L, R, 275L, R, 276L, R, 285L, 288L, 289L, R, 292L, R, 293L, R, 294L, R, 295L, R arrival of Mammuthus 270R-271R definition and characterization 269R-270R geographic distribution 276R-284R California 276R–278R Eastern Caves 284L, R Florida 283L, R Great Basin 278R Great Plains 280R-283L Rocky Mountain region 279L-280L Snake River Plain 276R Southwestern U.S. 280L, R Mexico 280R historical treatment 269L small mammal definition 271R, 272L zonation 273L-276L arvicoline rodents 274L, R Irvingtonian I subage 274R, 275L, R Irvingtonian II subage 275L, R, 276L Irvingtonian III subage 276L, R Sappan subage 273L, R Cudahyan subage 273L, R, 274L Sheridanian subage 273L, R, 274L isochron, isochroneity, isochronous xiiR, 3R, 6R, 7R, 8L, 14L, R, 15R, 215L, 249L, 293L Itaboraían mammal age 94L Itaboraían mammal subage 95L Itaboraí district, southeastern Brazil 92R, 93L, 94L Italy, Italian 237L, R, 238L, 295R IUGS (International Union of Geological Sciences) xiiiL, 237L Ixtapa Formation, Chiapas, Mexico 203L, 214R

intracontinental (correlation, disper-

sal) 138L, 254L

Jackrabbit Trail, California 259R Jackson Group, Arkansas 108R, 134L

⁷⁸R, 85R, 91L, 92R, 114R, 174L, 193L,

Woodburne_tosubtinx 2/1//04 1:42 PM Page 3/2

372 Subject Index

Jalisco, Mexico 251R Jaramillo magnetic polarity subchron of Matuyama Chron 233L, 240, 258R, 259R, 263L, 269L, 279R, 280L Javelina Member, Tornillo Formation, Texas 62L, 69R Jaw Face section, Wellsch Valley, Saskatchewan, Canada 281L Jbel Guersif Formation (Thanetian), Morocco 92L Jefferson Basin, Montana 160L Jeletzkytes nebrascensis Range Zone 34L John Day 'fauna,' Oregon 179R, 187L, 188R, 212R, 332L John Day Formation, Oregon 172R, 173L, 174R, 179L, R, 187L, R, 189L, R, 193L, 204L, R, 206L, 209R, 211L, R, 327L John Day region, Oregon 178R, 179L, 188R, 327R, 331L, 332L, 333R John Henry Member, Straight Cliffs Formation, Utah 23L Jones Spring, Missouri (early Bison) 286L, 289, 295L Judithian mammal age, faunas, rocks 21L, R, 23R, 24L, R, 25L, 28L, 37R, 318R definition and characterization 23R-24R Judith River Formation, Montana 23R, 24L, R Judith River Group, Alberta and Saskatchewan, Canada 24L Juntura Formation, Oregon 220R Kaena magnetic polarity subchron of Gauss Chron 240, 256R, 258L, 259L, 262L, 263L Kaiparowits Formation, Utah 24L Kaiparowits Plateau, Utah 23R Kansan glacial stage (Pleistocene) 237R, 238L, 281L Kansan till 237R KE (kaolinitic event, at LPTM) 320L, R Kemp Clay Formation, Texas 28L Kilgore flora, Nebraska 334R Kimbeto wash, San Juan Basin, New Mexico 45L, R, 48, 66R, 71L, 72R, 73R, 74L Kinney Rim Member, Washakie Formation, Wyoming 108R, 115L, 127R Kirkwood Formation, New Jersey 207R, 208L, R Kirtland Formation, New Mexico 24L, 25L, 27, 28L, 34, 36R, Kishenehn Formation, British Columbia, Canada 109R, 132R Kisinger Lakes flora, Wyoming 326R Kneehills Tuff, Scollard Formation, Alberta, Canada 32R

Knight Formation, Wyoming 107R, K-T boundary 9L, 21R, 32L, 35R, 36L, R, 37L, 38L, 320R Kutz Canyon, New Mexico 48, 71R, 72L, R, 73R, 74

LaBarge, Wyoming 108L, 128L LAD (Last Appearance Datum) xiiiL, R. 14L Laguna Umayo (area), southeastern Peru 92R, 93L, R Lake Titicaca, Peru 93L Lambdotherium Range-Zone (Lostcabinian, Wa-7) 113R, 121R Lance Creek, Wyoming 25R, 34L, R Lance Formation, Wyoming 25R, 26R, 27L, 34L, 36L Lancian mammal age, faunas, rocks 16R, 21L, R, 22L, 24R, 25–28L, R, 32L, R, 34–37L, R, 38L, 45R, 46, 53L, R, 61L, 62L, 63L, 64L, R, 92R, 318R, 320R, 321L, R definition and characterization 28L, R Lancian-Puercan boundary 21R, 35R, 36L, R, 62L, 64L land mammal age(s) viiL, viiiL, xivL, R, 8R, 15R, 21L, R, 22L, 23–25L, R, 26R, 27, 28R, 35L, 36L, R, 43L, R, 76R, 90R, 91L, R, 93L, 95L, 106L, 139L, 156L, R, 158L, 166R, 169R, 175R, 232L, 240, 244, 246R Laney Shale Member, Green River Formation, Wyoming 113R, 114R, 115L La Palca, Bolivia 94L Lapilli Tuff, California 220L LaPoint Ash, LaPoint Member, Duchesne River Formation, Utah 118R, 119L, 136 LaPoint horizon, Duchesne River Formation 112L LaPoint Member, Duchesne River Formation, Utah 109R, 112L, 118R, 119L, 126R Laramie Basin, Wyoming 108L, 111L, 132R Laramie Formation, Colorado 27R, 34 Laramie Range, Wyoming 158R Laredo Formation, Texas 109L, 118R, 134L Largo beds, New Mexico 109R, 130L, R last appearance(s) xiiiR, 5, 16R, 23R, 28R, 36R, 44L, 62R, 63L, R, 65R, 67R,

28R, 36R, 44L, 62R, 63L, R, 65R, 67R, 69R, 71R, 72L, 73R, 75L, 76L, 78R, 79R, 60R, 81R, 82R, 83L, 84L, R, 86L, 87L, R, 88L, 112R, 113L, 114R, 115L, 117R, 118L, 119L, R, 163R, 164L, R, 165L, 166L, R, 176L, 187L, 189R, 190R, 196R, 199R, 200R, 204L, 207R, 209R, 211L, R, 212L, 213R, 215L, 216L, 217R, 218R, 219L, 247R, 249R, 252R, 253R, 256L, 268L, 273R, 276R, 283R, 324R, 327R, 331L

- Late Cretaceous, faunas, rocks viiL, 16R, 21–22L, R, 23L, 26R, 32L, 36L, R, 37L, R, 38L, 62L, 64R, 92R, 93R, 315R, 317–318L, R, 319, 320–321L, R, 323L, 326R
- Lava Creek B Ash (Pearlette-O) 234, 237R, 240, 273R, 280R, 281R, 282L, R, 285R
- Laverne Formation, Oklahoma 197R, 198L
- Lawlor Tuff, Etchegoin Formation, California 219R, 234, 255L
- Lebo Formation, Montana 70R, 73L, R, 80R
- *Leptauchenia* beds, Brule Formation, Big Badlands, South Dakota 159, 165R, 166L
- *Leptauchenia major* Interval Zone (early Whitneyan) 165R
- *Leptomeryx mammifer* Interval Zone (middle Chadronian) 163L
- *Leptomeryx yoderi* Interval Zone (late early Chadronian) 168R
- Lepus LSD_k 259L
- Leslie Gulch Tuff, Sucker Creek Formation, Oregon 187R
- *Lignimus-Tardontia* Zone (Ba2), Hepburn's Mesa Formation, Montana 191L, R
- Lineage Chron xiiiR, xivL, 4, 15L
- Lineage Zone xiR, xiiiR, 2, 4, 5, 6L, 15L, 16L, 17L, 44L, 78R, 79–84L, R, 86R, 87L, R, 89L, 91R
 - Tiı lineage zone 79L, 80L, R, 81L, 82L, 83R
 - Ti2 lineage zone 78R, 79L, 80L, R, 81L, R, 82L Ti3 lineage zone 79L, 80L, 82L, R,
 - 83L
 - Ti4 lineage zone 79L, 80L, 82R, 83L Ti5 lineage zone 79L, 80L, 83L, R, 84L, 91R
 - Ti6-Cfi lineage zone 79L, R, 80L, 84L, R, 86R, 87L, 89L
- Cf2 lineage zone, 86R, 87L, R lithologic 2, 3L, 10R, 13L, 15R, 18L, 34, 45L, R, 70L, 94R, 107L, R, 111R, 112L, 113R, 115R, 116L, 124R, 128L, 131L, R, 158R, 160R, 187L, 196L, R, 200L
- lithostratigraphic (unit) viiL, xviiL, 2L, R, 3L, R, 7, 10L, 13L, 106R, 107R, 111R, 112L, 123R, 158L, 159, 161R, 162L, 163R, 164L, 165R, 170L, 179L, 187L, 193L
- lithostratigraphy xivL, 3L, 156R, 160R, 164L, 166L, 172L, R, 176R, 179L, 193L, 197L, 198R, 209R

Little Cove Point Unit, basal St. Mary's Formation, Maryland 208L Llajas Formation, California 124L, R Llano Estacado, Texas 266R Llaves Member, San Jose Formation, New Mexico 130R LMA (land mammal age) 106L, R, 107L, 111L, R, 112L, 113L, 114R, 115R, 119L, 128L, 138L LO (Lowest Stratigraphic Occurrence) xiiR, xiiiR, xivL, R, 6L, 14L, 15R Lobato Basalt, New Mexico 221L Local Fauna(s) xiiR, xiiiR, 169R, 170L 111 Ranch fauna (Blancan, Blancan V), Arizona 244, 255R, 257, 261L, R, 263L, 268L, R Adams Fauna (Irvingtonian, Sheridanian; Rancholabrean), Kansas 274L, 288R Agate Springs Local Fauna (Arikareean, Ar4), Nebraska 209R, 212R Aguila Fauna (Blancan), Texas 263R Ahearn Member faunas (late early Chadronian), South Dakota 162R Airstrip Local Fauna (Chadronian), Texas 130L, 160L Alamos Canyon Local Fauna (Arikareean, Ar2), California 172R Anceney Local Fauna (Barstovian, Ba1), Montana 190R, 191L Angus Fauna (Irvingtonian, Sheridanian), Nebraska 274L, 285R Archusa Marl Fauna (Uintan), Mississippi 134L Argonaut Fauna (early Blancan), Kansas 265L Aries A Fauna (latest Blancan; Sappan), Kansas 265R, 266L, 270L, 273R, 295L Aries B Fauna (latest Blancan/ Irvingtonian), Kansas 265R, 270L, 295L Arroyo Seco Fauna (middle Blancan), California 258R Artesia Road Fauna (Blancan), Arizona 261R Ash Hollow Formation faunas (Clarendonian-Hemphillian), Nebraska 177R, 195R, 216R Axtel Local Fauna (Hemphillian, Hh4), Texas 200R Ash Springs Local Fauna (late Chadronian), Texas 129R, 130L, 163L Balm Creek Member Fauna (Arikareean, Ar3), Oregon 187L Barker's Ranch Local Fauna (late Hemingfordian, He2), California 172L

Barstow Fauna (Barstovian, Ba2), California, 171R, 174L, 176L, R, 177R, 215R Bear Creek Local Fauna (Clarkforkian, Cf1) 50, 76R, 85R, 87L Beaver Fauna (Clarendonian, Cl2), Oklahoma 197R, 198L Beaver Quarry Local Fauna (Clarendonian, Cl2), Oklahoma 198L Beck Ranch Fauna (Blancan), Texas 250L, 257, 267L Bee Canyon Landfill Fauna (Hemingfordian, He1), California 174R Belen Fauna (Blancan), Albuquerque Basin, New Mexico 262R Benson Fauna (early Blancan), Arizona 261L, R Berends Fauna (Irvingtonian, Sheridanian), Oklahoma 274L Big Spring Canyon Local Fauna (Clarendonian, Ca1), South Dakota 216L Birch Creek Fauna (late Blancan), Idaho 258L Black's Beach Local Fauna (late Bridgerian/early Uintan), California 108R, 123L Black Butte Fauna (late Blancan), Idaho 258L Black Hawk Ranch Local Fauna (Clarendonian, Montediablan, Cl3), California 171L, R, 172R Blacktail Local Fauna (Lancian), Montana 26L, 27 Blacktail Deer Creek Fauna (Arikareean, Ar1/2), Montana 189L Blanco Fauna (early Blancan, Rexroadian), Texas 249L, R, 253L, R, 257, 266R, 267L, 268R Blufftop Fauna (early Blancan), Washington 256R Bolero Lookout Local Fauna (Hemingfordian, He1), California 174R Bone Valley Fauna (Hemphillian, Hh4) Florida 204R Borchers Fauna (late Blancan), Kansas 234, 245, 265R, 266L, 272R, 291L Boron Local Fauna (Hemingfordian, He1), California 176R Brea Canyon Local Fauna (late Uintan), Ventura County, California 109L, 124L, R, 125L Broadwater Fauna (early Blancan, Rexroadian; Arvicoline Zone II), Nebraska 253R Brooksville 2 Local Fauna (Arikareean, Ar2), Florida 205R

Buckeye Creek Local Fauna (Blancan, Bl1), Nevada 178L, 257, 260L Buckhorn Fauna (Blancan), New Mexico 257, 262R Buckman Hollow Local Fauna (Clarkforkian, Cf2), Wyoming 49, 87R Buda Local Fauna (Arikareean, Ar2), Florida 205L, R, 206L Buis Ranch Local Fauna (Hemphillian, He3/4), Oklahoma 198L, R, 200R Burkeville Fauna (Barstovian, Ba2), Texas 214R Burge Fauna (Clarendonian, Cl1), Nebraska 177R, 195R, 216L, R, 217L Butler Spring Fauna (Rancholabrean) 288R, 291L Cabbage Patch Fauna (Arikareean, Ar1/2), Montana 187R, 188R, 189L, R Calgary 2E Local Fauna (Torrejonian, To3?), Alberta, Canada 52, 75R California Wash Fauna (late Blancan), Arizona 261L Candelaria Local Fauna (Uintan, Ui-3), Texas 109L, 118R, 130L California Oaks Fauna (Blancan), California 265R Camp Cady Fauna (Rancholabrean), California 286L, 289 Cape Deceit Fauna (Irvingtonian), Alaska 257, 270R, 275R, 280L, 285L Carlton Bar Fauna (Irvingtonian), Alberta, Canada 270R Casa Blanca Local Fauna (late Uintan), Texas 109L, 118R, 134L, R Castle Butte Fauna (late Blancan), Idaho 258L Castolon Fauna (Arikareean, Ar3), Texas 201L, R, 211R Cathedral Bluffs Fauna, (Wasatchian, Wa-7), Wyoming 128L Cathedral Cave Fauna (Irvingtonian, ?Cudahyan), Nevada 272L, R, 274L, 275R, 276L, 277, 278R, 280L, 294L Cedar Ridge Local Fauna (Whitneyan), Badwater Creek area, Wyoming 160L Cedar Run Local Fauna (Arikareean, Ar3), Texas 204L, R, 205R Cedazo Fauna (late Blancan/ Irvingtonian), Aguascalientes, Mexico 257, 264R, 270L, 289, 295L Cerrillos Local Fauna (Wasatchian, Wa-5/Wa-6?), New Mexico 108L, 130R

Local Fauna(s) (continued) Cernay faunas (Cernasian, Thanetian; ?Ti6-Cfi equivalent, in part), France 89L, R Chattin Hill Fauna (late Blancan), Idaho 258L Cheetah Room Fauna (Irvingtonian), Pennsylvania 284L Chesapeake Bay Fauna (Barstovian), Maryland 207R, 208L, R Circle Local Fauna (Tiffanian, Ti4), Montana, 51, 83L Cita Canyon Fauna (Blancan, Blancan III), Texas 244, 255R, 257, 266R, 267L, 268R Claw Butte Local Fauna (Lancian), Montana 26L Clarendon Local Fauna (Clarendonian), Texas 216L Clarks Fork Fauna (Clarkforkian, Cf2), Wyoming 76R, 84R Cochrane II Local Fauna (Tiffanian, Ti1), Alberta, Canada 52, 76R, 80L Coffee Cup Local Fauna (Chadronian), Texas 129R Coffee Ranch Local Fauna (Hemphillian, Hh2), Texas 200R, 217R Coleman 2A Fauna (Irvingtonian), Florida 277, 282R, 283R Comanche Point Local Fauna (Clarendonian, Cl3, Montediablan) 172L, R Conard Fissure Fauna (Irvingtonian, Cudahyan), Arkansas 245, 274L, 277, 284L Concha Fauna (Blancan, Blancan I), Chihuahua, Mexico 252L Cook Ranch Local Fauna (Orellan), Montana 160L Corinto Fauna (Hemphillian, Hh1), El Salvador 201L, 203L, R Coso Mountains Fauna (middle Blancan), California 257, 259R Cotter Channel Fauna (early Duchesnean), Texas 109R, 129R Country Club Fauna (Blancan), Arizona 262L County Line Fauna (Irvingtonian), Illinois 275R Courtland Canal Fauna (Irvingtonian), Kansas 281R Cow House Slough Local Fauna (Arikareean, Ar2), Florida 204R, 205L, R, 206L Cragin Quarry Fauna (Rancholabrean), Kansas 288R, 291L Cragin Quarry Local Fauna (Clarendonian, Cl1), Oklahoma 198L

Crystal River Fauna (Irvingtonian), Florida 277, 283L Cudahy Fauna (Irvingtonian), Kansas 237R, 245, 270R, 281L, R, 282L, 291L Cumberland Cave Fauna (Irvingtonian, Cudahyan), Maryland 245, 274L, 275L, 277, 284L Cunningham Hill Fauna (Barstovian, Ba2), Wyoming 191R Curtis Ranch Fauna (latest Blancan), Arizona 261L, R, 270L, 280L Dad Local Fauna (Wasatchian, Wa-7), Wyoming 108L, 127L Deadman's Creek Fauna (Irvingtonian, Cudahyan), Texas 273R, 282R Deep River Fauna (Barstovian, Ba1), Montana 188L, 189R, 190L, R, 191L, 213R, 214R Deer Park Fauna (Blancan, Blancan III), Kansas 255L De Soto Shell Pit Fauna (latest Blancan), Florida 244, 267R, 268L, 270L, 283L, 295L Devils Nest Airstrip Fauna (Hemphillian, Hh4), Nebraska 251R Diamond O Local Fauna (Duchesnean/Chadronian), Montana 109R, 134R Diss Local Fauna (Torrejonian, To3?), Alberta, Canada 52, 75L, R Dixon Fauna (late Blancan, Senecan; Arvicoline Zone III), Kansas 253L, R Doe Spring Canyon Fauna (Barstovian, Ba2), California 174L Donnelly Ranch Fauna (Blancan), Colorado 257, 267L, 268R Dragon Local Fauna (To1), Utah 49, 62R, 70L, R, 71L, R, 72L, 73L, R, Douglass Draw Local Fauna (late Uintan), Montana 109L, 134R Duncan Fauna (Blancan), Arizona 257, 261R East Lake Local Fauna (early Arikareean), California 174R East Pilgrim 11 Local Fauna (Arikareean, Ar4), Wyoming 191R East Pilgrim 5 Local Fauna (Hemingfordian, He1), Wyoming 191R El Casco Fauna (latest Blancan/ Irvingtonian), California 259R, 260L, 270L, 272L, 278L, 295L El Golfo Fauna (Irvingtonian), Sonora, Mexico 251L, 277, 280R, 285L

Crazy Johnson Member fauna (mid-

dle Chadronian), South Dakota

163L

Ba2?), Oaxaca, Mexico 202R Elsinore Fault Zone Fauna (Irvingtonian), California 260L, 277, 278R Emerald Lake Fauna (Arikareean, Ar2), Wyoming 191L Eubanks Fauna (Barstovian, Ba1), Colorado 197R Fallen Angel Fauna (early Blancan), Kansas 265L Farmingdale Fauna (Arikareean, Ar3), New Jersey 208R Farrand Channel Local Fauna (To1), Montana 51, 70R, 73L Faunule A (Blancan), Mesilla Basin, New Mexico 263L Faunule B (Blancan), Mesilla Basin, New Mexico 263L Faunule C (Irvingtonian), Mesilla Basin, New Mexico 250R, 263L, 280L Feltz Ranch Fauna (Hemphillian, Hh1), Nebraska 195R Fish Creek Fauna (Blancan, Blancan V), Alaska 255R, 257, 272R Fish Lake Valley Fauna (Clarendonian, Cl2), Nevada 178L, 216L Fish Springs Flat Fauna (late Blancan), Nevada 257, 260L Flat Creek Local Fauna (Lancian), Montana 25R, 28L Flatiron Butte Fauna (late Blancan), Idaho 258L Flat Tire Fauna see 111 Ranch Fauna Fort Logan Fauna (Arikareean, Ar1/2), Montana 191L Fossil Bush Local Fauna (Orellan, Or2?), Saskatchewan, Canada 331L Four Mile Fauna (Wasatchian), Wyoming 108L, 126R Fox Canyon Fauna (early Blancan, Arvicoline Zone II), Kansas 253R, 265L, 267L Franklin Phosphate Pit 2 Local Fauna (Arikareean, Ar2), Florida 205R Friars Formation fauna (Uintan), California 109L, 115R, 117L, 118L, 123R, 124L Froman Ferry Fauna (latest Blancan), Idaho 245, 256R, 257, 258R, 260R, 272R, 276R, 295L Fullerton Fauna (Irvingtonian), Nebraska 250R Fyllan Cave Fauna (Irvingtonian), Texas 277, 282R, 283R Garbani Local Fauna (Puercan, Pu3), Montana 51, 68R, 69L, R, 73L

El Gramal Fauna (Barstovian?,

Gas Tank Local Fauna (Puercan, Pu2?), Utah 49, 67L Gilliland Fauna (Irvingtonian, Cudahyan), Texas 250R, 273R, 277, 281R, 282L Gordon Fauna (Irvingtonian, Sheridanian), Nebraska 274R, 285R Gracias Fauna (Hemphillian, H1), Honduras 201L, 203L, R Grand View Fauna (late Blancan, Senecan; Arvicoline Zone III), Idaho 244, 253L, R, 257, 258L, 269L Grayson Ridge Fauna (Tiffanian, Tii?), Wyoming 50, 77R Green Hills Fauna (Barstovian, Ba1), California 174L, 175R, 176L, 214R, 215L Gryde Local Fauna (Lancian), Saskatchewan, Canada 26R, 27 Hackberry Fauna (Hemingfordian, He1), California 176R Hagerman Fauna (early Blancan, Rexroadian), Idaho 244, 253L, 255L, R, 256R, 257, 258L Haile 7C Fauna (Blancan), Florida 257, 267R, 269L Haile 15A Fauna (Blancan), Florida 257, 267R, 268L, R Haile 16A Fauna (latest Blancan/ Irvingtonian), Florida 245, 267R, 268R, 270L, 283L, R, 295L Haile 21A Fauna (Blancan), Florida 277, 283L Hainin Local Fauna (Danian), Belgium 88R "Halfway Fauna" (Duchesnean), Utah 118R Halfway Fauna (Uintan, Ui-3), Utah 112L, 126R Halfway Hill Fauna (Tiffanian, Tii?), Wyoming 50, 77R Hall Ash Fauna (Irvingtonian), Kansas 240, 281R Hamilton Cave Fauna (Irvingtonian), West Virginia 244, 277, 284L, 285L Harrison Formation fauna (Arikareean, Ar3), Nebraska 191L, R, 194L, R, 197L, 198R, 204L, 205R, 209R, 211R, 212L Hartman Ranch Local Fauna (Uintan/Duchesnean), California 109R, 124R, 125L Hatchetigbee Bluff Local Fauna (Wasatchian), Alabama 108L, 134L Hay Springs Fauna (Irvingtonian, Sheridanian), Nebraska 274L, 285R Hemphill Local Fauna (Hemphillian, He2/3), Texas 200R, 217R

Hell's Hollow Local Fauna (Puercan, Pu1), Montana 51, 63R, 64L Hepburn's Mesa Fauna (Barstovian, Ba1/2), Montana 188L, 190R, 191L, R Hiatt Local Fauna (Puercan, Pu2), Montana 51, 65R, 67L, R Hidden Treasure Springs Fauna (Hemingfordian, He2), California 173R Higgins Local Fauna (Hemphillian, Hh1), Texas 198L, 217R Hill County Local Fauna (Judithian), Montana 24L Holloman Gravel Pit Fauna (Irvingtonian), Oklahoma 250R, 277, 281R, 284R Horse Room Fauna, Salamander Cave (Irvingtonian), South Dakota 281L Hough Draw Local Fauna (late Uintan), Montana 109L, 134R Hudspeth Fauna (Blancan), Texas 257, 263R, 268R Huerfano B fauna (Gardnerbuttean, Br1a), Wyoming 121R, 131L I-95 Local Fauna (Whitneyan), Florida 160L Inglis Fauna (Blancan), Florida 264R Inglis 1A Fauna (latest Blancan), Florida 245, 257, 267R, 268L, 269L, 270L, 283L, 285R, 289, 295L Inglis 1C Fauna (latest Blancan), Florida 245, 257, 267R, 268L, 270L, 283L, 295L Indian Meadows Fauna (Wa-2/ Wa-3) Wyoming 108L, 120R Iron Canyon Fauna (Clarendonian, Cl1/2), California 177L, R, 217L Irvington Fauna (Irvingtonian), California 269L, R, 272L, 274L, 277, 278L Itaboraí Fauna ("middle" Paleocene), Brazil 93L, 94L, R Ixtapa Local Fauna (Barstovian, Ba1), Chiapas, Mexico 203L, 214R Jackass Butte Fauna (late Blancan), Idaho 258L Jacks Channel Local Fauna (Puercan, Pu1), Montana 51, 63R, 64L Java Fauna (latest Blancan; Sappan), South Dakota 245, 257, 265R, 267L, R, 270L, 272L, 273R, 276L, 280L, 295L Jeff's Discovery Local Fauna (late Uintan), San Diego area, California 124L Jinglebob Fauna (Rancholabrean), Kansas 288R, 291L

Jones Fauna (Rancholabrean), Kansas 288R, 291L Kanopolis Fauna (Irvingtonian, Sheridanian), Kansas 245, 274L, 283L, 283R, 289 Kealey Springs Local Fauna (Arikareean, Ar2), Saskatchewan, Canada 192L Keefer Hill Local Fauna (Tiffanian, Ti1), Wyoming 50, 80L Kentuck Fauna (Blancan; Sappan), Kansas 245, 267R, 273R Keota Fauna (Barstovian, Ba2), Colorado 192R, 197R Kew Quarry Local Fauna (Arikareean, Ar1), California 173L Kishenehn Fauna (Duchesnean/ Chadronian), British Columbia, Canada 109R, 132R LaBarge Fauna (Wasatchian, Wa-7), Wyoming 108L, 128L La Colonia Local Fauna (Campanian-Maastrichtian), Argentina 92R Lac Pelletier Lower Fauna (Duchesnean), Saskatchewan, Canada 109, 133L, 329L Lac Pelletier Upper Fauna (Duchesnean), Saskatchewan, Canada 109, 133L Lake Casa Blanca Local Fauna (Uintan, Ui-3), Texas 109L, 118R, 134L, R Laguna Umayo Local Fauna (Paleocene), Peru 92R, 93L, R Laguna Riviera Local Fauna (Uintan/ Duchesnean), San Diego area, California 109R, 124L LaPoint Fauna (middle Duchesnean), Utah 118R, 120L, 133R Las Tunas Fauna (early Blancan?), Baja California del Sur, Mexico 257, 264L Laudate Local Fauna (Tiffanian, Ti1), California 53, 62R, 81L, R Layer Cake Fauna (early Blancan), California 258R Lebo Fauna (Torrejonian-Tiffanian), Montana 70R Leisey Shell Pit Fauna (Blancan/ Irvingtonian), Florida 267R, 270R, 271R, 277, 283L, R Lisco Fauna (early Blancan, Rexroadian), Nebraska 235L Little Egypt Local Fauna (earliest Chadronian), Texas 120L, 130L, 138R, 160L, 161R, 162R Little Pipestone Creek Local Fauna (middle Chadronian), Montana 163L

Local Fauna(s) (continued) Little Stave Creek Local Fauna (Wasatchian/Bridgerian), Alabama 108R, 134L Littleton Local Fauna (Puercan, Pu1), Colorado 49, 63R, 64R Logan Mine Local Fauna (Hemingfordian, He1), California 176R Los Alamitos Local Fauna (Campanian-Maastrichtian), Argentina 92R Love Bone Bed Local Fauna (Clarendonian, Cl3), Florida 171L Lower Cady Mountains Fauna (Hemingfordian, He1) 176R Lower Dome Spring Fauna (Barstovian, Ba1), California 174L Lower Hunter Wash Fauna (Judithian?), New Mexico 25L lower Monroe Creek Fauna (Arikareean, Ar2), Nebraska 193R Lower Snake Creek Fauna (Barstovian, Ba1), Nebraska 175R, 199R Macasphalt Shell Pit Fauna (Blancan), Florida 244, 257, 262L, 263R, 267R, 268L, 285R, 289 MacPherson Local Fauna (Hemphillian, He4), Kansas 219L Madison Valley Fauna (Barstovian, Ba1), Montana 188L, 190L, R, 191L, 214R Mantua Lentil Local Fauna (Pu1), Wyoming 45R, 50, 63R, 64R, 65L Marsland fauna (Arikareean, Ar3/ 4-Hemingfordian, He1), Nebraska 212R Martin-Anthony Local Fauna (Arikareean, Ar2), Florida 206L Martin Ranch Fauna (Irvingtonian), Texas 244, 250R, 282L Mascall Fauna (Barstovian, Ba1), Oregon 171R, 187R, 213R Massacre Lake Local Fauna (Hemingfordian, He2), Nevada 178R, 214R Matatlán Local Fauna (Barstovian, Ba2), Oaxaca, Mexico 202L Mathews Ranch Fauna (Clarendonian, Cerrotejonian, Cl1/2), California 174L, R Maxum Fauna (Blancan, Blancan I), California 244, 254L, 257 Mayfield Ranch Fauna (Irvingtonian), Texas 282R McCann Canyon Local Fauna (Arikareean, Ar2), Nebraska 193R, 205L McCarty's Mountain Local Fauna (late early Chadronian), Montana 162R

McGuire Creek Local Faunas (Puercan, Pu1), Montana 51, 53L, R, 63R McLeod Fauna (Irvingtonian), Florida 244, 277, 282L, 283R Medicine Hat Fauna (Irvingtonian), Alberta, Canada 232R, 270R, 277, 280R, 281L, 288L, 289 Merychippus Zone Fauna (Barstovian, Ba1), California 171R Midway Fauna (Hemingfordian, He2), Florida 206R Minnechaduza Fauna (Clarendonian, Cl2), Nebraska 216L, R Mollie Gulch Local Fauna (Arikareean, Ar3/4), Montana 188L Monroe Creek Fauna (Arikareean, Ar2), Nebraska, South Dakota 187R, 189L, 191L, 192L, 193R, 194L, 196R, 197L, 204L, 205L, R, 206L, 209R Morena Boulevard Local Fauna (Wasatchian, Wa-6/Wa-7), California 108L, 122R Mosquito Gulch Local Fauna (Torrejonian, To1), Montana 51, 73L Mount Eden Local Fauna (Hemphillian, Hh4), California 175L, 251R, 259R Mt. Eden see Mount Eden Mt. Blanco Fauna (Blancan), Texas 249L, 253L, R, 257, 266R, 267L, 268R Mt. Scott Fauna (Rancholabrean), Kansas 288R, 291L Muddy Creek Fauna (Arikareean, Ar2?), Wyoming 204R Muddy Tork Local Fauna (Lancian), Montana 26L Muddy Valley Fauna (Blancan), Nevada 257, 260R Mussentuchit Local Fauna (Albian-Cenomanian), Utah 22R Nash Fauna (latest Blancan; Sappan), Kansas 244, 265R, 266L, 270L, 272L, R, 273R, 275L, 295L Nettle Springs Fauna (Clarendonian, Cl2), California 174L, R Ninefoot Rapids Fauna (late Blancan), Idaho 258L Norden Bridge Local Fauna (Barstovian, Ba2), Nebraska 191R, 197R, 200L North Coalinga Local Fauna (Barstovian, Ba1), California 171R, 172L, 203L, 214R Northeast of Agate Local Fauna (Hemingfordian, He1), Nebraska 187L North Tejon Hills Fauna (Clarendonian, Montediablan, Cl3)

172L, R

Oldman assemblage (Judithian), Alberta, Canada 24L Olive Local Fauna (Tiffanian, Ti4), Montana 51, 83L Oreana Fauna (early Blancan), Idaho 258L Oshkosh Fauna (Hemphillian, Hh2), Nebraska 195R Otay Fauna (early Arikareean, Arı), California 174R Palmetto Fauna (Hemphillian, Hh4), Florida 207L, R, 251L Panaca Fauna (Blancan, Blancan I), Nevada 250L, 252L, 254L, 257, 260R Papago Springs Cave Fauna (Irvingtonian), Arizona 245, 276L, 285L, 289 Pawnee Creek Fauna (Barstovian, Ba2), Colorado 197R, 213R Payne Creek Mine Fauna (Irvingtonian), Florida 277, 283L Peanut Peak Member fauna (late Chadronian), South Dakota 168L Pearson Mesa Fauna (middle Blancan), Arizona 262L Pearson Ranch Local Fauna (early Duchesnean), California 109R, 119R, 124R, 125L, 138R Peterson Creek Local Fauna (Arikareean, Ar1/2), Montana 187R, 188L Phillips Ranch Local Fauna (Hemingfordian, He2), California 175R Pinole Local Fauna (Hemphillian, Hh4), California 251L Pipestone Springs Local Fauna (middle Chadronian), Montana 160L, 163L Pit Fauna, Porcupine Cave (Irvingtonian, ?Cudahyan), Colorado 245, 270R, 272L, R, 274L, 275R, 276L, 278R, 279L, 294L Plateau Valley Local Fauna (Clarkforkian), Colorado 125L Poison Creek Fauna (late Blancan), Idaho 258L Police Point Local Fauna (Tiffanian, Ti3), Alberta, Canada 52, 82L Pollack Farm Local Fauna (Hemingfordian, He1), Delaware 206R, 208L, R Pool Branch Fauna (Irvingtonian), Florida 277, 283L Port Kennedy Cave Fauna (Irvingtonian, ?Cudahyan), Pennsylvania 244, 274L, 277, 284L Porvenir Local Fauna (late Duchesnean), Texas 109R, 120L, 130L, 133L, 138R, 160L, 161R, 329R
Punta Peligro Fauna (late Paleocene), Argentina 92R, 93L, 94R Purgatory Hill Local Fauna (Puercan, Pu3), Montana 51, 68R, 69L, R Quarry A Local Fauna (Hemingfordian, He1), Colorado 200R Quincy Local Fauna (Hemingfordian, He2), Florida 206R Raben Ranch Local Fauna (middle Chadronian), Nebraska 163L Railway Quarry Local Fauna (Barstovian, Ba2), Nebraska 191R, 200L Rak Division Local Fauna (Hemingfordian, He2), California 175R, 176L, 200R, 215L Rancho del Oro Local Fauna (late Uintan), San Diego area, California 124L Rancho el Ocote Local Fauna (Hemphillian, He4), Guanajato, Mexico 178L, 201L, R, 218R (also Blancan) 257 Rancho La Brea Fauna (Rancholabrean), California 284R, 286R, 289 Rancho Gaitan Local Fauna (earliest Chadronian), Mexico 130L, 162R Rancho Viejo (Blancan), Guanajuato, Mexico 244, 257, 264L Randlett Fauna (Uintan, Ui-3), Utah 109L, 112L, 118R, 126R, 130L Red Division Quarry Local Fauna (Hemingfordian, He2), California 173R, 175R Red Fox Fauna (early Blancan), Kansas 265L Red Owl Local Fauna (Lancian), South Dakota 26R, 27, 32R, 34L, 35L Red Light Fauna (Blancan), Texas 257, 263R, 268R Rexroad Fauna (early Blancan, Rexroadian; Arvicoline Zone II), Kansas 253L, R, 267L Rexroad 3 Fauna (early Blancan), Kansas 244, 255L, 265L Rezabek Fauna (Irvingtonian, Sheridanian), Kansas 245, 274L, 283L, 289 Ricardo Fauna (Clarendonian, Cl2/3), California 175R, 176R, 177L, 216L, 217L Rick Forester Fauna (latest Blancan/ Irvingtonian), Kansas 265R, 266L, 270L, 295L Rigby Shell Pit Fauna (Irvingtonian), Florida 277, 283L, R Rio Chico Fauna (late Paleocene), Argentina 92R, 93L, 94R

River Road Fauna (Hemphillian, Hh4), Washington 256L Robert Fauna (Rancholabrean), Kansas 288R Rock Bench Fauna (Torrejonian), Montana 50, 70R, 74L, R Rock Creek Fauna (Irvingtonian), Texas 271L, 272R, 277, 282L Roche Percée Local Fauna (Tiffanian, Ti4), Saskatchewan, Canada 52, 82R, 83L Runningwater Local Fauna (Hemingfordian, He1), Nebraska 175L, 187L, 191R, 192L, 194R, 199L, 206R, 208L, R, 212R Rushville Fauna (Irvingtonian, Sheridanian), Nebraska 274L, 285R Sand Canyon Fauna (Barstovian, Ba2), Colorado 197R Sand Draw Fauna (early Blancan, Rexroadian; Arvicoline Zone II; Blancan III), Nebraska 244, 253L, R, 255L, 257, 266L Sandahl Fauna (Irvingtonian, Sheridanian), Kansas 274L Sanders Fauna (Blancan, Blancan III), Kansas 244, 255L, 267L Sand Point Fauna (early Blancan), Washington 256R, 258L Sand Wash Fauna (Uintan, Ui-1), Wyoming 117L Santa Fe River 1 Fauna (Blancan), Florida 244, 257, 267R, 268L, R, 271R, 272R Santana Mesa Fauna (Arikareean, Ar3), Texas 201L, R, 211R Santee Local Fauna (Hemphillian, Hh4), Nebraska 195R, 251L, R Santiago Canyon Landfill Fauna (Hemingfordian, He1), California 175L Santo Domingo Basin Fauna (late Blancan), New Mexico 262R Sappa Fauna (latest Blancan/ Irvingtonian; Sappan), Nebraska 257, 266L, 270L, 273R, 295L Saw Rock Canyon Local Fauna (Hemphillian, Hh3/4), Kansas 198R, (Blancan) 244, 250L, 254L, 257, 264R, 265L SB-1A Local Fauna (Arikareean, Ar2), Florida 205R, 206L Scabby Butte Local Fauna ("Edmontonian"), Alberta, Canada 25L School Well Local Fauna (Torrejonian) 51, 73R Seaboard Local Fauna (Hemingfordian, He1/2), Florida 206R, 207R

Second Division Fauna (Barstovian, Ba1), California 174L, 176L Seneca Fauna (late Blancan, Senecan; Arvicoline Zone III), Nebraska 244, 253L, R, 257, 266L Sespe Creek Local Fauna (Duchesnean), California 124R, 125L Serendipity Local Fauna (Uintan, Ui-3), Texas 109L, 118R, 129R, 130L, 134R Sharktooth Hill Local Fauna (Barstovian, Ba1), California 172L, 214R Shutt Ranch Fauna (Irvingtonian), California 278L Sheep Creek Fauna (Hemingfordian, He2), Nebraska 175R, 194R, 199L, R, 212R Shoddy Springs Fauna (Duchesnean), Montana 109R, 134R Shiloh Local Fauna (Arikareean, Ar3), New Jersey 208L, R Shotgun Butte Fauna (early Wasatchian), Wind River Basin, Wyoming 121L Silver Coulee Local Fauna (Tiffanian, Ti2), Montana 76R Simi Valley Landfill Local Fauna (middle Duchesnean), California 109R, 119R, 120L, 124R Slaton Fauna (Irvingtonian, Sheridanian), Texas 274L, 277, 282R, 283L, 284L Slim Buttes Fauna (Duchesnean), South Dakota 109R, 133R Skull Springs Fauna (Barstovian, Ba1), Oregon 187L, R, 214R South Mountain Fauna (Arikareean, Arı), California 173L South Tejon Hills Fauna (Clarendonian, Cerrotejonian, Cl1), California 172L, R, 174R Split Rock Fauna (Hemingfordian, He2), Wyoming 195R, 196L Standing Rock Quarry Local Fauna (Arikareean, Ar4) 198R Stewart Springs Fauna (Barstovian, Ba1), Nevada 171R, 177R, 178L Stonecrest Local Fauna (Uintan, Ui-3), California 109L, 123R Strathern Local Fauna, (Uintan/Duchesnean), Ventura County, California, 109R, 124L, R Suchilquitongo Local Fauna (Hemingfordian, He2), Oaxaca, Mexico 202L Sucker Creek Fauna (Barstovian, Ba1), Oregon 187R, 214R

Local Fauna(s) (continued) Swami's Point Local Fauna (Bridgerian, Br-2), California 108R, 122R Swift Current Creek Local Fauna (Uintan, Ui-3), Saskatchewan, Canada 109L, 118R, 133L Sycamore Creek Local Fauna (Clarendonian, Montediablan, Cl3), California 171R Tapo Canyon Local Fauna (Uintan, Ui-2), California 109L, 118R, 124R, 125L Taunton Fauna (middle Blancan, Blancan III), Washington 255L, 256R, 257 The Breaks Local Fauna (Torrejonian-Tiffanian, To3-Ti3), Wyoming 50, 77R, 78L, 81R, 82L Thomas Farm Local Fauna (Hemingfordian, He1/2), Florida 206L Three Mile East Fauna (late Blancan), Idaho 258L Tiupampa Fauna (early Paleocene), Bolivia 92R, 93L, R, 94L, R, 95L Tobin Fauna (Irvingtonian, Cudahyan), Kansas 273R, 282L Toledo Bend Local Fauna (Arikareean, Ar3), Texas 204L, R, 205R Tonopah Local Fauna (Barstovian, Ba1), Nevada 177R Tonque Local Fauna (Duchesnean), New Mexico 109R, 130R Tonuci Mountain Fauna (Blancan), New Mexico 263L Topaz Lake Fauna (Blancan/ Irvingtonian), Nevada 257, 259L, 260L, 278R Topham Local Fauna (Hemingfordian, He1), Saskatchewan, Canada 192L Tortugas Mountain Fauna (Irvingtonian), New Mexico 250R Tres Cruces Fauna (early Paleocene), Bolivia 92R, 93L, 94R Trinity River Local Fauna (Barstovian, Ba1), Texas 203R, 207L Trochu Local Fauna (Lancian), Alberta, Canada 26R, 27, 28L Trout Cave Entrance Fauna (Irvingtonian), West Virginia 284R Trout Cave No. 2 Fauna (Irvingtonian, Cudahyan), West Virginia 274L, 277, 284R Tusker Claims, Tusker Fauna (see 111 Ranch Fauna) Tyson Ranch Fauna (late Blancan), Idaho 258L Unnamed Butte Fauna (late Blancan), Idaho 258L

(Hemphillian/Blancan), California 244, 250L, 251L, 254L, 257 Upper Cady Mountains Local Fauna (Hemingfordian, He2), California 175R Upper Bone Valley Fauna (Hemphillian, Hh4), Florida 207L Upper Dome Spring Fauna (Barstovian, Ba1), California 174L Upper Harrison Formation faunas (Arikareean, Ar4), Nebraska 191R, 194L, R, 196R, 198R, 212L, R Upper Oso Dam Fauna (Hemingfordian, He1), California 174R Uptegrove Fauna (Hemphillian, Hh3), Nebraska 195R Vallecito Creek Fauna (late Blancan/Irvingtonian), California 244, 258R, 259R, 260L, 271L, 272R Vedder Local Fauna (Hemingfordian, He2), California 173R Vera Fauna (Irvingtonian, Cudahyan), Texas 273R, 277, 282L Verde Fauna (Blancan, Blancan I), Arizona 244, 254R, 255L, 257, 262L Vim-Peetz Fauna (Barstovian, Ba2), Colorado 197R Virgin Valley Fauna (Barstovian, Ba1), Nevada 171R, 178L, R, 213R, 214R Waubonsie Fauna (Rancholabrean), Iowa 289, 291R Wagonroad Local Fauna (Puercan, Pu3), Utah 49, 67L, 68L Wannagan Creek Local Fauna (Tiffanian, Ti4), North Dakota 52, 83L Warm Springs Local Fauna (Hemingfordian, He1), Oregon 187L Washoe Local Fauna (Hemphillian, He4), Nevada 178L Wathena Fauna (Irvingtonian; Sappan), Kansas 273R Wellington Hills Fauna (Blancan), Nevada 260L, 278R Wellsch Valley Local Fauna (Irvingtonian), Saskatchewan, Canada 191R, 250R, 257, 271R, 272L, 277, 281L West Dry Canyon Fauna (Barstovian, Ba1), California 174L White Bluffs Fauna (early Blancan), Washington 244, 256L, R, 257 White Narrows Fauna (early Blancan), Nevada 260R White Rock Fauna (late Blancan, Senecan; Arvicoline Zone III),

Upper Alturas Fauna

Kansas 244, 253L, R, 257, 265L, 266L White Springs Local Fauna (Arikareean, Ar2), Florida 205L, R, 206L Wild Horse Butte Fauna (late Blancan), Idaho 258L Willacoochee Creek Local Fauna (Barstovian, Ba1), Florida 206R, 207L, 213R Wilson Valley Fauna (Irvingtonian, Cudahyan), Kansas 273R, 282L Whisenhunt Quarry Local Fauna (Clarendonian, Cl2), Oklahoma 198L Wolf Ranch Fauna (Blancan), Arizona 267L, 269L Wood Mountain Fauna (Barstovian, Ba2), Saskatchewan, Canada 192L, R Woody Draw Fauna (Irvingtonian, Cudahyan), Texas 273R, 277, 282R Wounded Knee Local Fauna (Lancian), Saskatchewan, Canada 26R Wounded Knee-Sharps Fauna (Arikareean, Ar1), South Dakota 196L, R Yepómera Local Fauna (Hemphillian, He4), Mexico 178L, 200R, 201L, R, 202L, 218R, 251R, 257 Yoder Local Fauna (late early Chadronian), Wyoming 162R Z-line Channel Local Fauna (Puercan, Pu1), Montana 51, 63R, 64L Zoyotal Fauna (Arikareean, Ar3), Mexico 201L, R Localities, quarries, sites .6 miles east of Junction, Trans-Pecos, Texas (Uintan, Ui-1) 116L, 129R 7-Up Butte, Montana (Tiffanian, Ti2) 51, 81L "A" sites, Transverse Ranges, California (Hemingfordian, He1) 174R Aaron's locality, Alberta, Canada (Tiffanian, Ti2?) 52, 81L Adrar Mgorn 1 locality, Morocco (Thanetian) 92L Agate Springs quarries, Nebraska (Arikareean, Ar4) 212R Agua Fria sites, Trans-Pecos, Texas (Uintan, Ui1) 116L Airport site, Wyoming (Tiffanian, Ti4) 50, 83L Alexander Locality, Colorado (Puercan, Pu1) 49, 64R AMNH locality I, Colorado (Bridgerian, Br1) 114R

AMNH locality II, Colorado (Bridgerian, Br1) 114R AMNH locality III, Colorado (Bridgerian, Br1) 114R AMNH locality V, Colorado (Bridgerian, Br1) 114R AMNH locality VII, Colorado (Bridgerian, Bro) 114R AMNH locality 2, New Mexico (Puercan, Pu2, 3), 48 AMNH locality 4, New Mexico (Puercan, Pu₃), 48 AMNH locality 5, New Mexico (Puercan, Pu2), 48 AMNH locality 6, New Mexico (Puercan, Pu2), 48 AMNH locality 7, New Mexico (Puercan, Pu2), 48 AMNH locality 8, New Mexico (Torrejonian, To2) 74L AMNH locality 10, New Mexico (Torrejonian, To3) 48, 75L AMNH locality 230, New Mexico, (Torrejonian, To1) 71R AMNH locality 1482, New Mexico (Torrejonian, To2) 74L AMNH locality 2658, New Mexico (Torrejonian, To2) 74L Baca Formation sites, New Mexico (Uintan/Duchesnean) 109R, 115R, 130R, 131L Badwater locality 5, Wind River Basin, Wyoming (Uintan, Ui3) 121R Badwater locality 5A, Wind River Basin, Wyoming (Uintan, Ui3) 121R Badwater locality 6, Wind River Basin, Wyoming (Uintan, Ui3) 121R Badwater locality 7, Wind River Basin, Wyoming (Uintan, Ui3) 118R Badwater locality 17, Wind River Basin, Wyoming (early Bridgerian) 121R Badwater locality 18, Wind River Basin, Wyoming (early Bridgerian) 121R Badwater locality 20, Wind River Basin, Wyoming (early Duchesnean) 120L, 121R Bangtail locality, Montana (Tiffanian, Ti1) 51, 80L, R Battle Mountain locality, Wyoming (Tiffanian, Ti3) 49, 82L Bear Springs section, Arizona (Blancan) 262L Bechtold Site, Montana (Puercan, Pu3) 51, 68R, 69L

Bender locality, Kansas (Blancan, Blancan III) 244, 255L, 267R Big Multi Quarry, Wyoming (Clarkforkian, Cfi?) 49, 87L Bingo locality, Montana (Tiffanian, Ti1) 51, 80L, R Bitter Creek sites, Wyoming (Clarkforkian/Wasatchian) 126R, 127L Black Hawk Ranch Quarry, California (Clarendonian, Montediablan, Cl3) 171L, R, 172R Blick Quarry, New Mexico (Hemingfordian, He1) 199L Blindman River localities DW-1, DW-2, DW-3, Alberta, Canada (Tiffanian, Ti3) 52, 82L Bone Bed A, Tepee Trail Formation, Wyoming (Uintan, Ui-1, Shoshonian) 108R, 116L, R, 117L, 120R Brown Ranch localities, North Dakota (Torrejonian, To2) 52, 74R Bug Creek, Montana (?Lancian) 35L, R, 36L, 53L, R, 64L Bug Creek Anthills, Montana (?Lancian; Puercan, Pu1) 35L, 51, 53L, R, 63R, 64L, R Bug Creek West, Montana (?Lancian; Puercan, Pu1) 35L, 51, 53L, 63R, 64L Campo site, Spain (Paleocene, Thanetian; ?Tiffanian Ti4 equivalent) 88R Camp San Onofre Locality, San Diego area, California (Uintan/Duchesnean) 109R, 124L Canoe assemblage A, Big Bend area, Texas (Uintan, Ui-1) 108R, 129L, Canoe assemblage B, Big Bend area, Texas (Uintan, Ui-3) 109L, 129R, 130L Canyon Ski Quarry, Alberta, Canada (Tiffanian, Ti4) 52, 83L Carrot Top Quarry, Nebraska (Barstovian, Ba2) 195L Cathedral Cave, Nevada (Irvingtonian) 272L, R, 274L, 275R, 276L, 277, 278R, 280L, 294L Cave Without a Name, Texas (Rancholabrean) 289, 291R Cedar Point Quarry, Wyoming (Tiffanian, Ti3) 82L Chappo Type Locality, Wyoming (Tiffanian, Ti3) 49, 82L Cheek Bend Cave, Tennessee (Rancholabrean) 289, 291R Chris's Bonebed locality, Montana (Puercan, Pu1) 51, 63R, 64L Cochrane I locality, Alberta, Canada (Tiffanian, Ti1) 52, 80L

Cochrane II locality, Alberta, Canada (Tiffanian, Ti1) 52, 76R, 88L Coffee Ranch Quarry, Texas, (Hemphillian, Hh2) 217R Corral Bluffs locality, Colorado (Puercan, Pu2-3?) 67L Crestomere School site, Alberta, Canada (Tiffanian, Ti4) 52, 83L Croc Pot site, Saskatchewan, Canada (Puercan, Pu3) 52, 69L, R Cub Creek 1 site, Montana (Tiffanian, Ti1) 75R, 77L, 80R Cub Creek 2 site, Montana (Torrejonian, To3) 50, 75R, 77L Cub Creek 3 site, Montana (Tiffanian, Ti1) 75R, 77L, 80R Cudahy Ash Pit, Kansas (Irvingtonian, Cudahyan) 273R, 282L Dell Creek Quarry, Wyoming (Tiffanian, Ti5) 49, 83R Divide Quarry, Wyoming (Tiffanian, Ti4) 50, 83L Dogie site, Texas (Puercan, Pu3), 48, 69R Dolichorhinus Quarry, Utah (Uintan, Uinta B) 116L Donnybrook site, North Dakota (Torrejonian, To3?) 52, 75R Douglass Quarry, Montana (Tiffanian, Ti1) 51, 80L, R Dove Spring Formation basal faunal site, California (Clarendonian, Cl1) 177L Duchesneodus Quarry, Utah, (Duchesnean) 118R Eagle Quarry, Montana (Tiffanian, Ti1) 75R, 77L, 80R Edentulous Jaw Site, Califiornia (Tiffanian, Ti2) 53, 81L, R Egelhoff Quarry, Nebraska (Barstovian, Ba2) 195L Egg Mountain, Montana (Judithian) 24L El Gallo, Baja California del Norte, Mexico 25L, 321R Erickson's Landing locality, Alberta, Canada (Tiffanian, Ti2) 52, 76R Eureka Sound Group, Canada (Wasatchian/Bridgerian) 108R, 109R, 133R, 138L Fairmead Landfill locality, California (Irvingtonian) 277, 278R False Cougar Cave, Montana (Rancholabrean) 289, 291R Ferron Mountain locality, Utah (Puercan, Pu3?) 67L Foggy Day beds, N. Fork Owl Creek, Wyoming (Uintan, Ui-1) 121L Fort Union Formation sites, Wyoming (Puercan, Pu1) 63R

Localities, quarries, sites (continued) Fr1 (Frenchman 1), Saskatchewan, Canada (Puercan) 35R, 52, 53L, R, 62L, 63R, 64R Ferguson Ranch locality, Montana (Puercan, Pu1) 51, 63R, 64L Fisher/Sullivan site, Virginia (Wasatchian, Wa-3-Wa-5) 108L, 111R Flagstaff Peak locality, Colorado (Puercan, Pu2?) 67L Foster Gulch locality, Wyoming (Clarkforkian, Cf2) 50, 87R Fowkes Formation sites, Wyoming (Bridgerian) 108R, 128R Garbani Quarry, Channel, site, Montana (Puercan, Pu3) 69L, R, 73L Gas Tank Hill locality, Utah (Puercan, Pu2?) 49, 67L Gidley Gidley Quarry, Montana (Torrejonian, To2) 51, 74L, R, 80R Gidley's Horse Quarry, Texas (Irvingtonian) 282L Glenn Eleven site, Texas (Puercan, Pu3) 48, 69R Glennie locality, Montana (Tiffanian, Ti1) 51, 80L, R Goler Formation sites, California (Tiffanian, Ti2) 53, 62R, 70R, 77L, 81L Hagerman Horse Quarry, Idaho (early Blancan) 258L, 282L, R Hancock Quarry, Oregon (Uintan/Duchesnean) 109R, 133R Hand Hills West (lower level), Alberta, Canada (Tiffanian, Ti2?) 52, 81L Hand Hills West (upper level), Alberta, Canada (Tiffanian, Ti3) 52, 82L Hanna Basin sites, Wyoming (Puercan, Pu1) 50, 61L, 63R, 65L, 66R, 73L, 75R, 77L, R, 78L, R, 80R, 81R, 82L Hannold Hill sites, Texas (Wasatchian, Wa-7) 108L, 111L, 129L Hanover Quarry No 1, Pennsylvania (Irvingtonian) 277, 284L Hansen Bluff, Colorado (Irvingtonian, Cudahyan) 245, 272L, R, 274L, 275L, R, 277, 279L, R Harbicht Hill, Montana (?Lancian; Puercan, Pu1) 35L, 51, 53L, 63R Hardscrabble Creek, Wyoming (Wasatchian) 120L Hares site, North Dakota (Torrejonian, To3?) 52, 75R Hart Mine Formation sites, New Mexico (Bridgerian, Br-3) 108R, 130R, 131L

ington (early Blancan) 256R Herpijunk Promontory locality, Montana (Puercan, Pu1) 51, 63R Hidden Treasure Springs site, California (Hemingfordian, He2) 173R High Rock Lake sites, Nevada (Barstovian, Ba2) 178L, R, 214R Highway Blowout, Montana (Tiffanian, Ti2) 51, 81L Holy City beds, N. Fork Owl Creek, Wyoming (Uintan, Ui-1?) 121L Horse and Mastodon Quarry, Colorado (Barstovian, Ba2) 197R Horseshoe Canyon, Alberta, Canada ("Edmontonian") 25L Howard Ranch, Texas (Rancholabrean) 289, 291R Huerfano II, Colorado (Bridgerian) 114L Huerfano III, Colorado (Bridgerian) 114L Huerfano IV, Colorado (Wasatchian, Wa-7) 131L Huerfano V, Colorado (Bridgerian) 114L Huerfano VI, Colorado (Wasatchian, Wa-7) 131L Huerfano (AMNH) VII, Colorado (Bridgerian, Bro-Br1a) 114L, R, 51 Huerfano VIII, Colorado (Wasatchian, Wa-6) 131L Huerfano IX, Colorado (Wasatchian, Wa-6) 131L Huerfano XI, Colorado (Wasatchian, Wa-7) 131L Huerfano XII, Colorado (Wasatchian, Wa-6) 131L Huerfano XIII, Colorado (Wasatchian, Wa-5) 131L Ihadjamene locality, Morocco (Thanetian) 92L Iron Lightning locality, South Dakota (Lancian) 27, 32R, 34L, R Jeep Quarry, New Mexico (Hemingfordian, He1) 199L Joe's Bone Bed (TMM 41365-66), Texas (Tiffanian, Ti5) 48, 79L, 83R, 84L Joffre Bridge locality, Alberta, Canada (Tiffanian, Ti3) 52, 82L Jones-Miller site, Colorado (Rancholabrean) 289, 291R Junction locality, Trans-Pecos, Texas (Uintan, Ui-1) 108R, 116L, 118L, 129R Keefer Hill locality, Wyoming (Tiffanian, Ti1) 50, 80L Kemp Clay Formation, Texas (Lancian) 28L

Haymaker's Orchard locality, Wash-

289L, R Kissimmee River site, Florida (Blancan) 257, 267R, 268R KU locality 9, "Little Pocket" (Torrejonian, To2) 48, 74R L-41, Aycross Formation, Wyoming (Wasatchian/Bridgerian) 108L, 120R LACM [CIT] locality 104, California (Clarendonian, Montediablan, Cl3) 172R LACM[CIT] locality 292, California (Duchesnean) 124L LACM [CIT] locality 302, California (Clarendonian, Montediablan, Cl3) 172R LACM [CIT] locality 303, California (Clarendonian, Cerrotejonian, Cl1) 172L LACM [CIT] locality 304, California (Clarendonian, Cerrotejonian, Cl1) 172L LACM [CIT] locality 305, California (Clarendonian, Montediablan, Cl3) 172R LACM [CIT] locality 307, California (Clarendonian, Cerrotejonian, Cl1) 172L LACM [CIT] locality 315, California (Hemingfordian, He2) 173R Ladd's Quarry, Georgia (Rancholabrean) 289, 291R La Goleta, Michoacan, Mexico (Hemphillian-Irvingtonian) 244, 257, 263R, 264L, 277 Laramie Formation, Colorado (Lancian) 27R Laubach 3, Texas (terminal Rancholabrean) 286R Ledge site, Wyoming (Tiffanian, Ti3) 49, 82L Leidy Quarry, Wyoming (Puercan, Pu1) 50, 63R Leptarctus B site, Leptarctus Quarry, Nebraska (Clarendonian, Cl2) 216L Little Beaver Cave, Missouri (Rancholabrean) 289, 291R Little Dell Dam site, Utah (Irvingtonian) 272L, 276L, 277, 280L, 294 Little Muddy Creek locality, Wyoming (Tiffanian, Ti1) 49, 80L Live Oak site (SB-1A Local Fauna), Florida (Arikareean, Ar2) 205R Lloyd site, North Dakota (Torrejonian, To3?) 52, 75L

Kennewick sequence, Washington

(Irvingtonian) 276R, 277, 288R,

Long Fall, Saskatchewan, Canada (Puercan) 26R, 35R, 36L, 52, 53L, 62L, 63R, 64R Love Bone Bed, Florida (Clarendonian, Cl3) 171L Lundbreck, Alberta, Canada ("Edmontonian") 25L Marfil, Mexico (Bridgerian/Uintan) 108R, 131R, 132L Martin-Anthony oreodont site, Florida (Arikareean, Ar2) 206L Mason Pocket (Quarry), Colorado (Tiffanian, Ti4) 48, 76R, 79L, 82R McKeever Ranch localities, Montana (Puercan, Pu1) 51, 63R, 64L Medicine Rocks 1-Mehling Site, Montana (Torrejonian, To3?) 51, 75R, 81L Mel's Place locality, Alberta, Canada (Tiffanian, Ti3) 52, 82L Mesa Prospect, New Mexico (Hemingfordian, He2) 199L Monument Blowout, Wyoming (Wasatchian, Wa-3) 132L Mount Laurel Formation, New Jersey (Lancian) 28L Morales 1 locality, Montana (Puercan, Pu1) 51, 63R, 64L Mullen assemblage, Kansas (late Blancan, Senecan; Arvicoline Zone III) 253L, R, 275R Naashoibito Member, Kirtland Formation, New Mexico (Lancian) 28L Nejapa Valley sites, El Cameron Formation, Oaxaca, Mexico (Barstovian, Ba3) 202L, R Newell's Nook Quarry (USGS D-2003), Montana (Tiffanian, Ti1) 51, 80R New Year Quarry, California (Barstovian, Ba1) 176L Norden Bridge Quarry, Nebraska (Barstovian, Ba2) 191R, 197R, 200L North Cove, Nebraska (Rancholabrean) 289, 291R North Horn Formation, Utah (Lancian) 27R Nut Bed, Clarno, Oregon (Bridgerian) 108R, 133R Owl Creek, Wyoming (Bridgerian) 109L, 120R Pajarito locality (Laguna site), New Mexico (Blancan) 262R Patton Cave, West Virginia (Rancholabrean) 289, 291R Peccary Cave, Arkansas (Rancholabrean) 289, 291R Pipe Creek Sinkhole, Indiana (Blancan) 250L

Pita Flats locality, North Dakota (Puercan, Pu2-3) 52, 67L Pollack Farm site, Delaware (Hemingfordian, He1) 206R, 208L, R Pomerado Conglomerate sites, San Diego area, California (Uintan/Chadronian) 109L, 118R Porcupine Cave, Colorado (Irvingtonian) 244, 270R, 272L, R, 274L, 275R, 276L, 277, 278R, 279L, 285L, 294L Porcupine Hills Formation sites, Alberta, Canada (Torrejonian) 70R, 75L Post Ranch faunal horizon, Arizona (early Blancan) 261L Powder Wash sites, Utah (Wasatchian/Bridgerian) 108R, 126L Prince Creek, Alaska (Lancian) 26R Princeton Quarry, Wyoming (Tiffanian, Ti5) 50, 83R, 85R Railway Quarry, Nebraska (Barstovian, Ba2) 191R Rav-1, Saskatchewan, Canada (Puercan, Pu3?) 35R, 52, 69L, R (Rav W-1) Ray's Bonebed (TMM 40536-37), Texas (Tiffanian, Ti3) 48, 79L, 82L, R Red Creek, Wyoming (Clarkforkian) 120L Red Deer locality, Alberta, Canada, (Tiffanian, Ti2) 76R Red Division Quarry California (Hemingfordian, He2) 173R, 175R Red Hot Local Fauna, Mississippi (Wasatchian, Wa-1?) 108L, 133R Red Owl Quarry, South Dakota (Lancian) 26R, 27, 32R, 34L, 35L Rexroad 3 Locality, Kansas (Blancan, Blancan III) 244, 255L, 265L Rick Forester locality (late Blancan), Kansas 266L Ries locality, Wyoming (Clarkforkian, Cf2) 50, 87R Roche Percée localities, Saskatchewan, Canada (Tiffanian, Ti4) 52, 82R Rock Bench Quarry, Montana (Torrejonian, To2) 50, 70R, 74L, R Rock Creek Quarry, Texas (Irvingtonian) 277, 282L Rough Gulch locality, Wyoming (Clarkforkian, Cf2) 50, 87R Round Mountain Quarry, New Mexico (Clarendonian, Cl1) 200L, R Saddle Annex locality, Wyoming (Tiffanian, Ti3) 49, 82L

Saddle locality, Wyoming (Tiffanian, Ti2) 49, 81L Salamander Cave, South Dakota (Irvingtonian) 245, 276R, 277, 281L, 282L, 285L, 289R SAM Cave, New Mexico (Irvingtonian, ?Cudahyan) 274L, 275L, 276L, 277, 279L, R Sand Creek fauna, Wyoming (Tiffanian, Ti3?) 50, 82L San Jose Formation Locality 18, New Mexico (Wasatchian, Wa-6?) 108L, 130L San Jose Formation sites, New Mexico (Wasatchian, Wa-6?) 111L Santiago Formation sites, San Diego area, California (Uintan) 109L, R, 118R, 124L Savage Canyon site (Stewart Springs Fauna), Nevada (Barstovian, Ba1) 177R Scarritt Quarry, Montana (Tiffanian, Ti2) 51, 80R, 81L, R Schiebout-Reeves Quarry, Texas (Tiffanian, Ti1) 48, 80L, R SDSNH Locality 3495, San Diego area, California (Uintan/ Duchesnean) 124L Sebits Ranch Site 24B, Texas (Hemphillian, Hh1) 198L Sespe Formation sites, California (Uintan/Arikareean) 109L, R, 119R, 124R, 125L, 172R, 174R Silberling Quarry, Montana (Torrejonian, To2) 51, 74L, R, 80R Simpson localities 9, 65, 78, Montana (Torrejonian, To1?) 51, 73R Simpson locality 13, Montana (Tiffanian, Ti3) 51, 82R Simpson Quarry, Montana (Puercan, Pu2-3) 51, 69L, R Skyline Channels, Texas (early Duchesnean) 109R, 120L, 129R Sloth-Camel Quarry, Texas (Irvingtonian) 282L South Table Mountain sites, Colorado (Puercan, Pu1) 49, 64R Stadium Conglomerate sites, California (Uintan, Ui-2?) 109L, 118L, R, 123L, R Steepside Quarry, California (Barstovian, Ba1) 176L, 215L Stewart Valley sites, Nevada (Clarendonian, Cl2) 178L Sunbright Ash Pit, Kansas (Irvingtonian, Cudahyan) 273R, 282L "Sweetwater" Formation sites, San Diego area, California (Uintan/Duchesnean) 109R, 124L

woodburne_luSublinx 2/1//04 1:42 PM Page 382

382 Subject Index

Localities, quarries, sites (continued) Swain Quarry, Wyoming (Torrejonian, To2) 49, 62R, 74R Swan Hills site, Alberta, Canada (Tiffanian, Ti4) 52, 83L Swift Current Plateau, Saskatchewan, Canada (Uintan, Ui-3) 109L, 133L Thornton Beach, California (Irvingtonian) 271R Tijeras Arroyo, New Mexico (Blancan/ Irvingtonian) 262R, 270R Titanoides locality, Wyoming (Tiffanian, Ti5) 49, 83R TMM locality 40147, Texas (Torrejonian, To2?) 74R Togwotee Summit, Wyoming (Bridgerian, Br-2) 108R, 120R Tom's Top site, Texas (Puercan, Pu3) 48, 69R Tsentas Microsite (NMMNH locality L-312), New Mexico (Torrejonian, To2) 48, 74L UALP locality 7650, New Mexico (Torrejonian, To2) 74L UCM loc. 77039, Colorado (Wasatchian) 112R UCM loc. 77041, Colorado (Wasatchian, Wa-5) 131L UCM loc. 83120, Wyoming (Wasatchian/Bridgerian) 127L UCM loc. 84115, Wyoming (Bridgerian) 115L UCM loc. 84213, Wyoming (Bridgerian) 113R UCM loc. 84219, Wyoming (Bridgerian) 113R UCM loc. 84220, , Wyoming (Wasatchian, Wa-7) 113R UCM loc. 84211, Wyoming (Wasatchian, Wa-7) 113R UCM loc. 84228, Wyoming, (Wasatchian, Wa-7) 113R UCM loc. 88052, Wyoming (Wasatchian, Wa-3) 132L UCM loc. 92189, Wyoming (Uintan, Ui-1) 116L, 117L UCM loc. 96197, Colorado (Bridgerian) 112R UCMP locality V-5814, California (Uintan/Duchesnean) 124R UCMP locality V-72088, San Diego area, California (Uintan/ Duchesnean) 124L University of Michigan locality I, II, III, V, New Mexico (Bridgerian, Gardnerbuttean) 131L UM locality 263, Wyoming (Tiffanian, Ti2) 50, 81L

(Barstovian, Ba1) 176L Ventana Cave, Arizona (Rancholabrean) 289, 291R Verdigris Coulee (early Campanian), Alberta 23L, R Walbeck site, Germany (Paleocene, ?Tiffanian equivalent) 88R Wapiti Valley fauna (Lysitean-Bridgerian), Wyoming 122R West Bijou Creek-1 locality, Colorado (Puercan, Pu2-3?) 49, 67L West End site, Wyoming (Tiffanian, Ti3) 49, 82L Whistler Squat Quarry, Trans-Pecos, Texas (Uintan, Ui-1/Ui-2) 109L, 116L, 118L, 129R White Site, Montana (Tiffanian, Ti2) 51, 81L White's River Basin Survey Site, North Dakota (Tiffanian, Ti3) 52, 82L Wiggins Formation sites, Wyoming (Uintan) 109L, 117R, 118L, 121L, R, 122R Wind River Formation sites, Wind River Basin, Wyoming, (Uintan, Bridgerian) 107L, R, 108L, 113L, 114R, 121L, 122L, 132L, R Witter Quarry, Wyoming (Tiffanian, Ti4) 50, 52, 83L XMas and Kat quarries, Nebraska (Clarendonian, Cl2) 216L, R LOD, Last Occurrence Datum xiiiR Lomas de Tetas de Cabra Formation, Baja California 108L, 111L, 131R London Basin 324L Lost Cabin beds (Lambdotherium level) 107R Lostcabinian subage (Wa-7) of Wasatchian mammal age 107L, R, 113L, R, 121L, 122L, R, 135 characterized 113L, R, 122L Lost Cabin Member, Wind River Formation 107R, 108L, 113R, 114R, 121L, 122L Loup Fork beds 190L Love Formation, Texas 263R Loveland Loess, Colorado, Iowa, Nebraska 285R, 287R Love Ranch Formation, New Mexico 131L Lower Oreodon Beds, Big Badlands, South Dakota 165L Lower Nodular Zone, Big Badlands, South Dakota 164R Lower Pleistocene Series 236R Lower Rosebud Formation, beds, Nebraska, South Dakota 196R, 209R

Valley View Quarry, California

Lower Tuffaceous Zone, New Mexico 221L Lower variegated sequence, Togwotee Pass, Wyoming 85L, 108L, 120L Lower Whitney Ash, Nebraska 159, 166L LPTM (late Paleocene Thermal Maximum) 320L, R, 324R LRD (lowest range datum) 17L LSD, Lowest Stratigraphic Datum xiiiL, R, xivL, 4, 5, 14L, R, 15R, 259R LSD_k, lowest known stratigraphic occurrence 259L, 278L Ludlow Formation, Montana, North Dakota 62L, 63L, 65R, 67L, 68R, 71L, 74R Ludlow Member, Fort Union Formation, North Dakota 62L Luisian benthonic foraminiferal stage, California 171R, 172L, 214R Lusk, Wyoming 163L, 164L, R, 165L Lysite beds 107R, 108L Lysitean subage (Wa-6) of Wasatchian mammal age 107L, R, 111L, 113L, 122L, R, 130R, 135 characterized 113L Lysite Member, Wind River Formation, Wyoming 107R, 108L, 121L, 122L Ma (Megannum in the radioisotopic time scale) xivR Maastrichtian Stage/Age, rocks, faunas 21L, 24R, 35R, 37L, 92R, 93R, 317R, 318L macroevolutionary 37L Madison Valley Formation, Montana 188L, 190L, R Madrean shrubland, chaparral 327L magnetostratigraphic viiL, xivL, xviiiR, 10L, 16R, 17R, 18L, 35R, 44R, 46, 47, 63L, 69L, R, 71L, 74R, 75R, 76L, 79L, 86L, 88R, 93L, R, 94L, 95R, 123R, 134R, 138L, R, 159, 161R, 171L, 172R, 175L, 179L, 194L, 199R, 206R magnetostratigraphic polarity chrons, units, zones xivL, 9L, R, 10L Brunhes Chron 233L, 238L, 259R, 261L, 263L, 274L, 276L, 278L, 279L, R, 280L, 281L, 285R, 287L Gauss Chron 233L, 253L, 255L, R, 256R, 258L, 259L, 261L, R, 262L, 263L, R, 265R, 267L, 268L, 269L, 279R Kaena subchron of Gauss Chron 240, 256R, 258L, 259L, 262L, 263L Mammoth subchron of Gauss Chron 240, 258L, 261R, 262L Gilbert Chron 200R, 233L, 256R, 258L, 259R, 261L

Cochiti subchron, Gilbert Chron 240, 256R, 258R, 259L Nunivak subchron, Gilbert Chron 240, 251R, 154R, 262L Sidufjall subchron, Gilbert Chron 200R, 240, 251R, 252L, 256R Thvera subchron, Gilbert Chron 233R, 240, 252L Matuyama Chron 233L, 253L, 255R, 258L, 259L, 261R, 262L, 263L, 267L, 268L, 269L, 271R, 274L, 278L, 279L, R, 281L, 285R, 294L Cobb Mountain subchron of Matuyama Chron 240, 263L Jaramillo subchron of Matuyama Chron 233L, 240, 258R, 259R, 263L, 269L, 279R, 280L Olduvai subchron of Matuyama Chron 233L, 237L, 240, 258R, 259L, 261L, R, 263L, 272L, R, 275L, 278L, 279R, 280L, R Reunion subchron, Matuyama Chron 240, 279R Chron C1n, Brunhes Chron 233L, 238L, 261L, 274L, 276L, 279R, 281L, 282R, 287L Chron C1r 258R, 278L, 279R, 280L C1r.1r 271R, 278L, 281L C1r.1n, Jaramillo subchron of Matuyama Chron 258R, 279R C1r.2r 260L, 263L, 269L, 289L Chron C2n, Olduvai subchron of Matuyama Chron 233L, 237L, 240, 258R, 259L, 261L, R, 263L, 272L, R, 275L, 278L, 279R, 280L, R Chron C2r 253L, 258L C2r.1r 259L, 278L C2r.1n, Reunion subchron of Matuyama Chron 279R C2r.2r 253L, 258L, 266R Chron C2An 253L, 259L, 263L, 269L C2An.1n 258L, 259R, 262L, 263R, 266R, 267L, 268L, 279R C2An.1r, Kaena subchron of Gauss Chron 256R, 258L, 259L, R. 263L C2An.2r, Mammoth subchron of Gauss Chron 258L, 261R C2An.3n 255L, 258L, 259L, R, 262L, 265L Chron C2Ar 251R, 256R, 258L, 259R, 261L Chron C3n 251R C3n.1n, Cochiti subchron of Gilbert Chron 256R, 258R, 259L C3n.2n, Nunivak subchron of Gilbert Chron 251R, 254R C3n.2r 251R C3n.3n, Sidufjall subchron of Gilbert Chron 200R, 251R, 256R

C3n.3r 252L C3n.4n, Thvera subchron of Gilbert Chron 233R, 252L Chron C3r 175R, 200R, 218R, 251R, 252L, 259R Chron C3An 218R, 251R (3An.2n) Chron C3Bn 200R Chron C4r 171R (C4A) Chron C4Ar 172R, 177L Chron C5n 177L, R, 200R Chron C5r 172R, 174L, R, 177L Chron C5An 172R, 174L, R, 215R (C5An2) 199R Chron C5ABn 217L Chron C5ABr (C5AB) 200L Chron C5ACn 176L Chron C5ACr (C5AC) 200L Chron C5ADn 191L, 199R Chron C5ADr (C5AD) 176L Chron C5Bn 176L Chron C5Br 176L, 191L, 214R (C5B) 199R, 207L Chron C5Cn 173R, 196L, 199L (C5C) 199L (C5Cn2) 215L Chron C5Cr 173R, 175R Chron C5Dr 175L, 194R Chron C5Er 175L, 194L (C5E) 194R Chron C6n 194L Chron C7r 193R Chron C7Ar 193R Chron C8n 193R Chron C8r 193R Chron Con 193R Chron C9r 172L, R, 193R Chron C10n 173L, 179R Chron Cior 173L, 174R Chron C11n 166R Chron C11r 166L Chron C12r 165L, 166L Chron C13n 164R, 165L, 330L Chron C13r 163L, 164L, R Chron C15n 162R, 163L Chron C15r 163L Chron C16r 162R Chron C17n 138R Chron C17r 136, Chron C18n 125L, 138R Chron C18r 125L, 136, 138R Chron C19n 125L Chron C19r 123R, 125L, 136 Chron C20n 123R, 125L, 136, 138L Chron C20r 116L, 117L, 120R, 123R, 136, 138L Chron C21n 123L, R, 135, 138L Chron C21r 123L, 135 Chron C22n 135 Chron C22r 135, 138L Chron C23n.1n 135 Chron C23n.1r 135

Chron C23n.2n 135 Chron C23r 131R, 135, 138L Chron C24n 131R Chron C24n.1n 135 Chron C24n.1r 135 Chron C24n.2n 135 Chron C24n.2r 135 Chron C24n.3n 135, 138L Chron 24r 12L, 79L, 86L, 87L, R, 88L, 89R, 90L, 92L, 106L, 135, 138L Chron C25n 79L, 84L, R, 86L, 87L Chron C25r 79L, 82R, 83L, 84L, 89L, 92L Chron C26n 79L, 82L, 83L, 88R Chron C26r 75R, 77L, 79L, 80R, 81R, 82L, R, 93R, 94L Chron C27n 71R, 72R, 74L, 75R, 76L, 77L, 78L, 79L Chron C27r 71L, 72R, 73R, 74L, R, 79L, 91L, 93R, 94L Chron C28n 71L, R, 73R Chron C28r 63L, 68L, 69R, 71L, 73L, R, 93R, 94L Chron C29n 65R, 66L, 67R, 68L, 69L, R, 71L Chron C29r 12R, 34R, 63L, 65L, R, 67R, 91L, 93R Chron C3on 34R Chron C31n 34R Chron C31r 34R, 317R Chron C33n 25L magnetic polarity stratigraphy, magnetostratigraphy viiR, xivL, 9L, R, 10L, 32L, R, 34, 63L, 65L, R, 67R, 68L, 69L, R, 71L, R, 72R, 73L, R, 74L, R, 75R, 76L, 77L, 78L, 79L, 80R, 81R, 82L, R, 83L, 84L, R, 86L, 87L, R, 88L, R, 89R, 91L, 92L, 93R, 94L, 117R, 157R, 158L, 160L, 162L, R, 169L, 172R, 173R, 175L, 177L, 179R, 191L, 193L, R, 198R, 200R, 202L, 206R, 217R, 218R, 233L, R, 271L magnetic polarity time scale viiR, 9R, 10L, 117R Mammal age viiR, xiL, xivL, R Mammoth magnetic polarity subchron of Gauss Chron 258L, 261R Mantuan Mammal Age 43L Marshalltown Formation, New Jersey 25R Marsland Formation, Nebraska 212R Mascall flora, Oregon 333R Mascall Formation, Oregon 187L, 220R Masuk Formation, Utah 23R MAT (mean annual temperature) 318L, 319, 320R, 321L, 326L, R, 327R, 328L, 330L, R, 332L, 333R, 337L

Matilija Sandstone, California 124R

Matuyama magnetic polarity chron 233L, 253L, 255R, 258L, 259L, 261R, 262L, 263L, 267L, 268L, 269L, 271R, 274L, 278L, 279L, R, 281L, 285R, 294L Mazama Ash, Washington, Oregon 288R MBE (Mammal dispersal event, at LPTM) 316, 320L McCone County, Montana 64L McCullough Peaks Formation, Wyoming 17R McGuire Creek, Montana 32L, 53L, R, 64L Meade Basin, Kansas 257, 270L, 288R Meade County, Kansas 232R, 265L, R, 270L, 273R, 277, 281R, 289, 291L Meade County, South Dakota 26R Medicine Hat sequence, Alberta, Canada 232R, 270R, 277, 280R, 281L, 288L, 289 Medicine Rocks, Montana 51, 81L Mediterranean Sea (area) 233R, 237L, 251L megathermal climate, floras 319, 321L, 324R, 327L, 328L, 330L, 332L Melville Formation, Montana 80R Merced Formation, California 271R Merycoidodon major Interval Zone (late Whitneyan) 166L Mesa Chijuilla, New Mexico 72R, 75L Mesa Falls Ash, Nebraska 234, 266L, 273R, 280R Mesa de Cuba, New Mexico 48, 71R, 72R, 73R Mesa de Cuba-Mesa Portales 48 "Mesaverde" Formation, Wyoming 24L Mesilla Basin, New Mexico 250R, 257, 263L, 277, 280L mesothermal climate, floras 218R, 319, 320R, 321L, 326L, 330L Mesozoic Erathem 25R Messinian salinity crisis 233R, 251L Messinian Stage, Italy 233R methane hydrates 320L Mexico 37L, 106L, 130L, 131R, 162R, 169L, 200R, 201L, R, 202L, R, 217L, 218L, R, 219L, 239L, 251L, R, 254R, 256L, 257, 263R, 270L, 277, 280R, 289, 294L, 285L, 327L, R microthermal climate, floras 318R, 319, 324L, 327R Middlegate flora, Nevada 332L middle Wasatchian see Graybullian Milk River Formation, Alberta, Canada 23R Minimal Overlap Assemblage Fossilzone 5, 6R Miniochoerus affinis Interval Zone (late early Orellan) 164R

Miniochoerus chadronensis Inverval Zone (late Chadronian) 163R Miniochoerus gracilis Interval Zone

(early late Orellan) 164L Miocene Chronofauna 195L, 197R,

209L, 218L

Miocene (medial) climatic optimum 331R, 333L

Miocene-Pliocene boundary 218R, 233R, 251L, 295R

Miocene-Pliocene Chronofauna 335R, 337L

Miocene Series/Epoch, faunas, rocks 176R, 188L, 191R, 192R, 195L, 197R, 198R, 201L, R, 202L, 203L, R, 207L, R, 208L, 209L, 211R, 214L, 215R, 217R, 218L, R, 233L, R, 251L, 260R, 269L, 295R, 327L, 330L, 331R, 332L, R, 333L, 334R, 335R, 336R, 337L,

Miramar Sandstone Member, Pomerado Conglomerate, San Diego area, California 109L, 124L

Mission Valley Formation, San Diego area, California 109L, 118R, 123R, 124L, 136 *Mixodectes pungens/Plesiadapis prae*-

cursor Interval Zone (To₃) 72R, 75L *Mixodectes pungens* Taxon-range Zone (To₂) 16R, 17L

Mojave Desert, California 172L, 174R, 175L, R, 176R, 214R, 217L, 335L molecular 37L, 246L

Molina Member, Debeque Formation, Colorado 125R

Mongolia 90R

Monroe Creek Canyon, Nebraska 193R, 194L

Monroe Creek Formation, Nebraska, South Dakota 189L, 191L, 192L, 193R, 194L, 196R, 197L, 204L, 205R, 206L, 209R

Montediablan Stage, Clarendonian, Cl3, California 171L, 172R, 174R, 177L

Moraga Formation, California 219R Morris Skinner, American Museum of Natural History, New York 160R, 166R

Mount Eden Formation, California 175R, 251R

Mount Laurel Formation, New Jersey 28L

Mount Soledad Formation, California 122R

Mt. Eden flora, California 337L Muddy Valley beds, Nevada 257, 260R Mud Hills, California 175L, 214R

M.Y. (or m.y.) xivR

Myton Member, Uinta Formation (= Uinta C), Utah 109L, 111R, 117R, 118L, 126R M Zone (= *Pantolambda* Zone, To₃) ₇₂R

Naashoibito Member, Kirtland Formation, New Mexico 28L, 34, 36R
Nacimiento Formation 45R, 62L, 63L, 66R, 67R, 70L, R, 72R, 73L, R, 74R, 75L, 76L, 78R
NALMA xivL, R, 21L, 22, 34L, 35L, R, 43L, R, 45L, R, 53R, 70L, 90R, 93L, 106R, 107L, 112L, 134R, 135, 136, 137, 138L, R, 158L, 169R, 209L, R, 210, 212R, 214L, 218L
Nambé Member, Tesuque Formation, New Mexico 199L, R

Nanjemoy Formation, Virginia 108L, 133R

Nanxiong Basin, China 91L

Navahoceros LSD_k 259L

Nebraskan glacial stage (Pleistocene) 237R

Nebraskan till 237R

Neogene xivR 237L, 331R

Neotropical (taxa) 263L, 268R, 269L

New Fork Tongue of Wasatch Formation 113R, 128L

Niland Tongue, Green River Formation, Wyoming 180L, 127L Niobrara County, Wyoming 25R

No. 4 White Ash, New Mexico 221L

non-analog faunas (see analog)

- Nongshanian, Asian land mammal age (approx. correlative with Tiffanian/ Torrejonian) 90R, 91R, 32RL
- Nonpareil Ash, South Dakota 166R, 196L
- North American Land Mammal Age viiL, 8R, 21L, 43L, R, 106L, 135, 158L, 169R, 208R, 210, 232L
- North American Stratigraphic Code (NACSN) 43R, 44L, 164L

Northern Great Basin, North America 175L

Northern Hemisphere 106L, 336R Northern Rocky Mountains, North

America 179L, 187L, 188L, 191L, 214R North Great Plains, North America 191R

North Horn Formation, Utah 27R, 20L, R, 21L, 67L, 68L, 70L, R, 71L, R, 73R

Northwestern Nevada, North America 178L

notophyllous broadleaved evergreen forest 318R, 319, 320, 321L, 327L, 332L

NP (nannoplankton) zones 11L, R, 12L, 89R, 133R, 134L

Nunivak magnetic polarity subchron of Gilbert Chron 240, 251R, 254R, 262L Woodburne_losublinx 2/1//04 1:42 PM Page 385

Oak Grove flora, Oregon 337L

Oaxaca, Mexico 202L

Ocean Point, Alaska 26R

Subject Index 385

Ogallala Formation, Great Plains 192L, 197L, R, 198L Ogallala Group, Great Plains 188R, 194R, 213L Ojo Caliente Member, Tesuque Formation, New Mexico 200L Ojo Encino Member, Nacimiento Formation 45R, 72R, 75L Olcott Formation, Nebraska 197L, 214L Oldman Formation, Alberta, Canada 24L Olduvai magnetic polarity subchron of Matuyama Chron 233L, 237L, 240, 258R, 259L, 261L, R, 263L, 272L, R, 275L, 278L, 279R, 280L, R Oligocene Series/Epoch, faunas, rocks 133L, 156L, R, 160R, 164L, 172R, 174R, 176R, 198R, 205R, 209L, 320R, 326L, 329R, 330L, R, 331L, R Oligocene-Miocene boundary 331R Olyorian faunas, Siberia 285R One Mile Creek flora, British Columbia, Canada 326R Opal, Wyoming 111R Orella A, (Big Cottonwood Creek Member, Chadron Formation), Nebraska 158L, 161L, 162L, 163R Orella B, Nebraska 164R Orella C, Nebraska 165L Orella D, Nebraska 165L Orella Member, Chadron Formation, Nebraska, Wyoming 158L, 160L, R, 163R, 164L Orellan mammal age, faunas, rocks 156L, R, 158L, 159, 160L, R, 161L, R, 162L, 163R, 164–165L, R, 330R definition and characterization 164L zonation 164L, 164R Hypertragulus calcaratus Interval Zone (earliest Orellan) 164R Miniochoerus affinis Interval Zone (late early Orellan) 164R Miniochoerus gracilis Interval Zone (early late Orellan) 164R, 165L Merycoidodon bullatus Interval Zone (latest Orellan) 165L Orellan-Whitneyan boundary 166L Oreodon beds, Brule Formation, Big Badlands, South Dakota 159, 163R Oreodont Tuff, Barstow Formation, California 9L, 219R Otay Formation, San Diego area, California 174R Ouarzazate Basin, Morocco 92L Ouled Abdoun Basin, Morocco 92L Owyhee Basalt, Columbia Plateau, Oregon 187R, 214R

oxygen isotope sea water values 316, 317L, R, 318L, 320L, 330L, 332L oxygen isotope stages 238R

Pacific Northwest 254R, 256L Palaeosyops borealis Assemblage-Zone (Br-o) 113L, 114R Paleocene Series/Epoch, faunas, rocks xivR, xviiR, 1L, 11L, R, 16L, R, 17L, 26R, 35L, R, 36L, 37L, R, 43L, R, 44R, 45L, 64R, 76R, 77R, 78–79L, R, 80L, 83L, R, 85L, 88R, 89-95L, R, 96L, 320–321L, R, 323L, 324L, 325R Paleocene-Eocene boundary 11L, R, 43L, R, 79L, 89L, R, 90L, R, 92L, 93L, 106L, R, 107R, 128R, 132L, 134L, R, 139L, 320L, R, 324L, R Paleogene xivR, 202L, 318L, 324R paleomagnetic viiR, xiiiL, 1R, 8L, 14L, 15R, 17R, 26L, 34, 46, 63L, 66L, 68L, 71R, 73R, 74R, 78R, 79L, 81R, 82R, 83L, 87L, R, 88L, 89L, 90L, 91L, R, 92L, 94L, R, 95R, 106L, 120L, R, 123L, R, 125L, 131R, 208L, 214L, 237L, 238L, 239L, 240, 247R, 251L, 252R, 255R, 256L, R, 258L, R, 260R, 261L, 262L, 263L, R, 264R, 266R, 267L, R, 268R, 270R, 276R, 279L, R, 280R, 281L, 283L, R, 291L, Paleontologically Distinct Lithozone 16R Palm Park Formation, New Mexico 131L Palm Springs Formation, California 250L, 258R Palousie Prairie, northwest US 337L Panaca Formation, Nevada 252L, 260R Panama 203R, 212L Isthmus of (Panamanian isthmus; land bridge) 253L, 268R, 269L, 335R, 338L Panhandle, Texas, Oklahoma 264R Pantolambda Chronozone 72L Pantolambda-Plesiadapis praecursor (To₃) biochron 17L Pantolambda-Plesiadapis praecursor Interval Zone (To3) 72L, R Pantolambda zone 70L, 71R, 72L Pants Butte, Nebraska 193R, 194L paratropical forest 319, 320R, 321L, 324L, 327L, 328L Paris Basin 324L Paronychomys-Borophagus littoralis Assemblage Zone (Hh1) 177L Paskapoo Formation, Alberta, Canada 76R, 77L, 81L, 82L, 83L Pass Peak Formation, Wyoming 108L, 128R Paunsaugunt Plateau, Utah 23R Pawnee Buttes, Colorado 197L

Pawnee Creek Formation, Colorado 192R, 195L, 197L, R, 213R, 214L, 215R, 221L P-E Zone (= part of *Deltatherium* Zone, To2) 7RR, 74L Peace River Formation, Florida 207L Peach Springs Tuff, Arizona, California 176R, 219R Peanut Peak Member, Chadron Formation, South Dakota, Nebraska 158L, 162L, 163L Pearlette Ash 237R, 280R, 281R Pearlette B Ash 261L Pearlette O Ash 273R, 281R Peligrian mammal subage, South America 93L, 94R Peninsular Ranges, California 174R, 175L, 176R Penny Farms Formation, Florida 206L Peridiomys-Parahippus Zone (Ba1), Hepburn's Mesa Formation, Montana 191L Periptychus-Loxolophus Chronozone 71R, 72L Periptychus-Tetraclaenodon (To1) biochron 17L Periptychus carinidens/Protoselene opisthacus Interval Zone (To) 17L, 71R, 72R, 73L Periptychus carinidens/Tetraclaenodon Interval Zone (To1) 72L, R Periptychus cavirictum-Mixodextes pungens Interval Zone 17L Periptychus opisthacus-Ellipsodon grangeri Interval Zone 17L Persistent White Layer (= purplish white layer, PWL) 159, 161L Peters Gulch ash, Idaho 234, 240, 258L Pewelagus HSD₁, 259L Phenacodus-Ectocion Acme Zone (Cf3) 17L, 44L, 86R, 88L Piceance Creek Basin, Colorado 85L, 87R, 88L, 108L, 109L, 111L, R, 112R, 114L, R, 115L, 125L, R Pickles Butte basalt, Idaho 258R Picture Gorge Ignimbrite, John Day Formation, Oregon 179R, 189L, 220R Piedra Parada Member, Zia Formation 198L Pine Nut Mountains, Nevada 178L Pine Ridge Escarpment, Nebraska,Wyoming 158R, 194L, 196R Pine Ridge Reservation, South Dakota 193R, 196R Pinole Tuff, California 219R planktonic foraminiferal zonations 89R, 124R, 133L, 134L, 206R, 237L Pleistocene-Holocene boundary 238L, R, 247R

Pleistocene Series/Epoch, faunas, rocks 232–239L, R, 240, 244, 246L, 249R, 252R, 266R, 269R, 270L, R, 272L, 275R, 276R, 280R, 281L, 284-287L, R, 288L, 290L, 291–295L, R, 336, 337R, 338R Plesiadapis anceps/Plesiadapis rex Lineage Zone (Ti2) 80L, 81L, R Plesiadapis cookei Lineage Zone (Cf2) 86R, 87R Plesiadapis churchilli/Plesiadapis simonsi Lineage Zone (Ti4) 80L, 82R, 83L Plesiadapis gingerichi/Plesiadapis cookei Lineage Zone (Ti6-Cfi) 8oL, 84L, 86R, 87L Plesiadapis gingerichi/Rodentia Interval Subzone (Cf1) 80L, 84L, R Plesiadapis praecursor/Plesiadapis anceps Lineage Zone (Ti1) 44L, 80L-81L Plesiadapis rex/Plesiadapis churchilli Lineage Zone (Ti3) 80L, 82L, R Plesiadapis simonsi/Plesiadapis gingerichi Lineage Zone (Ti5) 80L, 83R, 84L Pliocene-Pleistocene boundary 233R, 237L, R in North America 237L, R Pliocene Series/Epoch, faunas, rocks 191R, 201L, 232–233L, R, 237L, R, 239L, R, 240, 244, 246L, 249R, 251L, 252R, 260R, 262L, 266R, 269L, 276R, 285L, 287L, 288L, 290L, 292L, R, 293L, 294L, R, 295R, 330L, 336, 337L, R, 338R Plum Point Member, Calvert Formation, Maryland 207R Pojoaque Member, Tesuque Formation, New Mexico 199R, 200L polar broad-leaved deciduous forest 318R, 319, 321L, 324L, 327L Polecat Bench, Wyoming 17R, 77L, 81L, 84R Poleslide Member, Brule Formation, South Dakota 160L, 165R, 166L Pomerado Conglomerate, San Diego area, California 109L, 118R, 123R, 124L Porcupine Hills Formation, Alberta, Canada 70R, 75L Powder River Basin, Montana, Wyoming 77L, 80R, 107R, 108L, 111L, 121, 132L, R, 158R Powder Wash, Ravens Ridge, Green River Basin, Utah 108R, 115L, 126L P-P zone (Dragonian, To1) 72L Preboreal pollen zone 238R precision (in correlation) xiL, xviiR, xviiiR, 6R, 8R, 9L, 10R, 13L, 16R,

26R, 36R, 85R, 92L, 106R, 121L, 132L, R, 160L, 167R, 194R, 206L, 209L, 214L, 233R, 236R, 259L, 271L, 293R Priabonian Stage 330L

Principle of Paleontological Correlation xviiL

Principle of Superposition xviiL

Principle of Original Horizontality xviiL

Principle of Original Continuity xviiL proboscicean datum 171R, 172L, 176L, 177R, 189R, 190L, 195L, 197R, 200L, 203L, 206R, 214L, R, 215L, R

Protoceras beds, Brule Formation, Big Badlands, South Dakota 165R, 166L

Protoceras-Leptauchenia beds 165R *Protoselene opisthacus/Mixodectes pun-*

gens Interval Zone (To2) 72R, 74L–75L

Protungulatum/Ectoconus Interval Zone (Pu1) 44L, 63R–65R

provincial (ism, ity) 24R, 28L, R, 36L, R, 68R, 69L, R, 95L, R, 119L, 178L, 203R, 209L, 214L, 215R, 232R, 249L, 252R, 272L, R, 273L, 274R, 280R, 290R, 291R, 292–294L, R, 295L, 319, 326R, 327L, R, 328R, 331L, 332L, 335L, 338R

Pui-Pu3 see Puercan

Puercan mammal age, faunas, rocks 16R, 17L, 21L, R, 26R, 27L, 28L, R, 32L, 35L, R, 36-37L, R, 43-45L, R, 46, 53L, R, 54, 61R, 62–70L, R, 71L, 73L, R, 78L, 91L, 92R, 94L, 95L, R, 320, 321L, R, 323R, 324L definition and characterization 62L-63R zonation 63R-70L Hanna Basin sole succession for superposition of all zones 66R Protungulatum/Ectoconus Interval Zone (Pu1) 63R-65R Ectoconus/Taeniolabis taoensis Interval Zone (Pu2) 65R-67R Taeniolabis taoensis/Periptychus carinidens Interval Zone (Pu3) 16R, 67R-70L Puercan-Torrejonian boundary 71L Puerco Formation 45L, R, 68L, 70L "Puerco Marls" 45L Pumpkin Buttes, Powder River Basin, Wyoming 132R, 158R Punta Peligro, Argentina 92R, 93L,

94R Punta Prieta, Baja Califiornia del Norte 131R

PWL (Purplish White Layer; see Persistent White Layer; Ash J, Flagstaff Rim) 159, 161L, 163L, R, 164R, 165L Pyramid flora, Nevada 333R

- Quaternary System/Period, faunas, rocks 232R, 237L, 287R, 290L, 291L, R, 293R
- radiocarbon dates, dating 238L, R, 286L, R, 287L, 288L, 291L, R, 293R, 294R, 295L

radioisotopic dates, dating viiL, R, xiiL, xiiiL, xivR, xviiiL, 1R, 8R, 9R, 10L, 14R, 15R, 22L, 24L, 26R, 32R, 44R, 47, 91L, R, 94L, 95R, 106L, 120L, 134R, 138R, 169L, 172R, 176L, 177L, 178L, 179R, 193L, 206L, 208R, 214L, 233L, 247R, 280R

fission-track method 192R, 194L, 195L, R, 201R, 219L, 237R, 251L, R, 258L, 259L, 261L, R, 264L, 266R

- ⁴⁰Ar/³⁹Ar method viiR, xviiiL, 8R, 9L, 11L, 22R, 25L, 26R, 63L, 65R, 123R, 135–137, 156L, 158L, 161R, 162L, R, 163L, 164L, 166L, R, 173R, 177R, 178L, R, 179L, 187L, R, 195R, 197R, 199R, 200L, R, 251R, 258R, 264L, R
- K-Ar method viiR, xviiiL, 8R, 9L, R, 26R, 132L, 173L, R, 187R, 194L, 195L, 201L, 202L, R, 203L, 208L, 251L, 256R, 259R, 271L

radiometric 14L, 26R, 36R, 91L, R, 160L, 171R, 178L, 196L, 219L, 233L, 237R, 238L, 239L, 240, 251L, 252R, 256L, 258L, 260R, 263R, 264R, 267R, 268L, R, 270L, 281L, R, 283L, 285L, R, 286L, 287L, 294R

Rak Tuff, California 219R

Rancholabrean mammal age, faunas, rocks 232L, 233L, 239L, 240, 244, 246L, R, 247R, 248, 249L, 264L, R, 269R, 270L, R, 273L, 274R, 276L, R, 280R, 282R, 283–288L, R, 289, 292L, 293L, R, 294R arrival of *Bison* 285L, R

definition and characterization 284R–285L

geographic distribution 288L–290L Kennewick sequence 288R, 289R

Meade Basin sequence 288R

Medicine Hat sequence 288L, R historical treatment 284R

zonation 287L, R

Bison chronology 287L, R

Loess stratigraphy 287R Randlett horizon, Duchesne River For-

mation 112L Randlett Point, Uinta Basin, Utah 118R

Range Chron xiiL, xivR, 4, 5, 15L

Range Zone xiL, R, 3R, 4, 5, 6L, R, 15L, 17R, 34L, R, 44L, 113R, 114R, 121R,

156L, 162L, 166R, 173L, 177L, 179R,

197R, 198L, 258R, 259L Raton Basin, Colorado 108L, R, 111L, R, 125R, 131L Rattlesnake Fm., Oregon 220R Raven Ridge, Uinta Basin, Utah 108L, R, 114R, 115L, 125–126L, R Ravenscrag Formation, Saskatchewan, Canada 26R, 35R, 53L, 62L, 64R, 69L, 76R, 321L Rawls Formation, Big Bend area, Texas 201L Recent (temporal interval) 238L, 288R Red Bird, Wyoming 34R Red Light Bolson, Texas 257, 263R Regina Member, San Jose Formation, New Mexico 130L Relizian benthonic foraminiferal stage, California 171R, 214R Relizian-Luisian boundary 171L, R, 214R Renova Formation, Montana 160L, 188R Reunion magnetic polarity subchron of Matuyama Chron 240, 279R resident faunal elements 321R Rexroad Formation, Kansas 264R Rexroadian subage, Blancan age 253L, R Ricardo Faunas, faunal sequence, California 175R, 176R, 177L, 216L, 217L Ricardo Group, California 175R, 176R Ringold Formation, Washington 232R, 135 256L, R Riochican mammal age, South America 93L, 94L Riochican mammal subage, South America 95L Rio Chico Formation, Argentina 93L, 94R Rio Grande rift, New Mexico 130L Riverside County Landfill, California 259R Robin's Egg Blue Tuff, Washakie Formation, Sand Wash Basin, Wyoming 116R, 127R Rock Springs Uplift, Wyoming 83L, R, 109L rock unit vs temporal unit 106R, 160R, 161R, 162L, 163R, 164L, 165R Rockyford Ash, South Dakota 166R, 196L Rocky Mountains 107L, 117L, R, 179L, 187L, 188L, 191L, 214R, 217L, 254R, 255R, 272L, R, 273L, 274R, 275L, 279L, 280L, 292R, 294L, 318L, 320R, 321L, 326L, 327R, 328L, R, 330L, R, 331R, 332L, 334R, 336R, 338L Rodentia/Plesiadapis cookei Interval

Rodentia/Plesiadapis cookei Interval Subzone (Cfi) 86L, 87L, R Rosebud Formation, beds, South Dakota 196R, 197L, 209R, 212L Rose Creek Member, John Day Formation, Oregon 187L Roundhouse Rock Ash, Nebraska 220R Rubio Peak Formation, New Mexico 131L Runningwater Chronofauna 331R, 332R Runningwater faunas, Nebraska 194R, 199L, 206R Runningwater Formation, Nebraska 175L, 187L, 191R, 192L, 194R, 208L, R, 212R Rupelian Stage 330L Saddleback Basalt, California 219R Safford Basin, Arizona 257, 261R Sage Creek Formation, Beaverhead County, Montana 108R, 134R Sage Creek Limestone, Bridger Formation 115R Sage Creek Mountain, Wyoming 115R, 128L Sage Creek White Layer (SCWL), Bridger Basin, Wyoming 115L, R Salamanca Formation, Argentina 94R Salmon flora, Idaho 326R San Andreas fault, California 175L Sand Coulee beds 107R, 108L Sandcouleean subage (Wa-o-Wa-2) of Wasatchian mammal age (early Wasatchian) 107L, 113L, 122L, 132L, characterized 113L Sand Creek facies, Willwood Formation 107R San Diego area, California 116L, R, 118R, 122R, 123R, 124L, R, 125L Sand Wash Basin, Colorado 107R, 108L, R, 115L, R, 116R, 117L, 126R, 127R San Francisco Bay Area 171L Sangamonian interglacial stage (Pleistocene) 237R, 238L San Jacinto fault, California 175L San Joaquin Valley, California 171R, 172L, R San Jorge Basin, southern Argentina 92R, 93L, 94R San Jose Formation, New Mexico 76L, R, 108L, 109R, 111L, 130L San Juan Basin, Colorado, New Mexico 16L, R, 24R, 27, 34, 36R, 45L, R, 63L, 64R, 65L, 66-69L, R, 70L, 71–74L, R, 75L, 76L, 78L, 83R, 93R, 94L, 95R, 107R 108L, 109R, 125R, 130L San Pablo Group, California 171L San Pedro Valley, Arizona 232R, 256L, 257, 261L, R, 270L, 280L

Santa Ana Mountains, California 174L Santa Fe Marls, New Mexico 198R Santa Margarita Formation, California 172L Santee Ash, Ash Hollow Formation, Nebraska 195R, 220R Santiago Formation, San Diego area, California 109L, R, 118R, 124L San Timoteo Badlands, California 232R, 251L, 259R, 269L, 277, San Timoteo Formation, California 175L, 251R, 278L Santa Ana Mesa basalt, New Mexico 262R Santa Lucia Formation, Bolivia 93R Santonian Stage/Age, faunas, rocks 23L, R Sao Jose de Itaborai, Brazil 94L Sao Jose de Itaborai Formation, Brazil 94L Sappan subage, Irvingtonian age 247L, 273L, R Scollard Formation, Alberta, Canada 26R, 27, 32R, 34 Scottsbluff National Monument, Nebraska 161L Scenic Member, Brule Formation, South Dakota 160L, 166L Scripps Formation, San Diego area, California 108R, 115R, 123L sea level 315L, R, 317L, R, 318L, 323–324L, R, 325, 326L, 327R, 328L, R, 329, 330L, 331R, 333L, 335, 337L Seaman Hills, Wyoming 160R, 161L, 163-164L, R sea surface temperatures 317R, 318L, R, 320L, 324R, 326L, 330L second Nonpareil Ash Zone of the "brown siltstone," Nebraska 166L Seldovian (floral) stage, Alaska 334R Senecan subage, Blancan age 247L, 253L, R Sentinel Butte Formation, North Dakota 76R, 77L Sentinel Butte Shale Member of Fort Union Formation, North Dakota 132L sequence stratigraphy 315R Sespe Formation, California 109L, R, 118R, 119R, 123R, 124L, R, 125L, 138R, 172R, 173L, 174R, 175L Seymour Formation, Texas 282L Shanghuan(ian), Asian land mammal age 90R, 91L, R, 324L Shanyang Basin, China 91L Shark River Marls, New Jersey 132L Sharps Formation, South Dakota 166R, 179R, 187R, 188R, 189L, R, 193R, 196L, R, 197L, 209R Sheep Creek Formation, Nebraska 175R, 194R, 220R

Sheep Mountain Table, Big Badlands, South Dakota 165L, 166L Sheridanian subage, Irvingtonian age 247L, 273L, R, 274L, 285R Shirley Basin, Wyoming 132R Shoshonian subage, Uintan mammal age 116L, R, 117L, 136, 138R Shotgun Butte, Wyoming 121L Shotgun Member, Fort Union Formation, Wyoming 77L Sidufjall magnetic polarity subchron of Gilbert Chron 200R, 240, 251R, 252L, 256R Siebert Tuff, Nevada 177R Sierra Ladrones Formation, New Mexico 270R Sierra Nevada 332L, 336R, 337L Siesta Formation, California 219R Sigmodon LSD₁, 259L Simi Valley area, California 109R 119R, 120L, 124L, R, 125L, 172R, 173L Sinostylops Interval Zone 91R Six Mile Creek Formation, Montana 188R Skull Ridge Member, Tesuque Formation, New Mexico 199R, 199L, 200L Slim Buttes, South Dakota 196R, 197L Slim Buttes Formation, South Dakota 109R, 133R Smilodon LSD_k 259L Smoky Hollow Member, Straight Cliffs Formation, Utah 23L Snake River Plain, Idaho 232R, 253R, 256L, 256R, 276R Soldier Meadow Tuff, Nevada 178L South America 37L, 91R, 92R, 93-94L, R, 95L, 218L, 253L, 259L, 268L, R, 269L, 316, 317L, 335R, 336L, 337R Southern Great Basin, North America 169L, 214L Southern San Joaquin Valley, California 171R, 172L South Mountain, California 173L South Tejon Hills, California 172R South Townsend Basin, Montana 160L South Pass, Green River Basin, Colorado 113L, 128R Spanish Peaks, Colorado 131L Sparnacian Stage/Age, faunas, rocks 16L, 89–90L, R Spain 88R, 89L, 334R Spitzbergen (dispersal) 90R Split Rock Formation, Wyoming 195R, 220R ⁸⁷Sr/⁸⁶Sr isotope ratios 205–206L, R, 267R, 270R, 283R Stadium Conglomerate, California 109L, 118L, R, 123L, R Stage 1L, 2, 7, 8L, R, 16L, 171–172L, R, 172R, 174R, 233R, 236R, 234R, 334R

112I stasis 290L St. David Formation, San Pedro Valley, Arizona 261L, 267L St. Mary River Formation, Alberta, Canada 25L St. Mary's Formation, Maryland 208L Steens Basalt, Oregon 220L Stewart Valley flora, Nevada 334L Straight Cliffs Formation, Utah 23L stratigraphic classification 1R, 2L stratigraphic (position) 1L-8R, 45L, 46, 47, 53L, R, 62L, 63L, 65L, 67L, 68L, 71R, 72L, R, 73R, 74L, R, 77L, R, 78L, 80R, 83L, 85L, 89L, R, 90L, 93R, 115R, 116L, R, 120L, 124R, 126L, 128L, 133R, 134R, 156R, 162L, 163R, 164L, 166R, 169L, R, 170L, 174L, 175R, 179L, 187R, 190L, R, 193L, R, 195L, 198–199L, R, 200L, 203L, R, 206R, 207L, 208R, 215L, 216L, R, 237R, 239L, 247L, 250R, 251L, 252R, 254R, 256L, R, 258-259L, R, 261L, R, 263L, 264L, R, 265R, 266L, R, 271L, R, 272L, 278L, 279L, 280R, 281L, R, 286L, 287R, 288R, 290R, 291L, R, 294R, 317R, 338R stratotype (type section, area) 1R, 2, 3R, 5, 7, 8L, R, 13L, 15R, 16L, R, 17R, 21R, 23L, R, 25R, 26R, 27L, 28L, 34L, 36R, 45L, R, 49, 53R, 64R, 65L, 66L, R, 67R, 69L, 70L, 71R, 72L, 75L, 79L, 82L, R, 84R, 85L, R, 86L, 87L, 89L, R, 90L, 106R, 107L, R, 111L, 115L, 118R, 120R, 123R, 126L, 127R, 134R, 139L, 158L, 160R, 161R, 162R, 163L, R, 164–165L, R, 166L, 167L, 175R, 178R, 187L, 189L, R, 190L, 193R, 194L, R, 195R, 197L, R, 198R, 203L, R, 206L, 208R, 213R, 233L, R, 237-238L, R, 239L, 261L, 269R, 273R, 275R, 278L, R, 282L, 287R, 295R Strict Overlap Assemblage Fossizone 4, 5, 6L, R, 15L subtropical forests 324 R, 326L, 327L, 331L, R, 332L, 332L Summit Lake Tuff (Tuff of Big Basin), Nevada 178R superposition(al) xviiL, 5, 16R, 18L,

Starr Flat Member, Duchesne River

Formation, Utah (unfossiliferous)

superposition(a) xviil, 5, 16K, 18L, 27L, 45R, 65–66L, R, 68L, 71L, 73R, 74L, 75R, 77R, 94R, 95L, 118L, 121L, 129R, 131L, 133L, 169L, 171R, 172R, 174L, R, 178L, 188L, 198R, 200R, 212R, 215R, 216L, 217R, 251R, 252L, 258R, 260L, 262R, 280R, 282L, 283L, 286L, 287R, 288L, R, 290L
Sunrise Pass Formation, Nevada 260L
Susanville flora, California 326R, 327L

Sutro flora, Nevada 332L

- Swallow Ash, Ash Hollow Formation, Nebraska 195R, 220R
- "Sweetwater" Formation, San Diego area, California 109R, 124L
- Swift Current Plateau, Saskatchewan, Canada 133L
- Suchilquitongo Formation, Mexico 202L

Sucker Creek Formation, Oregon 187R Suwanee Limestone, Florida 205R

Sycamore Canyon Formation, California 171L, 219R

synchronous 21R, 32L, 37L, 91R, 106R, 176L, 268L, 317R, 320R, 324L, 236R, 332L

Tabernacle Butte, Wyoming 108R, 113R, 128L, R

Taeniolabis-Periptychus (Pu₃) biochron 16R

Taeniolabis taoensis/Periptychus carinidens Interval Zone (Pu3) 16R, 63R, 67R

Talkeetna Mountains, Alaska 111L

Tamiami Formation 251L

Tampa Limestone Member, Arcadia Formation, Florida 204R

Tapicitos Member, San Jose Formation, New Mexico 130R

Tatman Formation, Wyoming 108R, 122L

Taxon-range Chron xivR, 4, 5, 15L

Taxon-range Zone xiR, 2, 4, 5, 6L, 15L, 16R, 17L

Tecuya Formation, California 171L, 219R Teewinot Lake flora, Wyoming 337L Tehachapi flora, California 332L Tehachapi Mountains, California 175R Teichert Gravel Pit, California 286L Tejon Hills, California 172L, R Temblor Formation, California 171R Temecula Arkose, California 257, 260L temperate climate, flora 318R, 324R,

327L, R, 328L, 330R, 334R, 327L temperature gradient (poleward) 315L, 318R, 230R, 326R

- Tepee Trail Formation, East Fork Basin, Wyoming 108R, 116L, 117L, R, 118L, 120R, 121L, 122L
- Tertiary System/Period, faunas, rocks 9L, 21L, R, 32L, R, 35L, 35R, 36L, R, 37L, 43R, 62L, 64R, 115R, 116L, R, 127L, 129R, 171L, 188L, R, 191R, 195R, 202L, R, 232R, 230L

Tesuque Formation, New Mexico 199L, R, 200L, 214L

Tetraclaenodon/Pantolambda Interval Zone (To2) 72L, R

Texas Coastal Plain 204L

Thanetian Stage/Age, Europe, Africa 88R, 89L, R, 92L, R thermoluminiscent (TL) dates 285R, 287R Thousand Creek beds, Nevada 178R Three Forks Basin, Montana 160L Thunder Mtn. flora, Idaho 326R Thvera magnetic polarity subchron of Gilbert Chron 233R, 240, 252L Ti1–Ti6 see Tiffanian Tiffanian mammal age, faunas, rocks 17L, R, 43L, R, 44L, 48, 62R, 64L, 70R, 71R, 73L, 75R, 76-80L, R, 321L, 323R, 324L definition and characterization 78R, 79L, R zonation 79R Plesiadapis praecursor/P. anceps Lineage Zone (Ti1) 79R, 80L-81L, 82L, 83R *Plesiadapis anceps/P. rex* Lineage Zone (Ti2) 78L, 79L, 80L, R, 81L-R, 82L Plesiadapis rex/P. churchilli Lineage Zone (Ti3) 77L, 79L, 81R, 82L-R, 83L Plesiadapis churchilli/P. simonsi Lineage Zone (Ti4) 79L, 80L, 82R-83R, 89L, 91R Plesiadapis simonsi/P. gingerichi Lineage Zone (Ti5) 79L, R, 80L, 83L, R-84L, 91R Plesiadapis gingerichi/Rodentia Interval Subzone (Ti6) 79R, 80L, 84L-R Plesiadapis gingerichi/P. cookei Lineage Zone (Ti6-Cf1) 79L, R, 80L, 84L, R, 85R, 86R, 87L, 89L Tiffanian-Clarkforkian boundary 84L, 85L, 85R, 86L, R Tiffany beds, Colorado 76L, R Tiffany, Colorado 76L Tijeras Arroyo, Bernalillo County, New Mexico 262R, 270R, 271L, 271R, 277, 280L time-average(d) 35L, 293R Tin Roof Tuff, John Day Formation, Oregon 173L, 179R, 211R, 220R Tipton Tongue, Green River Formation, Wyoming 127L Titanotherium beds 160R Tiupampian mammal subage, South America 93L *Tetraclaenodon-Pantolambda* (To2) biochron 17L To1–To3 see Torrejonian Toadstool Park, Nebraska 160R, 161L, 162L, 164R, 165L, 166L Togwotee Pass, Wyoming 77L, 85L, R, 87L, 87R, 108L, R, 111L, 120L, R

Tongue River Formation, Montana, North Dakota; member of Fort Union Fm. 76R, 77L, 80R, 81L Tornillo Formation, Texas 62L, 69R, 70R, 71R, 74R, 79L, 85L Tonopah Tuff, Nevada 220L Torrejon Formation 45L, R, 70L Torrejon Wash, New Mexico 45L, 74L Torrejonian mammal age, faunas, rocks 16R, 17L, 43L, R, 44L, 45L, R, 47, 48, 62R, 69R, 70-73L, R, 74R, 75L, R, 76R, 77–79L, R, 80R, 81R, 88R, 91L, R, 92R, 94L, 95L, 323L, R, 342L definition and characterization 71L-72L zonation 72L-76L Periptychus carinidens/Protoselene opisthacus Interval Zone (To1) 17L, 63L, 71–73L, R, 74L Protoselene opisthacus/ Mixodectes pungens Interval Zone (To2) 72L, R, 73R, 74L-75L, 91L, 93R, 94L Mixodectes pungens/Plesiadapis praecursor Interval Zone (To3) 72L, R, 73L, 74L, 75L-76L, 77L, R, 79L, 80R, 81R, 91R Torrejonian-Tiffanian boundary 75R, 77L–79L, 80R Torrey Sandstone, California 123L Torreya Formation, Florida 206R Trail City Member, Fox Hills Formation, South Dakota 34L Trans-Mexican Volcanic Belt, Mexico 201L, R Trans-Pecos (area), Texas 112L, 115R, 116L, 136, 138R, 160L, 161R, 162R Transverse Ranges, California 172L, R, 174R Tres Cruces, Bolivia 92R Triceratops Zone, Scollard Formation, Alberta, Canada 32R tropical forest 318R, 319, 321L, 324L, R, 326-327L, R, 328L, 330L, 331L, 332L, 335R Trout Peak Trachyandesite, Wyoming 122R Trubi Formation (Trubi Marls), Italy 233R Trunk Butte (= Big Cottonwood Creek) Member, Chadron Formation, Nebraska, Wyoming 161L Tuff of Big Basin, Nevada 178R, 220L Tule Formation, Texas 250R, 262R, 271L, 282L Tulelake flora, California 337L Tullock Formation, Montana 28R, 36L, R, 53L, 62L, 63L, 64L, 68R, 70R, 71R,

73L, 95R

Turlock Lake Formation, California 278R Turonian Stage/Age, faunas, rocks 23L, 317R, 318L Turtle Butte Formation, South Dakota 196R Turtle Cove Member, John Day Formation, Oregon 179L Tuscahoma Formation, Mississippi 108L, 111L, 133R Turtle Bluffs Member, Bridger Formation, Wyoming 108R, 111R, 117L Twinbuttean subage (Br-3), Bridgerian mammal age 115R Twin Buttes Member, Bridger Formation 108R, 111L, 115L, R Two Medicine Formation, Montana 24L type locality 107R Uinta A-C 111R, 115R, 116L, 117L, 126L, R. 136 Uinta B1 111R, 116L, 117L, R, 118L, 120R Uinta B2 111R, 118L Uinta Basin, Colorado, Utah 107L, 108-109L, R, 111R, 112L, 114L, R, 115L, R, 118L, R, 125L, R, 126L, 131L, 136, 138L Uinta Formation, Colorado, Utah 111R, 112, 117R, 118L, 125L, R, 126L, R, 138R Uintan-Duchesnean boundary 118R, 119L, 138R Uintan mammal age, faunas, rocks 107L, 109, 111R, 112L, 115–118L, R, 119L, 120R, 121-124L, R, 125L, 126L, 127R, 128L, 129L, R, 130R, 132L, 133L, R, 134L, R, 136, 138L, R, 327R, 328L, R definition and characterization 117L, R zonation 117R-118R Shoshonian subage (Ui-1?) 116L, R, 117L, 136, 138R Bridger E (early Uintan) 108L, 111L, 116L, R, 117L, 128L, 129R, 136 Uinta A 111R, 115R, 116L Uinta B 111R, 116L, 117R, 126L Uinta B1 109L, 111R, 116L, 117L, R, 118L, 120R Uinta B2 109L, 111R, 117R, 118L Uinta C 111R, 116L, 117R, 126R, 136 Ui1, Shoshonian 116L, R, 117L, 136, 138R Ui2 108, 109, 116L, 117L, R, 118L, 123R, 126R, 127R, 129R, 136 Ui3 108, 109, 116L, 117R, 118L, 121R, 123R, 124L, 126R, 129R, 130L, 131R, 133L, 134L, R, 136, Umayo Formation, Peru 92R unconformity (ies), unconformably xiiiL, xviiiR, 3L, 6R, 10L, R, 11L, 13L, 18L, 113R, 116L, 122L, 129L, 130L, 131L,

woodburne_lusublix 2/1//04 1:42 PM Page 390

390 Subject Index

unconformity (continued) 177L, 187L, 188L, R, 193R, 198L, 202L, 233R, 258R, 263R, 276L, 281L, 288L, R Upper Bone Valley Formation, Florida 251L Upper John Day Formation, Oregon 179L Upper Harrison beds, Nebraska 191R, 194L, R, 196R, 198R, 212L, R Upper Harrison Formation, Nebraska 194L Upper Oreodon Beds, Brule Formation, Big Badlands, South Dakota 159, 165L, R, 166L Upper Nodular Zone, Big Badlands, South Dakota 165L Upper Tuffaceous Zone, New Mexico 221L Upper Whitney Ash, South Dakota 166L Uquian mammal age (South America) 269L Ustatochoerus profectus/Copemys russelli Assemblage Zone (Cl1) 177L Uzbekistan 23R Valentine Formation, Nebraska 177R, 191R, 192R, 193R, 195L, R, 197L, R, 200L, 215R, 216L, R Vallecito-Fish Creek section, Anza-Borrego Desert State Park, California 244, 245, 258R, 259R, 260L, 271L, 272R Valle de Oaxaca Gaben, Mexico 202L Vaqueros Formation, California 174R Ventura County area, California 118R, 122R, 124L, 125L, 172R Vieja Group, Texas 130L, 160L Vieja-Ojinaga area, Presidio County, Texas 129L, R, 138R Villafranchian Stage, Italy 236R, Virgin Valley beds, Nevada 178R, Virgin Valley Formation, Nevada 178R, 220L Vista Member, Brule Formation, Colorado 160L, 166L volcaniclastic deposit(s) 173L, 178L, R, 188R, 194L, R, 198R, 202L, 203R, 213L Vrica, Italy 237L Wa-o-Wa7 see Wasatchian Wagon Bed Formation, Wind River Basin, Wyoming 108L, R, 109L, 115L, 118L, 121R, 132R, 134R Wagonhound Member, Uinta Formation (= Uinta A and B), Utah 109L, 111R, 117R Wahweap Formation, Utah 23R Wapiti Formation, Wyoming 122L

Wapiti Valley, Wyoming 122R

warm-temperate forests 324R, 328L, 330R, 331R, 332L, 333R, 337L Wasatch beds 107R Wasatch Formation, Wyoming, Utah 77L, 85L, 107–108L, R, 112R, 113L, 114–125L, R, 126R, 127L, R, 128R, 132L, R type locality 107L, R Wasatch Group 107L, 128R Wasatchian mammal age, faunas, rocks 43R, 46, 74R, 77R, 85R, 86L, R, 87L, 89L, R, 90L, R, 92L, 106R, 107L, R, 109, 111L, 112–114L, R, 115R, 120L, R, 122L, R, 123L, 125–128L, R, 129L, 130-134L, R, 135, 138L, 139L, 324R, 235R, 326L, 327R, 338R definition and characterization 112R-113L zonation 113L Sandcouleean subage 107L, 113L, 122L, 132L, 135 Graybullian subage 107L, 111L, 113L, 122L, 130R, 132L, 135, 325R Lysitean subage 107L, R, 111L, 113L, 122L, R, 130R, 135 Lostcabinian subage 107L, R, 113L, R, 121L, 122R, 135 Wao, Sandcouleean 107L, 113L, 122L, 125R, 131R, 132L, 135, 320L, 323, 324R, 325L, R Wa1, Sandcouleean 125R, 131R, 133R Wa2, Sandcouleean 108, 111L, 113L, 120R, 126L, 132L Wa3, Graybullian 108, 113L, 120L, 122L, 127L, 131L, 132L, R, 133R Wa4, Graybullian 113L, R, 135, 138L Wa5, Graybullian, 108, 111L, 113L, 125R, 126L, 130L, 131L, 132R, 133R, 135, 138L Wa6, Lysitean 111L, 113L, 122L, R, 130R, 135 Wa7, Lostacbinian 107L, R, 113L, R, 121L, 122R, 135 Wasatchian-Bridgerian boundary 113L, R, 114L, 138L, 139L Wasatchian Stage/Age 16L Wasatch Station, Weber Canyon, Summit County, Utah 107L, R Washakie A (faunal level) 127R Washakie B (faunal level) 127R Washakie Basin, Wyoming 70R, 74R, 75R, 85L, 87L, 107R, 108L, 115L, R, 116R, 126R, 127L, R, 135, 136, 138L Washakie Formation, Wyoming, Colorado 108R, 109L, 115L, 116R, 117L, R, 127L, R, 136 Western Interior 24R, 26R, 28L, 32L, 34L, 35R, 36L, R, 37L, R, 39L, 93R, 122R, 321R

western montane coniferous forest 326L, 332L, 333R, 335L, 337L Western Nevada, North America 177R West Fork, Gallegos Canyon, San Juan Basin, New Mexico 45R, 48, 66L, 67R, 72R Weta Paleosol, South Dakota 158L Wheatland County, Montana 24L White Ash No. 4, Skull Ridge Member, Tesuque Formation, New Mexico 199R White River Chronofauna 166R, 173L, 179R, 193L, 205L, 206L, 209R, 328R, 330L, R, 331L, R White River Group, Colorado, Nebraska, North Dakota, Montana, South Dakota 156R, 158L, R, 160L, 166R, 167L, 179R, 188R, 193L, 194R, 196L, 209R deposition 158R White River relicts (taxa from White River faunas) 171R, 196L, 204R, 205L, R Whitneyan mammal age, faunas, rocks 156L, R, 159, 160L, 165-166L, R, 167L, 325, 330R definition and characterization 165R zonation 165R Leptauchenia major Interval Zone (early Whitneyan) 165R, 166L Merycoidodon major Interval Zone (late Whitneyan) 166L, R Whitneyan-Arikareean boundary 166R, 209R Whitney A, Brule Formation, Big Badlands, South Dakota 166L Whitney B, Brule Formation, Big Badlands, South Dakota 166L Whitney C, Brule Formation, Big Badlands, South Dakota 166L Whitney Member, Brule Formation, Nebraska, Wyoming 158L, 160L, R, 165R, 166R Wiggins Formation, Wyoming 109L, 117R, 118L, 121L, R, 122R Wild Horse Mesa Tuff, California 176R, 219R Willard Canyon Tuff, Sespe Formation, California 173L, 219R Wilkins Peak Member, Green River Formation, Wyoming 113R, 114L, 127L, 128L Williamsburg Formation, South Carolina 77L Williams Fork Formation, Colorado 25L Williston Basin, Montana, North Dakota 26L, 51, 52, 77L, 82L, 83L, 111L

- Willwood Formation, Wyoming 11R, 17L, R, 85L, R, 107L, R, 108L, 114L, 122L, R, 126R, 132L, R, 135 Wind River Basin, Wyoming 24L, 77L, 80L, 83L, 84R, 87L, R, 107R, 108–109L, R, 111R, 113L, R, 114L, 118R, 120–121L,
- R, 122L, 125R, 131L, 132L, R, 134R, 158R Wind River Formation, Wyoming 107L, 108L, 113L, 114R, 121L, 122L,
- 132L, R Wisconsinan glacial stage (Pleistocene) 237R, 238L, 287L, 288L, R
- Wodehousia spinata Assemblage Zone 32L
- woodland-savanna forest 326L, 327L, 332L

Wood Mountain Plateau, Saskatchewan, Canada 192L

- Woods Mountain volcanic center, California 176R
- Yarmouthian interglacial stage (Pleistocene) 237R, 238L Yautepec Tuff, Mexico 221L Yellowstone National Park 111L, 191L Yepómera, Chihuahua, Mexico 178L, 200R, 201L, R, 202L, 218R Younger Dryas pollen zone 238R Ypresian Stage/Age, Europe 89R, 92R Yukon Territory 239L, 249L, 277, 280L, 321L Yushe Basin, China 254R
- Zanclean Stage, Capo Rossello, Sicily 233R, 251L Z coal complex 28R

- Zia Formation, New Mexico 196L, 198R, 199L
- zoogeography (ic); provinces 169L, 170L, 174R, 177R, 178L, 179L, 187R, 191L, 192R, 199L, R, 204R, 206L, 209L, 213L, 214L, 215R, 324L, 338R zone, zonation xi–xivL, R, xviiR, xv–iiL, 2–3L, R, 4, 5, 6–7L, R, 8L, 10L, 11L, 14R, 15–17L, R, 32L, R, 34L, R, 35L, 43R, 44L, R, 53R, 61L, R, 63–88L, R, 107L, 111L, R, 113L, R,
- 114R, 121R, 127R, 133R, 134L, 138L, 156L, 162R–163R, 164L–166L, 170L, 171R, 173L, 177L, R, 179R, 180, 188L, 191L, R, 198L, 206L, R, 247R, 248, 253R, 258R, 259L, 263L, 280L
- Zoyatal Tuff, Mexico 201R

Woodburne_IUSubInx 2/1//04 1:42 PM Page 392

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