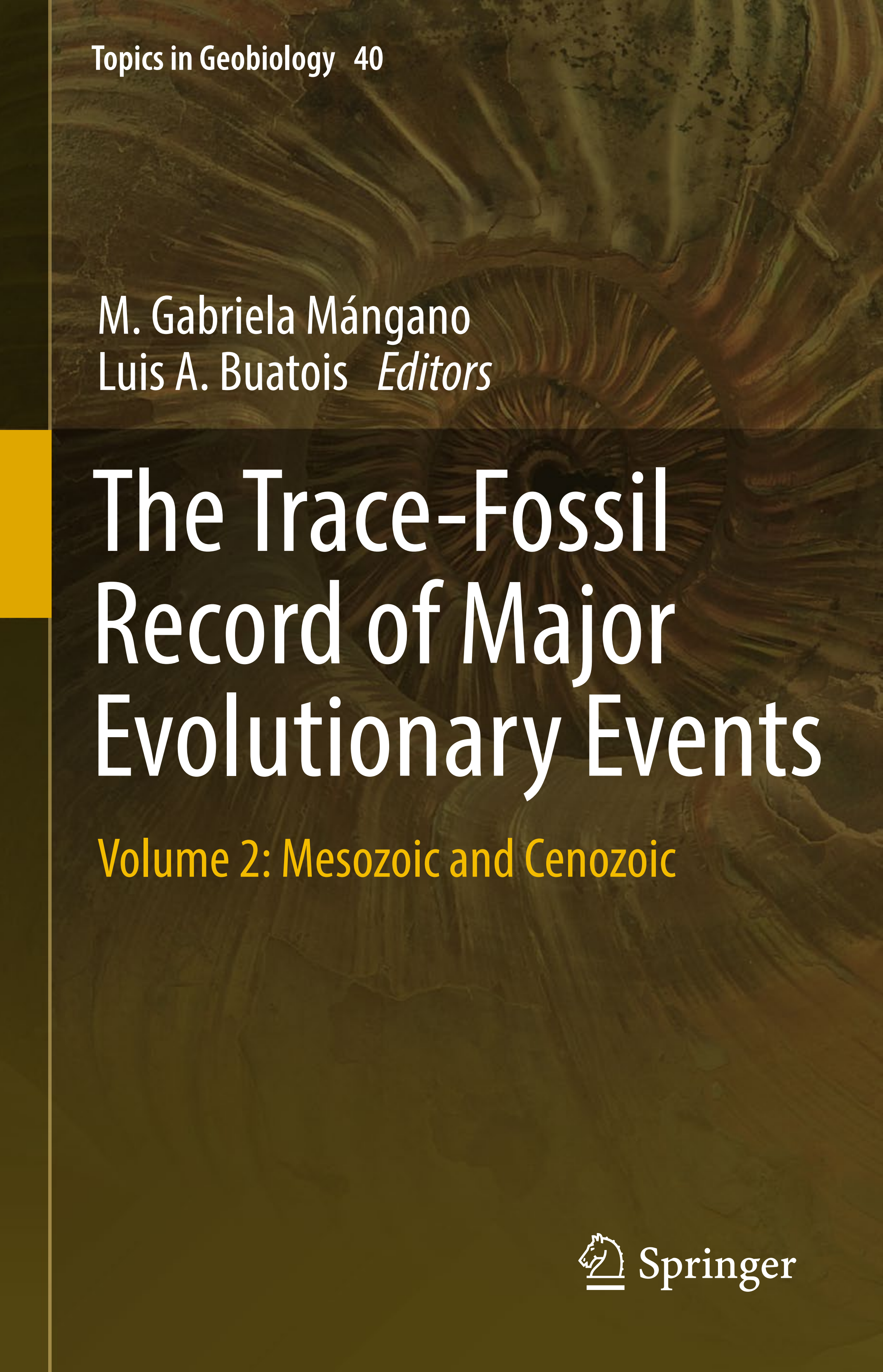

Topics in Geobiology 40

M. Gabriela Mángano
Luis A. Buatois *Editors*

The Trace-Fossil Record of Major Evolutionary Events

Volume 2: Mesozoic and Cenozoic

Springer

Topics in Geobiology

Volume 40

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Editors

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To Dolf Seilacher, who, as usual, thought about these issues long before us.

Foreword

Imagine a world much like our own: an oxygen-rich atmosphere, dynamic tectonic activity, and a rich and diverse biota of plants, animals, and teeming associations of microbes. Indeed a world just like ours, with a similarly deep history of life, but with one slight difference: no body fossils. No shark teeth eroding from cliffs, no trilobites, no dinosaur bones cluttering up museums and the dreams of impressionable 5-year-olds (and Hollywood moguls). Worst of all, of course, we would be missing the remarkable schnozzle of *Opabinia*. Much of the rich morphological detail provided by body fossils would be irretrievably lost, but how much of the history and diversity of life could we recover? Would we be able to identify the explosive evolutionary dynamism of the Cambrian diversification? Would the paleontologists of this imaginary world be able to chart changing patterns of animal diversity and morphological disparity? Identify the invasion of land or the great mass extinctions? Chronicle advances in behavioral patterns? Would changing climate patterns be evident, or the rise of great plodding vertebrates?

If we stipulate that tracks, trails, and burrows were preserved in all the detail documented in the chapters of this volume and the richly informative photographs and diagrams, then a remarkable detailed view of animal diversity, morphological disparity, and behavior emerges. For those not intimately acquainted with the extensive strides made over the past couple of decades of research in ichnology, this volume illustrates the range of information which can be recovered from the primary record of organismal behavior to analysis of changing patterns of diversity and disparity.

As a graduate student during the early 1980s the focus of ichnology seemed to be on describing new structures and providing them (mystifyingly to those of us who did not study trace fossils) Latin binomials. Yet ichnology was already undergoing a conceptual shift in concert with changes within the broader field of paleobiology. As facies concepts spread through sedimentology, the concept of ichnofacies was adopted. The increased emphasis on taphonomy, preservation, and the quality of the fossil record beginning in the 1980s found a similar expression in ichnology in the recognition that the same animal could produce very different structures depending on the environment and the nature of the sediment, and that tracks can look very different depending on what level one examines within their stratigraphy. One result of such studies has been considerable revision in the diversity of ichnotaxa. As described in Chap. 2 of this volume, many fossils that we happily accepted as burrows in the mid-1990s have now been recognized as components of a diverse assemblage of latest Ediacaran tubes, and not trace fossils at all. Restudy of Ediacaran traces has drastically reduced the number of accepted ichnogenera.

To a non-ichnologist, what is particularly striking about this book is how faithfully the general outlines of evolutionary dynamics are visible with trace fossils alone. As illustrated by Chaps. 2 and 3, the integration of trace fossils has long been standard for studies of the Ediacaran and Cambrian diversification. It is not just that the base of the Cambrian is currently defined by the first occurrence of the ichnotaxon *Treptichnus pedum*, rather it is hard to imagine any survey of the Ediacaran–Cambrian diversification *not* including a discussion of the trace-fossil record. Data from ichnological studies has been essential to revealing patterns of morphological novelty and innovation, which is why several generations of workers, from Dolf Seilacher and Peter Crimes to Mary Droser, Soren Jensen and the editors of this volume, have played critical roles in expanding our integrated understanding of this interval. Indeed, Chap. 3 notes that in important ways the trace-fossil record may provide a more reliable picture of the diversity dynamics during the Fortunian, the first stage of the Cambrian, than do other fossils.

The pattern continues with later chapters. The Ordovician biodiversification event reveals breakthroughs in paleoecology including movement into infaunal habitats with increased tiering, increased bioturbation, and colonization of new environments (Chap. 4). Unlike the Cambrian, the Ordovician increase in the diversity of ichnotaxa was not accompanied by an increase in ichnodisparity. Indeed a thread throughout the chapters is the frequency of “early burst” patterns of diversification. The exploration and exploitation of new habitats is a consistent theme throughout this volume. The invasion of land, discussed in Chap. 5, reveals a pattern of colonization, a rapid exploration of new behaviors and architectural designs, followed by variation on the established themes. Other episodes that are addressed are the expansion of terrestrial ecosystems, the Mesozoic marine revolution, and lacustrine revolutions. Chapter 14, on the Cenozoic mammalian radiation, suggests that the tracks of this episode, like the traces of the Cambrian, may provide a richer record of evolutionary change than does skeletal elements, and in addition provides unique information on locomotion, body size, and ecology. I must confess that I had never considered the nature of trace fossils associated with soils, but Chap. 15 illuminates the unexpected complexity in the evolutionary exploitation of paleosols. Chapter 16 provides an insightful analysis of patterns of ecospace occupation through the Phanerozoic, advances in ecosystem engineering, and patterns of ichnodiversity and ichnodisparity. I was particularly struck by the proposal that a space of all possible “ichno-structures” that was explored relatively early by marine invertebrate clades, with similar architectures subsequently discovered independently by different clades. Not surprisingly, this pattern matches studies of ecospace by Bambach and colleagues, and of morphological disparity by many writers.

But of course the diversity and disparity of these structures varied with events in the history of life, as demonstrated by ichnological studies associated with the end-Permian, end-Triassic, and end-Cretaceous mass extinctions, as discussed in Chaps. 7, 8, and 12. The early Triassic aftermath of the end-Permian mass extinction reveals as complicated a pattern of ichnofaunal re-emergence as has been found looking just at body fossils. Returning to the counterfactual musings with which I began this foreword, the evidence presented in Chap. 7 makes it clear that we would be able to recover much of the complexity of the biotic recovery from the trace-fossil record alone. (I must confess to a certain pleasure in Chap. 7 as a proposal I made in 1993 which had been discarded by later workers is resurrected therein.)

Sadly of course, the trace-fossil record on my mythical, alternate Earth would be no more complete than the record we possess today. Trace fossils might hint at morphologies not found among extant animals, but phylogenetic analysis, to take one example, would be greatly hampered by a loss of character information from the early history of many clades: the origins of turtles might forever remain a mystery. There would be many questions accessible with our extant fossil record that would be unanswerable. But of course this is just the strength of the fossil record that we possess. The trace and body fossil records each have their strength, and their weaknesses. This volume wonderfully elucidates the power of the ichnofossil record, properly interpreted, to reveal much of the ecological and evolutionary dynamics of life on this Earth. As students read this volume (and I hope many do), the chapters here should provide a plethora of questions to pursue. While I am sure that this book will attract many students to ichnology, in some ways the most significant impact of the book would be to convince paleontologists to more fully integrate ichnological data and analyses into projects on evolutionary diversifications and radiations, mass extinctions, and paleoecological dynamics.

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Prologue

"A beginning has been made and the discipline has been advanced to the point where some of the highlights in the history of life may be examined from a paleoecological perspective"

(Valentine 1973, Evolutionary Paleoecology
of the Marine Biosphere)

In a remarkable book on the meaning of geologic time, Stephen Jay Gould explored the dichotomy between time's arrow and time's cycle (Gould 1987). According to this view, time's arrow encompasses history as an irreversible sequence of unrepeatable events, whereas time's cycle refers to a nondirectional time characterized by repetition according to a recurrent pattern. As we have emphasized elsewhere (e.g., Mángano and Buatois 2012, 2015), ichnology can be viewed as an expression of the tension between these two faces of geologic time.

The remarkable success of ichnology to solve problems in facies analysis, paleoenvironmental reconstruction, and sequence stratigraphy is clearly an expression of the emphasis on recurrence. In fact, the very same definition of archetypal ichnofacies, as trace-fossil suites that record responses of benthic organisms to a given set of environmental conditions and that recur through geologic time, epitomizes time's cycle. In this view, regardless of the age of the unit animals should respond to ecological parameters in a similar way, reflecting their adaptation to the environment they inhabit. This nomothetic program for ichnology, with its power as a predictive conceptual tool, is the reason that sedimentary geologists now typically include trace fossils in their toolkit to scrutinize the stratigraphic record.

However, this success when dealing with practical issues, often of economic importance, should not prevent us from the realization that ichnology has much to contribute to our understanding of the changing ecology of the past by recovering a time's arrow perspective. While working on a previous book (Buatois and Mángano 2011), it became increasingly obvious to us that this other face of ichnology has received far less attention. However, even a cursory review of the recent paleobiologic literature shows that there is an increased awareness of the importance of bioturbation and bioerosion as driving forces in the history of life, playing major roles as a connecting players between biotic and abiotic factors involved in complex feedback loops that result in evolutionary change (e.g., Erwin and Tweedt 2012).

There are two strategies to bring back the time's arrow perspective of ichnology. One would be to assess the trace-fossil record of the colonization of specific depositional settings, being the main focus on the reconstruction of major trends in global ichnodiversity. In fact, this approach has a relatively long history, starting with the colonization of the deep sea through geologic time due to pioneer papers by Seilacher (1974, 1977) and Crimes (1974), continuing with more recent studies on the same topic (Orr 2001; Uchman 2003, 2004), as well as on the colonization of continental environments (Buatois and Mángano 1993; Buatois et al. 1998), estuaries (Buatois et al. 2005), and tidal flats (Mángano and Buatois 2015). Another approach would be to evaluate how the interactions between animals and substrates were shaped by major macroevolutionary events, such as the Cambrian explosion and the Permian mass extinction. These changes are analyzed from an ecological perspective. For this book we have decided to follow this later approach.

In its essence, this book reflects the growing interest within the ichnologic community in expanding the potential of ichnology to contribute to evolutionary paleoecology. The authors of the different chapters are eclectic in their perspectives and methodologies. However, there are some common themes and conceptual tools, such as ichnodiversity and ichnodisparity, ecospace utilization, environmental expansion, innovation associated to major radiation events, and the re-organizations of ecological units, in particular communities and ecosystems, after mass extinctions. What emerges is a wealth of information and the idea that the history of life can be accurately reconstructed looking through the ichnologic glass.

The first volume opens with Chap. 1, where Minter et al. briefly revise the conceptual and methodological tools of ichnology, with the aim of providing the reader with the basic information necessary to explore the rest of the book. The approach is eclectic with brief summaries of the basic principles and concepts in the field, as well as revisions of the ichnofacies model and the ichnofabric approach. The chapter also introduces a number of concepts and methods that are used in subsequent chapters, including the notion of ichnodiversity and ichnodisparity as a novel approach to unlock the potential of ichnofaunas to provide insights into mode of life, ecospace colonization, and ecosystem engineering.

Chapter 2, by Buatois and Mángano, starts our journey through time by evaluating the highly controversial trace-fossil record of the Ediacaran. The chapter can be understood as an attempt to revisit from an ichnologic perspective the so-called Darwin's dilemma on the supposed absence of evidence of life in the Precambrian by critically searching for the roots of animal life in the Ediacaran. In addition, ichnologic data is used to reveal the nature of Ediacaran ecosystems and the complexities involved in the transition to the Phanerozoic world.

In Chap. 3, Mángano and Buatois look at the other side of the great divide, by exploring the trace-fossil record of the Cambrian explosion. The chapter emphasizes the importance of trace-fossil data to calibrate the Cambrian diversification event. Also, the profound changes that took place at ecosystem scale are analyzed in detail, emphasizing the role of bioturbation as an agent of evolutionary change. The chapter closes with an evaluation of the paleoenvironmental breadth of the Cambrian explosion, the significance of the ichnofaunas associated with Burgess shale-type deposits, and the dual nature of the Fortunian from an evolutionary standpoint.

Chapter 4, by Mángano et al., examines the following evolutionary radiation, the Great Ordovician Biodiversification Event. This chapter analyzes ichnodiversity and ichnodisparity trajectories through the Ordovician, comparing patterns in different depositional environments and paleocontinents. The contrasting nature of diversification in soft-bottom and hardground communities is emphasized by showing that innovation in macrobioerosion was significantly delayed when compared with bioturbation.

Minter et al. explore the initial steps of life on land in Chap. 5 focusing on the Ediacaran–Ordovician timespan. The chapter traces the early stages of animal expansion from fully marine settings into marginal-marine coastal environments and ultimately truly continental settings by the Late Ordovician. This prelude to terrestrialization involves the gradual colonization of new environments followed by rapid filling of ecospace, the establishment of new architectural designs, and diversification within the framework of these new behavioral programs. Links between these evolutionary innovations, and the incipient establishment of a land flora and changes in fluvial styles are discussed.

In Chap. 6, Minter et al. continue with the analysis of terrestrialization by examining the trace-fossil record of marginal-marine and continental environments during the remainder of the Paleozoic. Following the protracted prelude reviewed in the previous chapter, the Silurian to the Permian was characterized by an explosion of diversity and expansion into newly colonized environments, such as river channels, overbanks, deserts, and lakes, coupled with increasing exploitation of the infaunal ecospace. The chapter underscores how colonization of continental settings by benthic organisms parallels changes in vegetation and fluvial styles.

Hofmann closes the first volume with Chap. 7, addressing the trace-fossil record of the end-Permian mass extinction. By carefully evaluating ichnologic data, he provides insights into the extinction event and the subsequent recovery. The impact of burrowing organisms on geochemical conditions of the marine sediment is emphasized, providing a critical evaluation of previous ideas regarding the role of oxygen-depleted conditions as a cause of delayed recovery. It is argued that bioturbation was strongly reduced as a result of the end-Permian mass extinction, leading to the collapse of the mixed layer. The large-scale consequences of such collapse are evaluated in detail.

Volume 2 marks the passage to the post-Paleozoic world, opening with Chap. 8, where Barras and Twitchett analyze the end-Triassic mass extinction. The authors revised the ichnologic record of both terrestrial and marine environments through the Triassic-Jurassic transition, outlining how the benthic faunas responded to the mass extinction. Their review suggests that climatic and environmental change were main factors controlling benthic communities on land and in the sea.

In Chap. 9, Buatois et al. take the reader to the new world arisen from the Mesozoic Marine Revolution. The main group of bioturbators and bioeroders are reviewed, and the trace-fossil record of Mesozoic and Cenozoic marine environments is revised to track evolutionary innovations, discussing the timing of Mesozoic Marine Revolution. The environmental breadth of this major event is evaluated by summarizing evolutionary innovations not only in shallow-marine environments but also in marginal-marine and deep-marine settings. It is argued that infaunalization predated an increase of predation pressures by approximately 50 Myr, pointing towards a complex set of feedback mechanisms between the two.

In Chap. 10, Bernardi et al. explore the vertebrate radiation during the Mesozoic. By revising in detail available ichnologic data, they show how the trackway record yields insights into several issues, such as locomotor mechanics and behavior, therefore providing information that typically is not revealed by the body-fossil record. In turn, biases inherent to the trace-fossil record are discussed, arguing that the integration between the trackway and the skeletal record is essential to provide a more holistic picture of the evolutionary changes underwent by terrestrial vertebrates during the Mesozoic.

Chapter 11, by Buatois et al., discusses another series of evolutionary breakthroughs that took place in continental settings: those resulting from the Mesozoic lacustrine revolution. Lakes are evaluated from an ichnologic perspective, contrasting lacustrine ecosystems prior to this evolutionary event with those that arose after the Mesozoic lacustrine revolution. Aspects discussed in this chapter include ichnodiversity changes through time, the establishment of modern lacustrine food webs, and the role of behavioral convergence on both sides of the salinity divide.

In Chap. 12, Labandeira et al. shift our attention to another extinction event: the end-Cretaceous mass extinction. These authors evaluate both the record of plant–arthropod interactions on land and that of invertebrate trace fossils in the sea, therefore providing a comprehensive picture of the extinction event and its aftermath. A number of methodological, empirical, and theoretical advances resulting from the use of ichnologic data are outlined, including application of innovative methods to quantify ichnologic information, access to novel ecologic data, and evaluation of catastrophic vs. gradualistic scenarios based on the analysis of bioturbated sediment, among many others.

Chapter 13, by Genise et al., represents a general departure to the overall structure of the book in that it does not address a specific evolutionary event, but instead traces a series of dramatic changes in paleosols covering most of, if not all, the Phanerozoic. In doing so, they provide an in-depth characterization of four revolutions in paleosol ichnofaunas. In addition, this chapter provides an interesting twist to the concept of ichnofacies by showing that their establishment in terrestrial settings is fully linked to a series of evolutionary innovations by soil-burrowing organisms.

In Chap. 14, Krapovickas and Vizcaino explore the evolution of mammals based on their footprint record. Although this chapter summarizes the Mesozoic and Cenozoic record of tracks attributed to mammals worldwide, emphasis is on changes in South American mammals during the Cenozoic. The authors show that Eocene-Oligocene trackway assemblages mostly consist of forms of uncertain affinity, whereas later assemblages consist of trackways of both native South American and North American mammals that arrived during the Great American Biotic Interchange. This chapter emphasizes the strong provincialism of mammal faunas, representing a starting point towards a more global examination of their ichnologic record.

Chapter 15, by Lockley et al., deals with the trackway record of hominin evolution. Starting with the famous 3.6 Ma tracks from Laetoli, the reader is taken through a journey that explores the expansion of our ancestors from Africa to Eurasia, the New World, and Australasia. References to footprints on the Moon and tracks of robotic vehicles on Mars add another dimension to the trip. Along the way, the authors discuss various controversies, including the alternative interpretations of the Laetoli trackways and the differences between early hominin footprints and those from modern humans.

The book closes with Chap. 16, where Buatois and Mángano take the challenge of trying to summarize possible recurrent trends revealed by the trace-fossil record that may provide insights into the underlying dynamics of animal–substrate interactions through geologic time. In particular, the chapter discusses organism–substrate interactions during evolutionary radiations, benthic fauna response to mass extinctions, patterns of ecospace colonization, and environmental shifts through time. In contrast to the other chapters, which by reviewing individual evolutionary events are anchored in an idiographic approach, this last chapter takes on a more nomothetic perspective by trying to find recurrent patterns and processes in evolutionary paleoecology.

In the process of planning this book, it became clear that, although there is an explicit attempt to bring a picture of the state of the art in the contributions of ichnology to the understanding of evolution at the macroevolutionary scale, our book does not offer a comprehensive treatment or a closure on the topic. In fact, during this process, we have identified numerous areas of interest where there is limited ichnologic information to the point that it was not possible to include chapters on these issues. For example, the end-Ordovician and Late Devonian mass extinctions have received significantly less treatment than any of the other so-called Big Five. Also, some of the chapters provide fresh approaches to our exploration of the colonization of infaunal ecospace and the impact of ecosystem engineers by using ichnologic data in an innovative fashion. This may serve as inspiration for applying new numerical and conceptual tools to a wider spectrum of paleobiologic issues. This book is a tangible testimony that ichnology counts with a solid theoretical framework and sufficient methodological tools to tackle evolutionary questions and offer crucial pieces in the reconstruction of the puzzle of the history of life. Our ambition with this book echoes the Gouldian aim, paraphrased in Chap. 10, of sitting Ichnology at the High Table of Macroevolution and Paleobiology.

We would like to thank the reviewers of the many chapters, who did a great job of providing valuable feedback. These are: Andrea Baucon, Zain Belaústegui, Angela Buscalioni, Karen Chin, Matthew Clapham, Darin Croft, Phillip Currie, Bill DiMichele, Tony Ekdale, Russell Garwood, Sören Jensen, Dirk Knaust, Conrad Labandeira, Spencer Lucas, Ken McNamara, Christian Meyer, Nic Minter, Guy Narbonne, Eduardo Olivero, Paul Olsen, Roy Plotnick, Gustavo Politis, Charles

Savrda, Thomas Servais, Alfred Uchman, Jean Vannier, Sally Walker, Mark Wilson, and Anna Żylińska. Also we thank Doug Erwin for writing the Foreword.

Finally, as with almost all things ichnologic, Dolf Seilacher has been there before. He should be recognized as the scientist who started to think along this line of evidence, putting forward the idea that trace fossils represent the "other" fossil record, underexplored and immensely valuable. Not necessarily an alternative archive for the history of life, but more of an essential companion that should be integrated to the other lines of evidence to decipher the complex evolutionary pathways in the history of life. Needless to say, Dolf's influence has been huge in the field of ichnology and the same can be said of his influence in our personal careers. It all started long time ago when we were Geology students and he planted some "seed ideas" during a Trace Fossil course that he taught at the Argentinean Paleontological Association (APA). Sadly, he passed away during the completion of this book. We would like to dedicate this book to his memory.

M. Gabriela Mángano
Luis A. Buatois

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Chapter 8
The Late Triassic Mass Extinction Event

Colin Barras and Richard J. Twitchett

8.1 Introduction

The end of the Triassic (~200 Ma) was identified by Newell (1963) as marking one of the five largest extinction episodes of the Phanerozoic. From the perspective of ecologic impact on the biosphere, it ranks third (McGhee et al. 2004). In the marine realm some 23 % of families and 50 % of genera were lost (Sepkoski 1981, 1993) with ammonites, bivalves, radiolarians, and coral reefs suffering most (McElwain et al. 2007; Keissling and Simpson 2011). On land, plant biodiversity declined at genus and species levels in the latest Triassic, as shown by local palynologic studies and analyses of macrofossils (e.g., in East Greenland; McElwain et al. 2007; McElwain et al. 2009; Mander et al. 2010). Widespread floral change would have affected other terrestrial groups such as vertebrates, which suffered a 45 % decline at the family level in eastern North America during the final stages of the Triassic (Olsen et al. 1987). Some common archosaurs disappeared at this time, although the theropod dinosaurs appear to have increased in abundance and size across the Triassic–Jurassic (T–J) boundary (Olsen et al. 2002).

For decades this event was relatively poorly studied, but a concerted effort in recent years, especially following formal designation of the Global Stratotype Section and Point (GSSP) for the base of the Jurassic (Hillebrandt et al. 2007), has led to a clearer picture of the sequence of events and likely contributing factors. Competing scenarios included sea level change (Hallam and Wignall 1997), a bolide impact (Olsen et al. 2002), and the dissociation of gas hydrates (Beerling and Berner 2002). However, it

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now appears likely that the principal kill mechanism was concomitant changes in climate, atmosphere, and oceans associated with the formation of the Central Atlantic Magmatic Province (CAMP), a large igneous province stretching roughly 5000 km in a north–south direction and 2000 km in an east–west direction, and covering areas of northwest Europe, West Africa, eastern North America, and Brazil (McHone 2000; Fig. 8.8.1). CAMP is among the largest of all continental large igneous provinces (Marzoli et al. 1999), and the extinctions in marine and terrestrial realms coincide with the onset and early phases of volcanic activity in the latest Triassic (Marzoli et al. 2004; Knight et al. 2004; Deenen et al. 2010; Mander et al. 2013).

At around the time of emplacement of the earliest CAMP lavas there is good evidence that the level of atmospheric carbon dioxide rose rapidly. Studies of fossil leaf stomatal density (McElwain et al. 1999; Retallack 2001; Beerling 2002; Steinthorsdottir et al. 2011) and soil carbonates (Schaller et al. 2011) suggest a rise in atmospheric CO_2 across the extinction interval from 600–1000 ppm to 2000–2500 ppm or from 1000 ppm to 2000–3000 ppm, depending on the respective proxy. Disruption to the global carbon system is recorded by negative carbon isotope

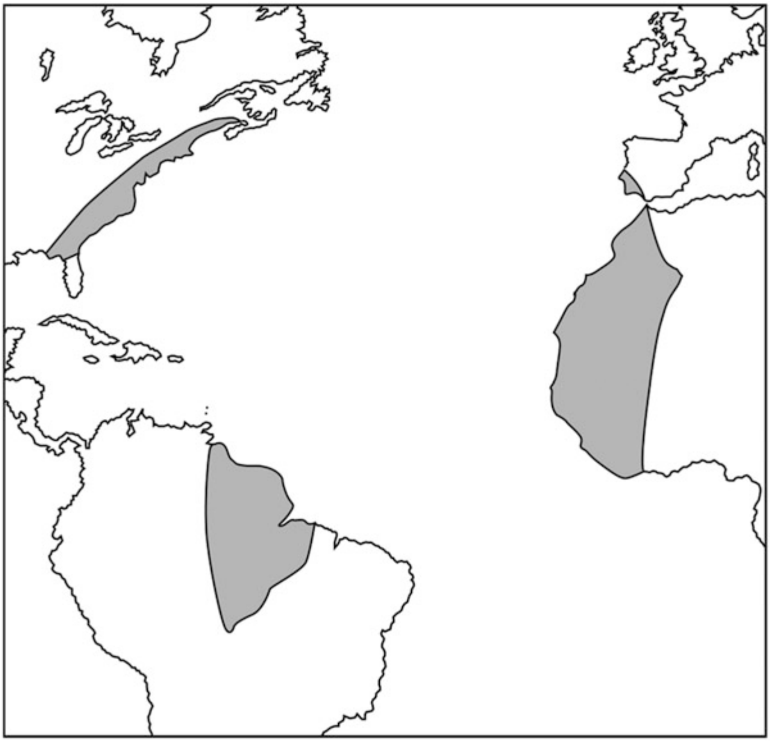

Fig. 8.1 Approximate extent of the Central Atlantic Magmatic Province, after Wignall (2001a), showing the two locations studied specifically for the effects of the end-Triassic extinction on the trace-fossil record

excursions from a number of localities worldwide, including among others example in Austria (Ruhl et al. 2009), Nevada, USA (Guex et al. 2004), the Newark Basin of eastern USA (Whiteside et al. 2010), East Greenland (McElwain et al. 1999), British Columbia, Canada (Ward et al. 2004; Williford et al. 2006), Italy (Galli et al. 2005), and England (Hesselbo et al. 2002; Whiteside et al. 2010).

Such a rapid increase in pCO_2 would have led to global warming, with dramatic effects on terrestrial climate zones, the global hydrologic cycle, and the circulation and dissolved oxygen content of the world's oceans (e.g., Kidder and Worsley 2010). Some authors have suggested that elevated CO_2 would have lowered the pH of surface waters, leading to ocean acidification that would have had detrimental effects for calcareous organisms (Hautmann 2004; Schootbrugge et al. 2007; Kiessling and Simpson 2011). Modern experiments suggest, however, that the responses to lowered pH vary dramatically between different marine taxa (Findlay et al. 2011), and there is evidence from the fossil record that calcification of some bivalves actually increased at this time (Mander et al. 2008).

Some have questioned whether extinction near the end of the Triassic was abrupt, or more gradual in nature (Hallam 2002; Cuny 1995; Tanner et al. 2004). Reported faunal changes often coincide with facies changes that might give a false impression of sudden extinction (Hallam 2002). For bivalves, at least, it appears that changes in facies, preservation, and other rock record biases have not significantly affected the extinction interval but may have led to the under-representation of some groups, such as aragonitic, deeper infaunal taxa, in the immediate aftermath (Mander and Twitchett 2008). Recent assessment of the fossil-plant record from East Greenland (McElwain et al. 2009) demonstrates that biodiversity decline was relatively abrupt and began around the time of initial CAMP volcanism. Furthermore, analysis of the palynologic records of East Greenland and St Audrie's Bay, UK, demonstrate that terrestrial ecosystems were affected at the same time as those in the sea, and the extinctions occurred during the steep rise in atmospheric CO_2 (Mander et al. 2013).

8.2 Trace-Fossil Record Across the T–J Boundary

While the body-fossil record across the T–J boundary has been relatively well studied, the trace-fossil record remains less well known. However, while trace fossils cannot usually be tied readily to the trace maker their study can still contribute to a better understanding of the nature of faunal turnover during extinction events such as the Late Triassic extinction, making the few studies that have been conducted important.

In terrestrial settings, such as the Newark Basin of eastern North America, which contains one of the best temporally constrained nonmarine vertebrate records through the extinction interval, skeletal remains are much less common than footprints making study of the footprints particularly useful for elucidating the nature of the vertebrate faunal response (Olsen et al. 2002) (Fig. 8.8.2). In the marine realm, trace fossils are important because most marine ecosystems are dominated by

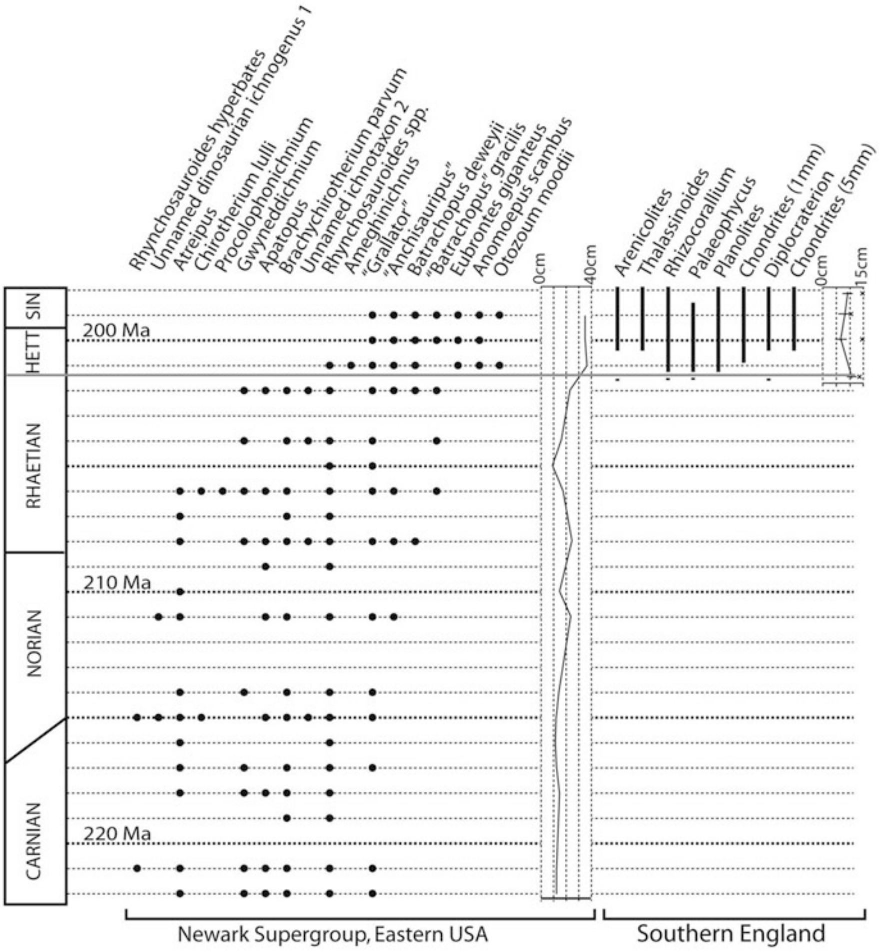

Fig. 8.2 Terrestrial ichnotaxonomic trends through the Triassic–Jurassic interval of the Eastern USA and shallow marine ichnotaxonomic trends of Southern England. *Gray horizontal line* shows approximate location of the initial carbon isotope excursion that marks the extinction interval. Graphs show trend in maximum length of theropod tracks in the Eastern USA, and trend in average diameter of *Diplocraterion* in southern England (X's mark the maximum diameter of *Diplocraterion*). H. = Hettangian. Sin. = Sinemurian. T–J = Triassic–Jurassic boundary. After Olsen et al. (2002) and Barras and Twitchett (2007)

nonmineralized taxa, which rarely fossilize (Allison and Briggs 1991). The traces that they leave may be more readily preserved, which makes the marine trace-fossil record the best, and sometimes only, window into the responses of these dominant, soft-bodied organisms to catastrophic extinction (Twitchett and Barras 2004). Finally, in both marine and terrestrial regimes, the trace-fossil record is spared from such taphonomic effects as transport or reworking (Barras and Twitchett 2007), making its study potentially less ambiguous than some body fossil studies.

8.2.1 Terrestrial Record

Terrestrial trace-fossil studies around the T–J boundary often focus on specific short sequences within either the Triassic or Jurassic, rather than longer successions that span the boundary and the extinction event itself. Low-diversity invertebrate trace-fossil assemblages associated with lake margins have been reported for both the Late Triassic (Lucas and Lerner 2006) and Early Jurassic (Lucas et al. 2006b) of the western United States, the Triassic of Greenland (Bromley and Asgaard 1979) and the Late Triassic of Germany (Schlirf et al. 2001).

Elsewhere in northern Europe the terrestrial record of invertebrate trace fossils is more extensive. In southern Sweden, for example, Late Triassic and Early Jurassic fluvio-deltaic deposits with some evidence of brackish marine influence preserve a moderately diverse ichnofauna, including horizontal (*Cochlichnus*, *Palaeophycus*, *Planolites*, *Rhizocorallium*, *Teichichnus*) and vertical (*Diplocraterion*, *Monocraterion*, *Skolithos*) burrows and grazing traces, as well as arthropod trackways (*Diplichnites*), and the bivalve resting trace *Lockeia* (Pieńkowski 1991a,b; Gierliński and Ahlberg 1994; Ahlberg 1994; Ahlberg and Arndorff 1994).

Further south, in Poland, exposures of Early Jurassic rocks formed in lacustrine and fluvial environments with some subaerial exposure contain a diverse ichnofauna. Finds here include *Lockeia*, arthropod resting traces (*Rusophycus*), arthropod trackways, burrows and borings (*Cruziana*, *Diplichnites*, *Linckichnus*, *Spongeliomorpha*, *Xylonichnus*) equilibrichnia formed by freshwater bivalves (*Calceoformites*, *Scalichnus*), and horizontal or vertical burrows (*Cochlichnus*, *Helminthoidichnites*, *Scoyenia*, *Planolites*, *Palaeophycus*). There are also possible arthropod nest structures. In brackish marine influenced deposits, the limulid trackway *Kouphichnium* also occurs (Pieńkowski 2004; Pieńkowski and Niedźwiedzki 2008).

Lacustrine assemblages associated with Triassic deltas in Argentina have been studied for their trace fossils (Melchor 2004). Ichnofaunas typically include horizontal or vertical burrows and grazing traces (e.g., *Palaeophycus*, *Skolithos*, *Planolites*, *Helminthoidichnites*, *Helminthopsis*, *Treptichnus*) and backfilled burrows (e.g., *Scoyenia*, *Taenidium*) with rare arthropod walking traces, such as *Diplichnites* (e.g., Lucas et al. 2006b). However, the invertebrate trace-fossil record is too sparse to reveal ichnotaxonomic trends, should they exist, through the extinction interval itself.

Likewise, most studies of the terrestrial vertebrate footprint fossil record often have as their focus particular formations within the Late Triassic or Early Jurassic. Nevertheless, there is evidence from the trace-fossil record that dinosaurs increased in abundance, diversity, and size through the Late Triassic and into the Early Jurassic. Hunt and Lucas (2007) summarized the record of Late Triassic tetrapod trackways of the western United States. The Revueltian (early to mid Norian) reveals a moderately diverse ichnofauna. *Rhynchosauroides*, considered by Hunt and Lucas (2007) to represent the tracks of a sphenodontian, is found in Arizona, New Mexico, and Utah. *Apatopus*, long considered the track of a phytosoaur (e.g., Foster et al. 2000), is found in Utah. Other ichnotaxa present in the region suggest the presence of dinosaurs: *Barrancapus*, possibly representative of a prosauropod trackway (Hunt et al. 2001), is found in New Mexico and Arizona; another prosauropod ichnotaxon (*Evazoum*) is found in Utah; and *Grallator*, interpreted as the tracks left by a small theropod, is also found in Utah.

The overlying Apachean (late Norian to Rhaetian) contains a diverse ichnofauna across several states, including a more diverse dinosaurian ichnofauna (Hunt and Lucas 2007). The possible sphenodontian track *Rhynchosauroides* is found in Colorado and New Mexico; carnivorous archosaur trackways (*Apatopus*) are found in New Mexico, while possibly herbivorous archosaur trackways (*Brachychirotherium*) are known from Utah, Colorado, New Mexico, and Oklahoma (Lucas and Tanner 2007). *Gwyneddichnium*, unambiguously linked to the Late Triassic reptile *Tanytrachelos*, is found in Utah and Colorado. There is also evidence of synapsid trackways (e.g., *Brasilichnium*) in Colorado. The dinosaurs, represented by three ichnotaxa in the preceding Revueltian, are more diverse and widespread in the Apachean. The small theropod trackway *Grallator* is abundant in Utah, and is also found in Wyoming, Colorado, Arizona, New Mexico, and Oklahoma. A larger theropod probably left *Anchisauripus* tracks in Utah and New Mexico, and *Eubrontes* is known from rocks that may date to the uppermost Triassic (Fig. 8.8.3e). Herbivorous saurischian dinosaurs are represented by the prosauropod trackway *Evazoum* in Utah, Colorado, and New Mexico, *Eosauropus* in Utah, Colorado, Arizona, and New Mexico, and sauropodomorph trackways *Pseudotetrasauropus* and *Tetrasauropus* in Arizona, Utah and Colorado (Lucas and Tanner 2007). *Atreipus*, found in Utah, may have been produced by an ornithischian (Olsen and Baird 1986).

In the lowermost Jurassic of Utah, Arizona and Colorado, large theropod tracks (*Eubrontes*) dominate, although smaller theropod tracks (*Grallator*) and sauropodomorph tracks (*Otozoum*; Fig. 8.8.3c) are also present. All three are also found in dinosaur-dominated trace-fossil assemblages dating to the Sinemurian (Fig. 8.8.3d), together with the tracks of ornithischian (*Anomoepus*) and prosauropod (*Otozoum*) dinosaurs, synapsids (*Brasilichnium*) and crocodilians (*Batrachopus*; Lucas and Tanner 2007).

More evidence for the rise of the dinosaurs through the T–J interval comes from Olsen et al. (2002), one of the few studies that consider the terrestrial trace-fossil record specifically from the perspective of the Late Triassic extinction (Fig. 8.8.2). The focus of the study is the Newark Supergroup, preserved in New York, New Jersey, and Pennsylvania in the eastern United States. The increase in dinosaur (ichno)taxonomic diversity that is apparent in the western United States is found here as well; Olsen et al. (2002) also reported a concomitant increase in the size of individual tracks, suggesting an increase in dinosaur body size in the latest Triassic.

Nondinosaurian ichnodiversity increases through the Norian and Rhaetian in the Newark Supergroup too, with *Rhynchosauroides* and *Gwyneddichnium* common. The probable silesaurian ichnogenus *Atreipus* is the most common member of the dinosauriform clade of dinosauromorphs (as opposed to dinosaur: Irmis et al. 2007) until the middle Rhaetian. Trackways attributed to theropods include *Grallator*, which occurs throughout the Carnian, Norian, and Rhaetian, and *Anchisauripus*, which first appears in the Norian.

In the Newark Basin, the Late Triassic extinction is marked by a facies change indicating wetter conditions, a coal bed, an apparent iridium anomaly, and a fern spore spike (Olsen et al. 2002). This horizon is correlated with the earliest phase of CAMP activity,

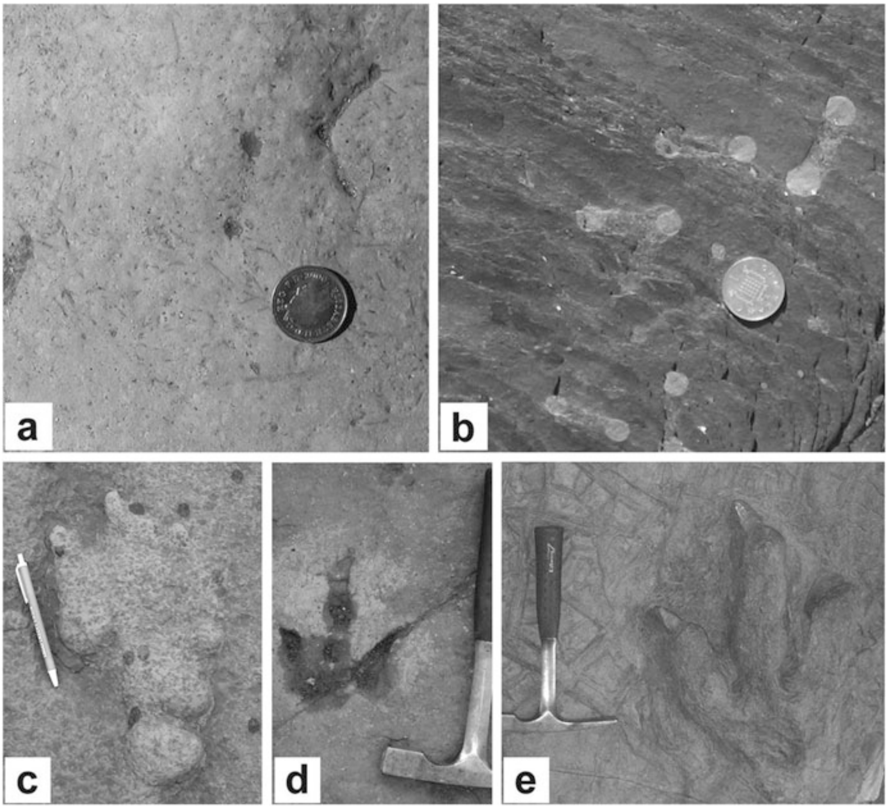

Fig. 8.3 Marine and terrestrial trace fossils of the Triassic–Jurassic interval. (**a**) Small *Diplocraterion* burrows in the *angulata* Zone (Hettangian) of Pinhay Bay, Dorset, UK; (**b**) Large *Diplocraterion* in the *semicostatum* Zone (Sinemurian) of Helwell Bay, Somerset, UK; (**c**) Track of a prosauropod dinosaur (*Otozoum*) in Wingate Sandstone (?Hettangian) of Gateway, Colorado; (**d**) Footprint of a theropod dinosaur (*Grallator*) in Kayenta Formation (Sinemurian to Pliensbachian) of St. George, Utah; (**e**) Footprint of a large theropod dinosaur (*Eubrontes*) in upper part of Dinosaur Canyon Member of Moenave Formation (?Late Triassic) of St. George, Utah. Images (**c**), (**d**), and (**e**) reproduced with permission of Spencer G. Lucas, New Mexico Museum of Natural History and Science, Albuquerque

recorded in Morocco, and the marine extinction event (Deenen et al. 2010; Mander et al. 2013). It marks a decline in the diversity of nondinosaurian tracks and an increase in both diversity and size of dinosaurian tracks (Olsen et al. 2002). The nondinosaurian ichnotaxa *Gwyneddichnium*, *Apatopus*, and *Brachychirotherium parvum* disappear, whereas *Rhynchosauroides* and *Batrachopus* span the extinction, the latter left by a crocodylomorph. Theropod dinosaurs survived the extinction, as evidenced by the records of *Grallator* and *Anchisauripus*, with new ichnotaxa such as *Eubrontes* appearing afterwards. Slightly higher in the section—an estimated >100 ky after the extinction—tracks belonging to prosauropods (*Otozoum*) and ornithischians (*Anomoepus*) appear. The prosauropod tracks increase in frequency, and the ornithischian tracks increase in size, through the remaining succession.

The Late Triassic extinction level also marks the first appearance of much larger theropod tracks (>25 cm in length) belonging to the ichnospecies *Eubrontes giganteus*, considered by some to be simply larger representatives of *Grallator* (e.g., Lucas et al. 2006a), despite differences in relative elongation of members of the two ichnogenera (e.g., Olsen 1980). *Eubrontes* may have been left by a ceratosaur such as *Dilophosaurus* (Lucas et al. 2006a), although some (Weems 2003) have argued the trackmaker was a *Plateosaurus*-like prosauropod.

Olsen et al. (2002) suggested that the increase in size of theropod tracks may represent either dispersal from an unknown location or indicate an evolutionary response to reduced competitive pressure and ecologic release in the aftermath of extinction. Lucas et al. (2006a) rejected this ecologic release hypothesis on the basis that the ichnogenus *Eubrontes* has been recorded from as far back as the Carnian. However, they failed to demonstrate that large-sized examples of the specific ichnospecies *Eubrontes giganteus* are known from preextinction strata, or that there is no size change through the extinction event, which would be a better test of the Olsen et al. (2002) hypothesis.

The vertebrate footprint record from Europe is broadly consistent with the North American picture. The theropod ichnotaxon *Grallator* has been reported from the Rhaetian of southern Sweden (Gierliński and Ahlberg 1994). Otherwise, Late Triassic vertebrate footprints are rare in Europe, although nondinosaurian tracks (possibly *Rhynchosauroides*) are seen in a Late Triassic lagoon in southwest England that evidently experienced occasional periods of emergence (Allington-Jones et al. 2010).

As in North America, *Grallator* is also found in Lower Jurassic European deposits—in Poland and southern Sweden—indicating that theropod dinosaurs in the region survived the extinction interval (Ahlberg 1994; Gierliński and Ahlberg 1994; Gierliński and Pieńkowski 1999). Indeed, the Early Jurassic (Hettangian) of Poland preserves a diverse dinosaur ichnofauna (Gierliński and Pieńkowski 1999; Pieńkowski 2004). Here, sauropod tracks (*Parabrontopodus*) and medium to large theropod footprints (*Anchisauripus* and *Kayentapus*) are found in rocks formed in an inland environment. A shoreline environment preserves ornithischians (*Anomoepus*, *Atreipus* and *Moyenisauropus*) and theropods (*Megalosauripus*, *Grallator*, and *Anchisauripus*), while *Plesiornis*, a possible protoavian track, is found in rocks formed under fluvial influence (Gierliński and Pieńkowski 1999; Pieńkowski 2004; Gierliński et al. 2010). Early mammalian prints also occur within Poland's nonmarine Lower Jurassic deposits (Pieńkowski 2004; Gierliński et al. 2010).

The Polish record, like that of North America, contains its first large theropod dinosaur footprints after the Late Triassic extinction. *Eubrontes* footprints (>34 cm in length) occur in the Hettangian, together with a single, unusually large (55 cm in length) footprint that may be *Megalosauripus* (Gierliński et al. 2010). Large sauropods are present too; some of the *Parabrontopodus* tracks found in the Early Jurassic of Poland are to 42 cm in length (Gierliński et al. 2010).

8.2.2 Marine Record

8.2.2.1 Deep-sea Ichnofauna Across the T–J Boundary

Nearly 30 ichnogenera inhabited the deep-sea in the Carboniferous, before a halving of ichnotaxonomic diversity in the Permian (Uchman 2004). Numbers remained low through the Triassic and Jurassic, rising again to Carboniferous levels only in the Cretaceous. However, a recent analysis of Upper Triassic deep-sea fan deposits in the Al Ayn Formation of Oman suggested ichnofaunal diversity was abundant at this time. Wetzel et al. (2007) recorded 32 ichnogenera, making this the most diverse deep-sea ichnofauna known until the Early Cretaceous. The ichnofauna includes predepositional forms that are cast by turbidites (*Belorhaphe*, *Circulichnis*, *Desmograpton*, *Glockerichnus*, *Gordia*, *Helminthopsis*, *Lorenzinia*, *Megagrapton*, *Paleodictyon*, *Strobiloraphe*, and *Treptichnus*) and postdepositional forms that penetrate the turbidites (*Arenicolites*, *Protovirgularia*, *Zoophycos*, *Thalassinoides*, and *Ophiomorpha*).

The deep-sea ichnofauna may have reduced in diversity in response to Permo-Carboniferous glaciation (Uchman 2004)—deep-sea ichnotaxonomic diversity also fell during episodes of glaciation in the Quaternary (Cronin and Raymo 1997). Warmer deep-sea conditions in the Late Triassic may then have contributed to an increase in ichnotaxonomic diversity. However, there is too little data as yet to search for any effects of the end-Triassic extinction on the deep-sea ichnofauna.

8.2.2.2 Shallow-Marine Ichnofauna Across the T–J Boundary

As with the terrestrial record, a number of studies have described shallow marine trace fossils from Upper Triassic or Lower Jurassic strata (e.g., Swift and Duffin 1999; Moghadam and Paul 2000), but few have studied ichnologic change through the extinction event.

A Late Triassic (Rhaetian) to Early Jurassic (Sinemurian) near-shore marine succession in southern Poland contains a moderately diverse ichnofauna including arthropod traces (*Cruziana*, *Thalassinoides*), asterozoan traces (*Asteriacites*), horizontal burrows (*Planolites*, *Palaeophycus*), and vertically branching *Chondrites* burrows (Uchman 1991).

Lower Jurassic lagoonal deposits in southern Sweden contain the bivalve traces *Lockeia* and *Protovirgularia* (Ahlberg 1994). Elsewhere in the region, the Early Jurassic is characterized by muds deposited in a tidally influenced environment. Horizontal and vertical burrows (*Cylindrichnus*, *Diplocraterion*, *Monocraterion*, *Phycodes*, *Planolites*, *Rhizocorallium*, *Skolithos*, *Teichichnus*, *Thalassinoides)*, bivalve traces (*Lockeia*), and arthropod traces (*Kouphichnium*, *Merostomichnites*) are found here (Pieńkowski 1991a; Ahlberg 1994). In deposits dating to the Sinemurian, the ichnofauna comprises *Diplocraterion*, *Planolites*, *Rhizocorallium*, and *Teichichnus* (Pieńkowski 1991a). Shales deposited in relatively deep and often dysaerobic conditions contain common *Chondrites*, with rare *Rhizocorallium* indicating occasional oxygenation (Pieńkowski 1991a). Hettangian to Sinemurian marine storm deposits in southern Sweden contain a burrow-dominated ichnofauna of *Teichichnus*, *Thalassinoides*, *Rhizocorallium*, and rare *Diplocraterion* (Pieńkowski 1991a). Storm-influenced shallow marine successions from the Early Jurassic (Sinemurian) of Poland are rich in *Diplocraterion* (Pieńkowski 1991b).

The T–J shallow-marine trace-fossil records of the UK, Austria, and Nevada, USA, have been examined by Twitchett and Barras (2004), with a more detailed analysis of the trace-fossil record in England by Barras and Twitchett (2007; Fig. 8.8.2). A key section is at St Audrie's Bay, Somerset, UK, which had been considered as a candidate for the Global Stratotype Section and Point for the base of the Jurassic (e.g., Warrington et al. 1994). Although the first appearance of the ammonite *Psiloceras spelae* in the Kuhjoch section of Austria was ultimately chosen as the GSSP (Hillebrandt et al. 2007), the St Audrie's Bay section remains critical for correlating the marine and terrestrial records (Deenen et al. 2010; Mander et al. 2013).

The Late Triassic extinction event correlates with an isotopic excursion in the middle of the Lilstock Formation in St Audrie's Bay, just prior to the boundary between the Cotham and Langport members (Hesselbo et al. 2004; Mander et al. 2013). Trace fossils formed prior to and possibly during the extinction event, in the Rhaetian Westbury and Lilstock formations, have been documented by a number of researchers (Wang 1993; Swift and Duffin 1999; Barras and Twitchett 2007; Allington-Jones et al. 2010). To the east of St Audrie's Bay, at Westbury-on-Severn, the Westbury Formation begins with siltstones formed in relatively oxygenated shallow marine conditions. These contain vertical burrows (*Diplocraterion* and *Skolithos*; Wang 1993). Above these marine siltstones, conditions become more restricted and indicative of a shallow lagoonal setting with lower oxygen. Bioturbation in discrete horizons here probably records storm events that brought in animals, sediment, and oxygen to the restricted environment (Wang 1993; Allington-Jones et al. 2010). Some trace fossils here (*Cruziana*, *Rusophycus*, and *Selenichnites*) probably show the activity of xiphosurids (Wang 1993). Allington-Jones et al (2010) report a diverse ichnofauna within these storm layers, including burrows (*Chondrites*, *Planolites*, *Rhizocorallium*, *Taenidium*, *Thalassinoides*), bivalve *(Lockeia*, *Protovirgularia)*, and arthropod (*Merostomichnites*, *Monomorphichnus*, *Oniscoidichnus*) traces, and a previously undescribed grazing trail, *Radichnus*. At St Audrie's Bay, the Rhaetian Westbury Formation is mostly thoroughly bioturbated, although few discrete trace fossils are preserved in the mudstone facies (Swift and Duffin 1999). Elsewhere in the region, shallower, sandier facies preserve a suite of trace fossils such, as *Arenicolites*, *Diplocraterion*, *Kouphichnium*, *Lockeia Palaeophycus*, and *Planolites* (Swift and Duffin 1999).

Following the extinction event, the Langport Member of the Lilstock Formation is well laminated and devoid of trace fossils at St Audrie's Bay, but elsewhere a low diversity, small-sized assemblage may be recorded. At Long Itchington, Warwickshire, for example, the Langport Member is moderately bioturbated with the beds measuring 2–3 on Droser and Bottjer's (1986) ichnofabric index for vertical sections (vii), while bedding planes assessed using Miller and Smail's (1997) ichnofabric index for horizontal exposures (hii) measure 2–4 (Barras and Twitchett 2007). Rare examples of *Arenicolites*, *Diplocraterion*, *Palaeophycus*, and

Rhizocorallium are found, although these are small in size; *Arenicolites* burrow diameter is generally 1–2 mm. Larger diameter *Diplocraterion* are locally abundant at the boundary between the Langport Member and the overlying Blue Lias Formation at Pinhay Bay in Dorset (Barras and Twitchett 2007).

The boundary between the Lilstock Formation and overlying Blue Lias Formation represents a significant deepening of the marine environment, probably linked to sea level rise during global warming, which needs to be borne in mind when comparing the ichnofaunas of the two formations. The lowermost beds of the Blue Lias Formation are termed the "Pre-Planorbis Beds," and were deposited during peak global warming around the T–J boundary. They are unbioturbated (vii1) in their lower part, but by the upper "Pre-Planorbis Beds" extensive bioturbation (vii4-5) is recorded. Milankovitch-scale lithologic cyclicity is evident in the Blue Lias Formation, and throughout the formation there is a small-scale alternation of laminated and bioturbated beds (Moghadam and Paul 2000). From the base of the *planorbis* Zone upwards, however, the latter are all well bioturbated (vii4-6) through to at least the Sinemurian *bucklandi* Zone (Barras and Twitchett 2007).

The lowest recorded ichnotaxa in the Blue Lias Formation are *Arenicolites* and *Thalassinoides* from the upper Pre-Planorbis Beds of Pinhay Bay. During the overlying Hettangian there is a stepwise increase in ichnotaxonomic diversity, which shows a similar trend at Pinhay Bay and St Audrie's Bay (Twitchett and Barras 2004; Barras and Twitchett 2007). At other locations, the rock record may be less complete but the trends are similar. At Long Itchington, for example, the ichnofauna of the Rugby Limestone Member is similar to that recorded in limestones of the same age (i.e. upper *angulata* and *bucklandi* zones) at Pinhay Bay and St Audrie's Bay. At its most diverse, in the upper *angulata* Zone and above, the Blue Lias Formation ichnofauna includes *Arenicolites*, *Chondrites*, *Diplocraterion*, *Palaeophycus*, *Planolites*, *Rhizocorallium*, and *Thalassinoides*. It is only within and above the *angulata* Zone that the four ichnotaxa recorded in the Triassic Lilstock Formation co-occur again (Barras and Twitchett 2007).

When they first (re)appear in the *angulata* Zone, *Diplocraterion* burrows are significantly ($p>0.95$) smaller than are similar burrows in the Langport Member at Pinhay Bay. Both *Diplocraterion* and *Arenicolites* significantly ($p>0.95$) increase in size from the *angulata* Zone through to the *bucklandi* Zone (Barras and Twitchett 2007; Fig. 8.8.3a, b).

As burrow size is correlated to body size (Savrda and Bottjer 1986), Barras and Twitchett (2007) inferred that the soft-bodied trace-making infauna was small in the "Pre-Planorbis Beds," the *planorbis* and *liasicus* zones, and increased in size from the later Blue Lias Formation. Given the link between small body size and low oxygen concentration (e.g., Rhoads and Morse 1971), and evidence of anoxic and euxinic conditions in the shales of the lower "Pre-Planorbis Beds" (e.g., Wignall 2001b), Barras and Twitchett (2007) further suggested that the ichnofauna records a gradual return to oxygen rich conditions following a period of anoxia in the "Pre-Planorbis Beds."

The ichnofaunal record in Austria and Nevada is less extensive than that in England, and has been little studied (Hallam and Wignall 2000, Twitchett and Barras 2004). Limestones belonging to the Rhaetian-aged Kössen Formation, exposed at Gaissau and Kendelbach Formation in Central Austria, are well bioturbated (vii3–4) and contain *Diplocraterion*, *Planolites*, *Rhizocorallium*, *Skolithos*, and *Zoophycos*. These ichnotaxa are absent from the uppermost beds of the Kössen Formation, and from the overlying Kendelbach Formation—a roughly 10-m-thick succession of limestones thought to encompass the Hettangian (Twitchett and Barras 2004). However, the shelly fossil record suggests any extinction here was followed by swift recovery before the first appearance of *Psiloceras* in the Kendelbach Formation (Hallam 1990).

In the New York Canyon area of the Gabbs Valley Ranges, Nevada, there is a modestly diverse ichnofauna in the Rhaetian-aged Mount Hyatt Member of the Gabbs Formation. *Arenicolites*, *Planolites*, *Rhizocorallium*, *Skolithos*, and *Thalassinoides* are found in the limestone-dominated succession, although the rocks are relatively poorly bioturbated (vii2; Twitchett and Barras 2004). Within the lower reaches of the overlying Muller Canyon Member of the Gabbs Formation, Guex et al. (2004) found evidence of a negative carbon excursion that they related to emplacement of CAMP. Locally intense bioturbation and thoroughly mottled horizons with the horizontal trace *Helminthoida* (now *Nereites irregularis*) have been reported (Hallam and Wignall 2000), but these were not located during a later study and in general trace fossils are rare within this member (Twitchett and Barras 2004).

The Ferguson Hill Member of the Sunrise Formation lies above and is dated as late Hettangian to early Sinemurian (Taylor et al. 1983). *Arenicolites*, *Planolites*, *Rhizocorallium*, *Skolithos*, and *Thalassinoides* all reappear in the Ferguson Hill Member of the Sunrise Formation, and *Chondrites* and *Diplocraterion* are also reported (Twitchett and Barras 2004). The reappearance of an abundant ichnofauna is associated with, and possibly the result of, facies and palaeoenvironmental changes; the Ferguson Hill Member is limestone dominated, and similar in appearance to the Mount Hyatt Member.

In summary, there are clear local changes in marine ichnofaunas through the T–J boundary interval in England, Austria, and Nevada that may relate to CAMP-induced warming-related environmental changes. While there is no evidence for extinction of trace makers in the Late Triassic, unlike the terrestrial record, there are clear ecologic changes in terms of burrow size, depth, and diversity during this interval. Locally, it appears that diverse Late Triassic ichnofaunas, representing a healthy benthic ecosystem, disappear around the extinction level and only reappear from the latest Hettangian onwards (Twitchett and Barras 2004). In between, although there are local differences, it appears that shallow marine ichnofaunas are typically of relatively low diversity, with small-sized and shallow penetrating burrows.

8.3 Discussion

It now seems likely that the Late Triassic extinction was largely a result of global warming and related environmental effects, associated with the widespread volcanism that led to the formation of CAMP. Furthermore, recent correlations (e.g., Mander et al. 2013) imply that atmospheric CO_2 remained high through the T–J boundary before declining to preextinction levels sometime in the later Hettangian, following cessation of CAMP activity. Although the data are currently sparse, and there is a clear need for more high resolution analyses from other localities worldwide, current evidence suggest that CAMP-related environmental changes and the associated Late Triassic extinction event are both reflected in the T–J trace-fossil record.

On land, the onset of CAMP-related volcanism is associated with the extinction of several groups of terrestrial vertebrate, as recorded in the disappearance of their footprints (Olsen et al. 2002). This warming-related event led to a dramatic increase in the dominance of dinosaur taxa and an associated increase in footprint, and therefore body, size during the Hettangian. While it is possible that the increase in maximum body size is simply a consequence of increased diversity and variance (Gould 1988), Olsen et al. (2002) suggested that it may be due to ecologic release following extinction of competing taxa. It is therefore intriguing that during the Hettangian a similar size trend is recorded in marine infaunal invertebrates, as evidenced by an increase in burrow diameter (Twitchett and Barras 2004; Barras and Twitchett 2007). The diameter of marine trace fossils reached a minimum during the peak warming interval spanning the T–J boundary, probably because of the combined stresses of elevated temperatures and an expansion in hypoxic or euxinic conditions at that time (Kidder and Worsley 2010). Although more data are required, it is possible that size increase in animals, on land and in the sea, is a response to the decline in atmospheric CO_2 back to preextinction levels coupled with a rise in atmospheric oxygen levels.

In the marine realm, the trace-fossil show as presently known does not show evidence of extinction of any tracemakers, but does indicate that there were significant ecologic changes to the marine benthic ecosystem. Apart from a reduction in burrow diameter, a reduction in diversity and maximum burrow depth is also recorded during peak global warming following the extinction event. Although this is an expected consequence of the associated environmental changes, such as reduced ocean circulation and expanding anoxia, these changes also have implications for ecosystem functioning. The depth and size of infaunal organisms affects the amount of bioturbation and a number of key nutrient cycles (Solan et al. 2004). The lower levels of bioturbation during peak global warming would have reduced efficient nutrient cycling, with consequences for the entire marine ecosystem.

The T–J interval was a time of major crisis, related to emplacement of a large igneous province and associated global warming. As a greater number of sedimentary successions across the T–J boundary are studied for their trace fossils, the impact of these major environmental changes on the marine and terrestrial realms should become clearer, providing a more complete picture of the degree to which Late Triassic global warming affected Earth's biosphere.

8.4 Conclusion

The trace-fossil record across the T–J boundary appears to preserve evidence of ecological and taxonomic change associated with the Late Triassic extinction event. There are well-documented changes in trace-fossil size and diversity through the interval—both in terrestrial and in shallow marine environments. Such findings are consistent with the current understanding that the Late Triassic extinction event was triggered by global warming and related effects of the emplacement of CAMP.

However, while there is evidence of (ichno)taxonomic extinction in the terrestrial realm, studies to date have yet to find evidence of extinction in the marine trace-fossil record. This might be more a reflection of a lack of study rather than a lack of evidence, because few trace-fossil studies have been conducted specifically from the perspective of documenting and understanding the extinction event.

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Chapter 9
The Mesozoic Marine Revolution

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9.1 Introduction

Modern-marine ecosystems are the result of numerous evolutionary innovations that took place during the Mesozoic, commonly referred to as the Mesozoic Marine Revolution (MMR; Vermeij 1977, 1987). This major evolutionary episode was responsible for the large-scale restructuring of shallow-marine benthic communities, including increases in the energy budgets of marine ecosystems (Finnegan et al. 2011) and predation levels, the latter resulting in a number of coevolutionary developments (Vermeij 1987). In particular, the intensification of grazing and the diversification of durophagous predators were conducive to increases in prey sturdiness and frequency of shell repair (Vermeij 1987; Kelley and Hansen 2001).

The MMR also signaled the rise to dominance of the Modern Evolutionary Fauna (MEF). The MEF actually had its origins in the early Paleozoic, but true displacement of Paleozoic faunas was not complete until after the end-Permian mass extinction

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(Sepkoski and Sheehan 1983; Sepkoski and Miller 1985; see Chap. 7). This shift from the Paleozoic Evolutionary Fauna (PEF) to the MEF involved the transition from sedentary epifaunal suspension feeders to mobile, energetic (high-metabolism) infaunal suspension feeders, deposit feeders, and predators (Wagner et al. 2006; Leighton et al. 2013). These changes included the appearance of ecologic guilds not represented within the Cambrian Evolutionary Fauna (CEF) and PEF (Thayer 1983; Bambach 1983). The number of utilized modes of life increased to present levels by the late Cenozoic, with all 20 Bambachian megaguilds being filled (Sheehan 2001; Bambach et al. 2007). At this point, marine paleocommunities had a much greater representation of infaunal organisms and a higher proportion of motile animals than mid-Paleozoic communities (Bush et al. 2007).

Not surprisingly, the majority of studies published on the MMR have been based on the body-fossil record. However, the trace-fossil record provides valuable additional evidence of the profound nature of this episode, particularly with respect to the degree of infaunalization, complexity of infaunal tiering structures, and predation intensity (e.g., Bertling 1999; Harper 2003; Bromley 2004; Glaub and Vogel 2004; Wilson 2007; Knaust 2007; Carmona et al. 2008; Buatois and Mángano 2011). In this chapter, the ichnologic record of the MMR is reviewed. The chapter is divided into three parts: first, the main groups of tracemakers involved in the rise of the MEF are analyzed; second, the trace-fossil record of post-Paleozoic shallow-marine environments is reviewed in order to provide insights into the timing of this evolutionary event; and, third, the ichnologic record is discussed with respect to how it can illuminate our knowledge of the MMR by assessing aspects, such as its environmental breadth, evolution of behavior, evolution of the mixed layer, potential paleogeographic patterns, and secular changes in infaunalization.

9.2 The Cast of Characters

9.2.1 The Main Groups of Burrowers

The MEF is dominated by bivalves, gastropods, echinoids, crustaceans, and marine vertebrates; other invertebrate groups, including gymnolaemate bryozoans, demosponges, corals and ammonites, were also members of this fauna (Sepkoski 1981). Of these groups, bivalves, echinoids, and crustaceans were important tracemakers during the MMR, and identification of their trace fossil “fingerprints” is relatively straightforward to detect in bioturbation structures, based on neoichnological observations and functional morphology analysis. Various types of worm-like organisms should be added to this list, as many are active bioturbators, although establishing a direct link between a given trace fossil and its producer(s) commonly is tenuous at best. If necessary, alternative interpretations are offered. In this section, some of the most important trace fossils produced by these groups of organisms are described (Table 9.1). Although not all of these ichnotaxa occurred for the first time during the MMR, most of them are particularly abundant in post-Paleozoic marine deposits.

Table 9.1 Common bioturbation ichnogenera in shallow-marine post-Paleozoic deposits (see main text for references). For explanation of modes of sediment interaction, see Chap. 1

Ichnogenera	Stratigraphic range	Potential producer	Ethology	Trophic type	Mode of sediment interaction
Arachnostega	Cambrian–Recent	Errant polychaetes	Fodinichnia	Deposit-feeding	Biodiffusive
Arcichnus	Devonian–Recent	Echinoderms (Ophiuroids)	Repichnia	Deposit-feeding/suspension feeding/predation	Biodiffusive
Arenicolites	Cambrian–Recent	Worm-like organisms (polychaetes)	Domichnia	Suspension-feeding	Gallery biodiffusive
Artichnus	Eocene–Recent	Echinoderms (Holothurians)	Domichnia	Deposit-feeding/suspension feeding	Conveyor
Asteriacites	Cambrian–Recent	Echinoderms (Asterozoans)	Cubichnia	Deposit-feeding/suspension feeding/predation	Biodiffusive
Asterosoma	Cambrian–Recent	Worm-like organisms (probably polychaetes)	Fodinichnia	Deposit-/detritus-feeding	Conveyor
Balanoglossites	Ordovician–Recent	Enteropneusts or polychaetes	Domichnia	Suspension-feeding	Gallery biodiffusive
Bichordites	Eocene–Recent	Echinoderms	Pascichnia	Deposit-feeding	Conveyor
Cardioichnus	Cretaceous–Recent	Echinoderms	Cubichnia	Deposit-feeding	Biodiffusive
Chondrites	Ordovician–Recent	Sipunculids, polychaetes	Fodinichnia	Detritus feeding/chemosymbionts	Gallery biodiffusive
Coenobichnus	Oligocene–Recent	Crustaceans (hermit crabs)	Repichnia	Scavenging	Biodiffusive
Curvolithus	Cambrian–Recent	Plathelminthes, nemerteans, gastropods	Repichnia	Predation	Biodiffusive
Cylindrichnus	Cambrian–Recent	Polychaetes	Domichnia	Deposit-/detritus-feeding	Gallery biodiffusive
Diplocraterion	Cambrian–Recent	Polychaetes	Equilibrichnia	Suspension-feeding	Gallery biodiffusive
Ereipichnus	Cretaceous–Recent	Worm-like organisms	Pascichnia	Deposit-feeding	Gallery biodiffusive/ conveyor
Euflabella	Cretaceous–Recent	Worm-like organisms	Fodinichnia	Deposit-/detritus-feeding	Conveyor
Foersterichnus	Cretaceous–Recent	Brachyuran crustaceans	Repichnia	Omnivory	Biodiffusive
Gastrochaenolites	Ordovician–Recent	Bivalves	Domichnia	Suspension-feeding	Gallery biodiffusive
Glyphichnus	Jurassic–Recent	Crustaceans	Domichnia	Suspension-feeding	Regenerator

(continued)

Table 9.1 (continued)

Ichnogenera	Stratigraphic range	Potential producer	Ethology	Trophic type	Mode of sediment interaction
Gyrochorte	Ordovician–Recent	Worm-like organisms	Fodinichnia	Detritus-feeding	Conveyor
Gyrolithes	Cambrian–Recent	Crustaceans	Fodinichnia	Deposit-feeding/gardening.	Gallery biodiffusive
Haentzschelinia	Jurassic–Recent	Worm-like organisms	Fodinichnia	Detritus/deposit feeding	Conveyor
Helicodromites	Devonian–Recent	Worm-like organisms	Fodinichnia	Deposit-feeding	Gallery biodiffusive
Hillichnus	Cretaceous–Recent	Bivalves	Fodinichnia	Deposit-feeding/chemosymbiosis	Biodiffusive/conveyor
Korymbichnus	Jurassic–Recent	Polychaetes	Fodinichnia	Deposit-feeding	Biodiffusive
Lapispira	Jurassic–Recent	Crustaceans or worm-like organisms, probably enteropneusts	Domichnia/ Fodinichnia	Deposit feeding/gardening/ omnivory	Gallery biodiffusive
Lockeia	Cambrian–Recent	Bivalves	Cubichnia/ Domichnia	Deposit feeding	Gallery biodiffusive
Lophoctenium	Devonian–Recent	Bivalve	Fodinichnia	Deposit-feeding	Gallery biodiffusive
Macanopsis	Jurassic–Recent	Brachyuran crustaceans	Domichnia	Omnivory	Regenerator
Macaronichnus	Permian–Recent	Polychaetes (opheliids)	Pascichnia	Deposit-feeding	Conveyor
Maiakarichnus	Miocene–Recent	Crustaceans	Calichnia	Suspension-/detritus-feeding	Regenerator
Nereites	Cambrian–Recent	Worm-like organisms, probably enteropneusts	Pascichnia	Deposit feeding	Conveyor
Ophioichnus	Cretaceous–Recent	Echinoderms (Ophiuroids)	Repichnia	Deposit-feeding/suspension feeding/predation	Biodiffusive
Ophiomorpha	Triassic–Recent	Crustaceans	Domichnia	Detritus-feeding	Regenerator
Palaeophycus	Ediacaran–Recent	Glycerid and nereid polychaetes	Domichnia	Predation/suspension-feeding	Gallery biodiffusive
Parmaichnus	Pleistocene–Recent	Crustaceans	Domichnia	Suspension-feeding	Regenerator
Patagonichnus	Miocene–Recent	Polychaetes (e.g., maldanids and capitellids)	Fodinichnia	Deposit-feeding/predation/ omnivory	Gallery biodiffusive
Pentichnus	Carboniferous–Recent	Echinoderms	Domichnia	Predation/suspension-feeding	Gallery biodiffusive

Phoebichnus	Jurassic-Pleistocene	Worm-like organisms, crustaceans	Fodinichnia	Deposit-feeding	Gallery biodiffusive
Pholeus	Triassic–Recent	Crustaceans	Domichnia	Suspension-/detritus-feeding	Regenerator
Phycosiphon	Ordovician–Recent	Worm-like organisms	Fodinichnia	Deposit-feeding	Conveyor
Planolites	Cambrian–Recent	Worm-like organisms (probably polychaetes)	Fodinichnia	Deposit-feeding	Conveyor
Polykladichnus	Devonian–Recent	Worm-like organisms (probably polychaetes), and anemones	Domichnia	Suspension-feeding	Gallery biodiffusive
Protovirgularia	Ordovician– Recent	Bivalves	Repichnia	Deposit-feeding	Biodiffusive
Psilonichnus	Late Jurassic onward	Crustaceans	Domichnia	Suspension-feeding	Regenerator
Rhizocorallium	Cambrian–Recent	Worm-like organisms/ crustaceans	Fodinichnia	Suspension-feeding/ deposit-feeding	Gallery biodiffusive
Rosselia	Cambrian–Recent	Polychaetes	Domichnia	Deposit-feeding	Gallery biodiffusive
Saronichnus	Pleistocene–Recent	Bivalves	Fodinichnia	Chemosymbiosis	Gallery biodiffusive
Scalichnus	Pliocene–Recent	Bivalves	Equilibrichnia	Suspension-feeding	Biodiffusive
Schaubcylindrichnus	Carboniferous–Recent	Polychaetes	Domichnia	Deposit-feeding	Gallery biodiffusive
Scolicia	Jurassic–Recent	Echinoderms	Pascichnia	Deposit-feeding	Conveyor
Sinusichnus	Cretaceous-Pliocene	Crustaceans	Fodinichnia	Deposit-feeding/farming	Regenerator
Siphonichnus	Carboniferous–Recent	Bivalves	Equilibrichnia	Suspension-feeding	Gallery biodiffusive
Skolithos	Cambrian–Recent	Worm-like organisms (e.g., phoronids, polychaetes)	Domichnia	Suspension-feeding	Gallery biodiffusive
Solemyatuba	Ordovician–Recent	Bivalves	Domichnia	Farming	Gallery biodiffusive
Spongeliomorpha	Triassic–Recent	Crustaceans	Domichnia	Suspension-feeding/farming	Regenerator
Taenidium	Cambrian–Recent	Worm-like organisms	Fodinichnia	Deposit-feeding	Conveyor
Teichichnus	Cambrian–Recent	Polychaetes, sipunculan worms, arthropods	Fodinichnia	Deposit-feeding	Conveyor
Thalassinoides	Cambrian–Recent	Crustaceans	Fodinichnia	Detritus-feeding	Regenerator
Tubotomaculum	Cretaceous–Recent	Crustaceans	Fodinichnia	Detritus-feeding/farming	Regenerator
Zoophycos	Cambrian–Recent	Sipunculids, echiuran worms	Fodinichnia	Detritus feeding/food cache/farming	Conveyor

9.2.1.1 Crustaceans

Crustaceans of the Order Decapoda (Superclass Crustacea, Class Malacostraca) are among the most important burrowers in the modern marine realm, constructing distinctive structures (Fig. 9.1a–g) that commonly extend to considerable depth within the substratum and occurring in abundance in the fossil record (e.g., Fürsich 1973; Schlirf 2000; Carmona et al. 2004). Seilacher (2007) described such branching decapod burrows with the general name "ophiomorphids" to comprise those structures that, although heterogeneous in taxonomy, share features such as having shaft and tunnel systems that tend to branch, forming a boxwork at depth, with enlargements at turning points and having preferential preservation due to their emplacement in deeper tiers than other burrows. Such burrows occur from supratidal to deep-marine settings. Most "thalassinidean" species (now gebiideans and axiideans, following De Grave et al. 2009) dwell in shallow-marine sediments, and especially for callianassids and upogebiids, the great majority live in water depths of less than 20 m at tropical to subtropical latitudes (Dworschak 2000, 2005; Dworschak et al. 2012). Less abundant in the fossil record are trackways attributed to crustaceans, such as *Coenobichnus* (Walker et al. 2003) and *Foersterichnus* (Pirrie et al. 2004). Other relatively common ichnotaxa, most notably *Rhizocorallium*, may have been produced by crustaceans (e.g., Rodríguez-Tovar et al. 2012), although worms cannot be disregarded in many cases (Knaust 2013). The same disagreement persists regarding *Phoebichnus*, traditionally regarded as produced by worms (Bromley and Asgaard 1972), but recently attributed to crustaceans (Evans and McIlroy 2016).

Integration of paleoecological data provided by trace fossils with information inferred from the body-fossil record (e.g., origin, radiation, and extinction patterns) is important for macroevolutionary analysis of these organisms, which have relatively poor preservation potential (especially for decapods that have weakly calcified exoskeletons). However, due to the presence of hard appendages, some decapods can excavate burrows in compacted mud, producing open tunnels as permanent domiciles. In looser sediments, some decapods also reinforce their burrow walls with characteristic linings. There are a number of distinctive trace fossils produced by decapods (Figs. 9.2a–k, 9.3a–f, 9.4a–f, 9.5a–e). Forms common in the ichnologic record are discussed below, approximately in order of most common occurrence.

Thalassinoides consists of large burrow systems comprising horizontal and vertical components, lacking a lining, and with characteristic "Y" or "T" branching patterns (Frey and Howard 1985; Figs. 9.2b and 9.3a–f). Such burrows usually are interpreted as dwelling or feeding structures of selective detritus-feeding crustaceans (Ekdale 1992), occurring commonly in fine-grained sediments of marginal- and shallow-marine environments, and also in deeper-marine settings. In a few instances, *Thalassinoides* has been reported from continental environments (e.g., Kim et al. 2002, 2005), but in this case a completely different set of producers was involved. *Thalassinoides* is known since the Cambrian (Myrow 1995), although a decapod origin is most likely only for post-Paleozoic occurrences (Carmona et al. 2004).

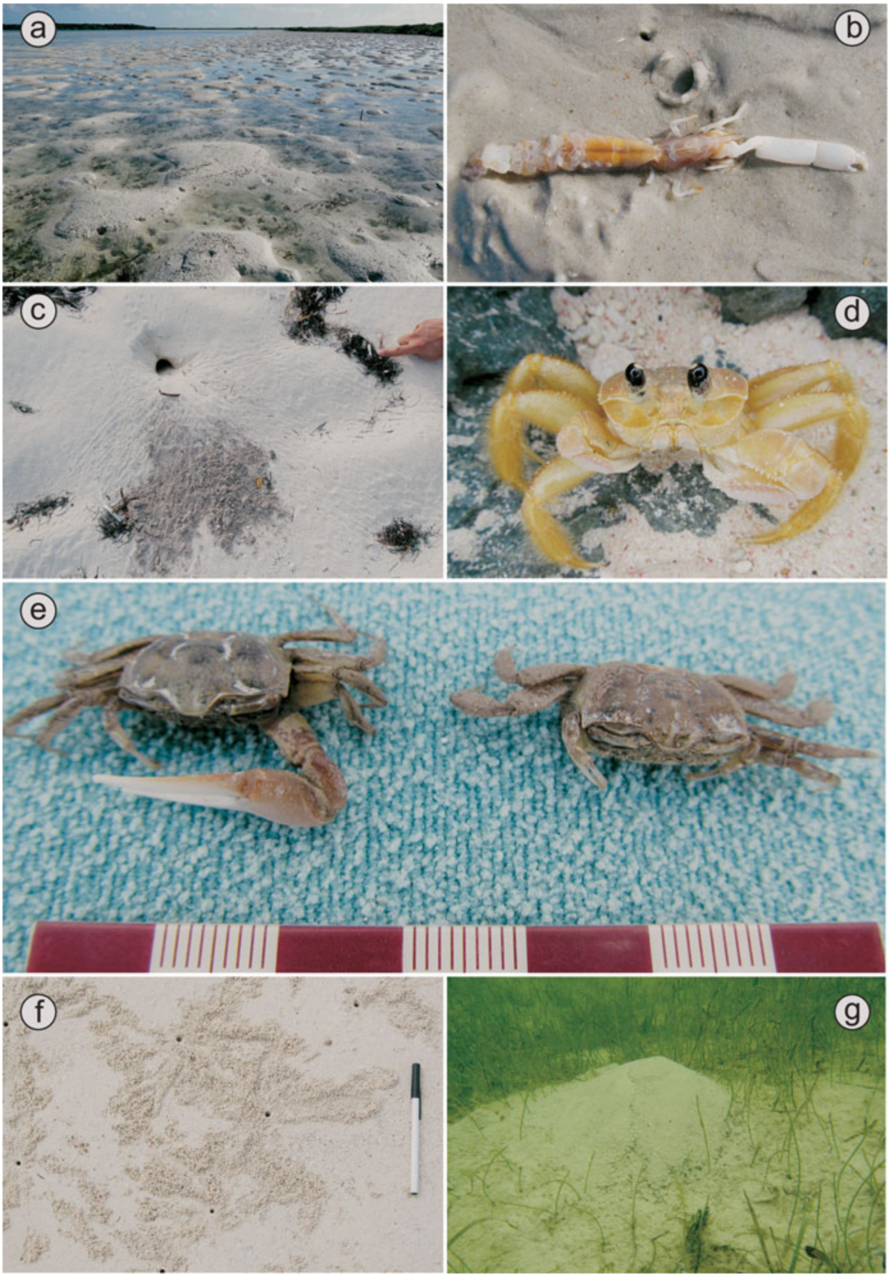

Fig. 9.1 Examples of typical decapod crustaceans and the structures they produce in modern shallow-marine environments. (**a**) Intertidal carbonate-sand flat completely re-engineered by callianassid burrowing, Pigeon Creek lagoon, San Salvador Island, Bahamas; (**b**) *Callichirus major* from the clastic northern Atlantic coast of Florida, USA, shrimp is 15 cm in length; (**c**) Ghost crab burrow in a Bahamian beach, opening is 4 cm in diameter; (**d**) The ghost crab *Ocypode quadrata*, on a Bahamian beach, Lee Stocking Island, front of carapace about 5 cm in length; (**e**) Male and female fiddler crabs, *Uca speciosa*, Pigeon Creek margin; (**f**) Fiddler crab burrows with radiate pattern of feeding pellets, sandy inlet area, Cockburn Town fossil reef quarry, San Salvador, pen is 15 cm in length; (**g**) Subtidal callianassid mound, Pigeon Creek lagoon, about 1 m in diameter

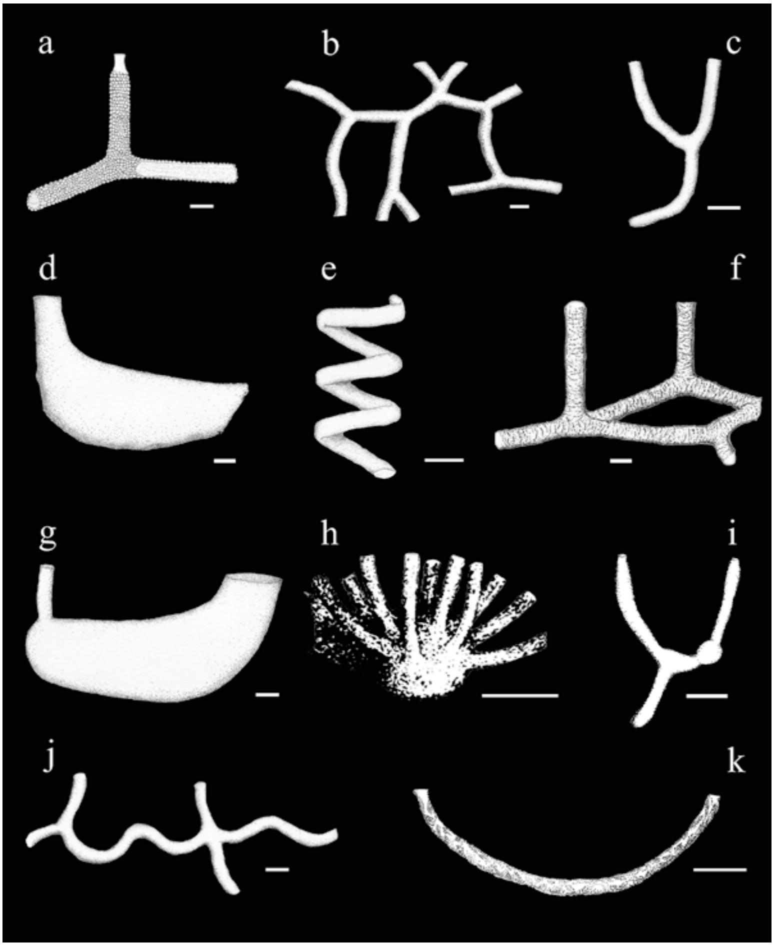

Fig. 9.2 Schematic reconstructions of burrow architecture of decapod ichnogenera. (**a**) *Ophiomorpha*; (**b**) *Thalassinoides*; (**c**) *Psilonichnus*; (**d**) *Macanopsis*; (**e**) *Gyrolithes*; (**f**) *Spongeliomorpha*; (**g**) *Pholeus*; (**h**) *Maiakarichnus*; (**i**) *Parmaichnus*; (**j**) *Sinusichnus*; (**k**) *Glyphichnus*. Scale bars in (**a**, **b**, **d**, **f** and **j**) are 5 cm; scale(s) in (**c**) is 10 cm; in (**e**) and (**h**) are 3 cm; in (**g**) is 2 cm; in (**i**) is 4 cm and in (**k**) is 20 cm

Ophiomorpha refers to simple to complex, branching burrows with distinctive, thick walls formed of agglutinated-sediment pellets, with the walls mamillated on the exterior and smooth on the interior (Figs. 9.2a and 9.4a–f). These structures represent the dwelling burrows of primarily selective detritus-feeding decapods, such as modern callianassids (Dworschak 2000; Dworschak et al. 2012, and references therein). The reinforcement of burrows in order to prevent substratum collapse is an adaptation to living in energetic commonly sandy sedimentary environments. *Ophiomorpha* occurs in both siliciclastic and carbonate deposits, typically attributed to shallow-marine, high-energy environments (Frey et al. 1978; Curran 2007) and also in deep-marine settings (Uchman 2009 and references

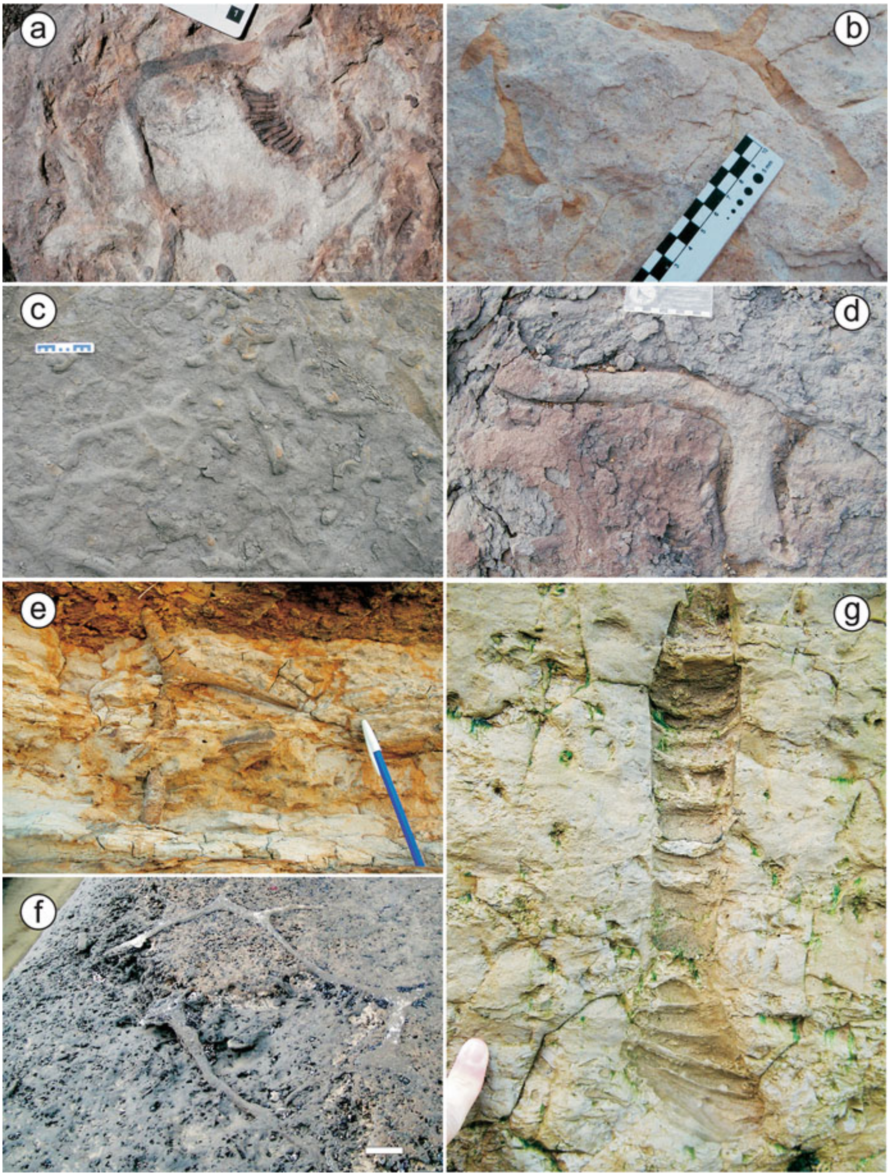

Fig. 9.3 Examples of *Thalassinoides* in Mesozoic–Cenozoic shallow-marine deposits. (**a**) Vaca Muerta Formation, Jurassic, Neuquén Basin, Argentina; (**b**) Quintuco Formation, Jurassic–Cretaceous, Neuquén Basin, Argentina; (**c**) Mulichinco Formation, Cretaceous, Neuquén Basin, Argentina; (**d**) Río Turbio Formation, Eocene, Austral Basin, Argentina; (**e**) Urumaco Formation, Miocene, Venezuela, scale is 20 cm; (**f**) Monte León Formation, Miocene, Austral Basin, Argentina, scale bar is 25 cm; (**g**) *Thalassinoides* isp. with tidal fill, Río Negro Formation, Miocene-Pliocene, Argentina

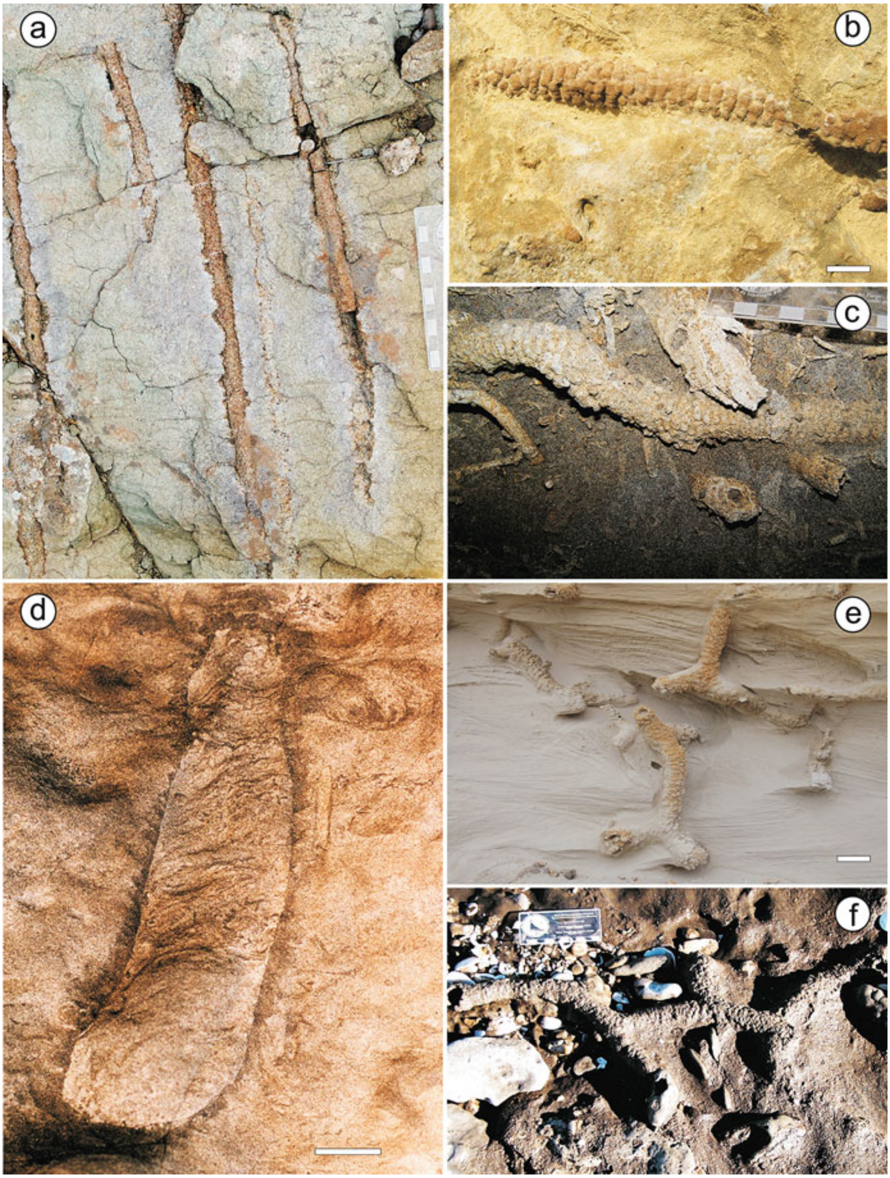

Fig. 9.4 Examples of *Ophiomorpha* in Mesozoic–Cenozoic shallow-marine deposits. (**a**) Lajas Formation, Jurassic, Neuquén Basin, Argentina; (**b**) La Vela Formation, Upper Miocene-Lower Miocene, Venezuela, scale bar is 1 cm; (**c**) Monte León Formation, Miocene, Argentina; (**d**) Chenque Formation, Lower Miocene, San Jorge Basin, Argentina, scale bar is 4 cm; (**e**) Chuí Formation, Pleistocene, Brazil, scale bar is 7 cm; (**f**) Upper Pleistocene, Pehuen-Co, Argentina

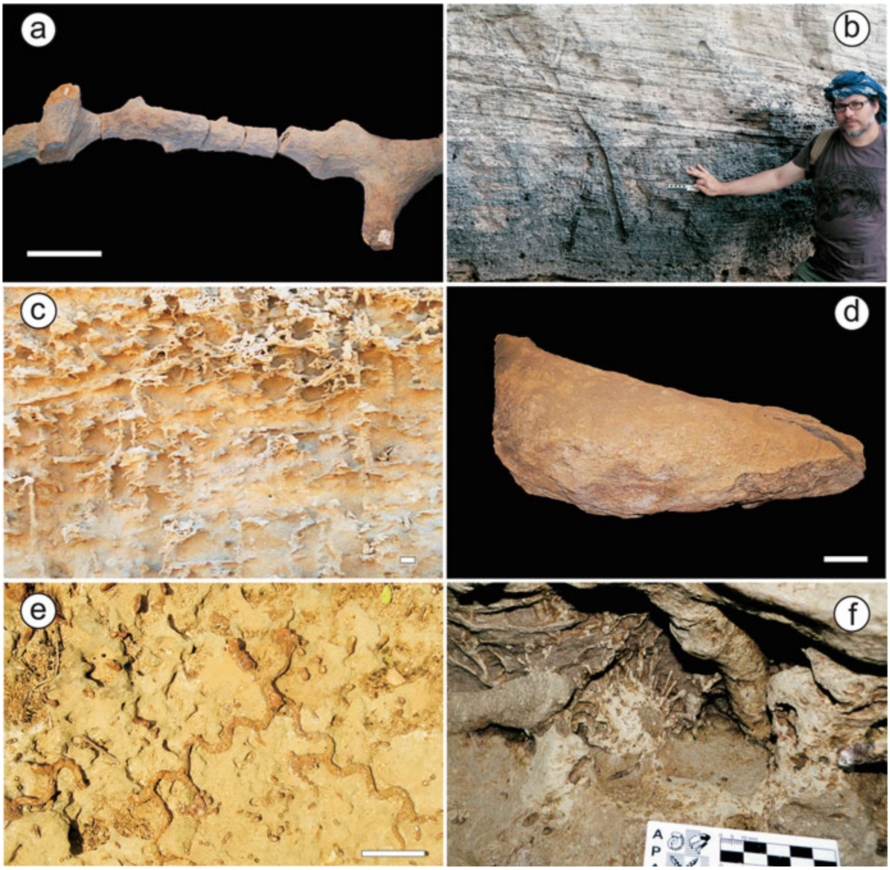

Fig. 9.5 Various decapod ichnotaxa in Mesozoic–Cenozoic shallow-marine deposits. All photos are from siliciclastic deposits with the exception of **b**, which is from carbonates. (**a**) *Spongeliomorpha* isp., Middle Miocene, Vallès-Penedès Basin, Spain, scale bar is 10 cm; (**b**) *Psilonichnus upsilon*, Holocene, San Salvador, Bahamas; (**c**) *Gyrolithes* isp., Pliocene, Araya Peninsula, Venezuela, scale bar is 3 cm; (**d**) *Macanopsis plataniformis*, lower Cretaceous, La Tejería de Josa, Spain, scale bar is 3 cm; (**e**) *Sinusichnus sinuosus*, Middle Miocene, Socorro Formation, Venezuela, scale bar is 11 cm; (**f**) *Maiakarichnus* isp., Miocene-Pliocene, Río Negro Formation, Argentina

therein). Although Paleozoic examples have been recorded since the Carboniferous (Driese and Dott 1984; Buatois et al. 2002), uncontroversial occurrences are in post-Paleozoic strata.

Spongeliomorpha consists of unlined, branching burrow systems with distinctive scratch marks (bioglyphs) on the walls (Figs. 9.2f and 9.5a). These burrows have been interpreted as domiciles produced by suspension-feeding decapods (Asgaard et al. 1997) and also as structures for gardening or breeding (D'Alessandro and Bromley 1995). *Spongeliomorpha* occurs in shallow- and deep-marine environments (Uchman 1998; Muñiz and Mayoral 2001a). There also are some records from non-marine deposits (Melchor et al. 2009). The presence of bioglyphs on the walls indicates that the tracemakers used a hard appendage (e.g., a chela) to excavate these burrows and that the sediment was firm at the time of construction. This ichnogenus is known since the Triassic (MacNaughton and Zonneveld 2010); specimens reported from the Permian (Carey 1979) do not display the diagnostic features (e.g., striated walls) of this ichnogenus.

Psilonichnus comprises predominantly vertical, cylindrical, unlined, J-, Y-, or U-shaped burrows, with passive fill, commonly interpreted as dwelling structures of upogebiid shrimp or ocypodid crabs (see Nesbitt and Campbell 2002, 2006; and Figs. 9.1c–d, 9.2c, and 9.5b herein). These burrows occur most typically in uppermost foreshore and backshore environments (Frey et al. 1984; Curran and White 1991; Netto and Grangeiro 2009; Seike and Curran 2014), and also in outer-estuarine and bay-mouth settings (Campbell and Nesbitt 2000; Nesbitt and Campbell 2002). This ichnogenus is present from the Late Jurassic onward (Fürsich 1981).

Gyrolithes consists of vertical, coiled burrows, forming a regular spiral, unlined to indistinctly lined, with bioglyphs and/or pellets (Figs. 9.2e and 9.5c) and, in some Mesozoic and younger examples, connecting to *Ophiomorpha* or *Thalassinoides* burrow forms. *Gyrolithes* is known from the Cambrian (e.g., Fritz 1980; Fedonkin 1981, 1983; Liñán 1984; Crimes and Anderson 1985; Hein et al. 1991; Jensen 1997; Jensen and Grant 1998; Stanley and Feldmann 1998) to the Recent (Dworschak and de Rodrigues 1997). However, worm producers have been indicated for the Paleozoic occurrences, particularly for the typical Cambrian ichnospecies (see Carmona et al. 2004; Netto et al. 2007). The robust forms of *Gyrolithes* from Mesozoic and younger deposits have been interpreted as resulting from a specific feeding strategy of decapods having a combined function of deposit feeding and possibly gardening (Mayoral and Muñiz 1993; Netto et al. 2007). Today, incipient *Gyrolithes*-like burrows made by axiidean shrimps are known to occur in modern mangrove and estuarine areas (Dworschak and de Rodrigues 1997; Wetzel et al. 2010).

Macanopsis refers to subhorizontal to horizontal, elongated, slightly curved burrow chambers, unbranched, and with a subvertical shaft (Fig. 9.2g); bioglyphs may be present. This ichnogenus has been interpreted as a dwelling structure constructed by decapods (probably brachyurans) and is known to occur in both shallow-marine and fluvial settings (Muñiz and Mayoral 2001b) since the Late Jurassic (Neto de Carvalho et al. 2010).

Pholeus consists of single or complex U-shaped, lined burrows with a longitudinal axis parallel to bedding, generally leading into an oblique shaft toward the surface and in the opposite direction with a smaller, rising vertical to oblique shaft (modified from Knaust 2002; Figs. 9.2d and 9.5d). These structures are interpreted as dwelling burrows of suspension- and detritus-feeding decapods ("thalassinidean" shrimps and lobsters), with the function of the small shaft related to ventilation of the burrow (Knaust 2002). This ichnogenus is typically associated with shallow-marine to lagoonal (intertidal to shallow subtidal) paleoenvironments and is known since the Middle Triassic (Knaust 2002).

Tubotomaculum consists of spindle-shaped burrows, displaying a spreite and containing ellipsoidal pellets (García-Ramos et al. 1984, 2014). This ichnogenus is interpreted as a feeding structure produced to store pellets that are subsequently used as a bacteria-enriched resource during times of limited food supply (García-Ramos et al. 2014). The presence of bifid bioglyphs on the basal and lateral surfaces of the structure suggests production by crustaceans (García-Ramos et al. 2014). *Tubotomaculum* is known from deep-marine environments, ranging in age from the Cretaceous to Miocene (García-Ramos et al. 1984, 2014).

Sinusichnus comprises distinctive burrow systems consisting of horizontal and regularly sinuous branches (Gibert 1996; Figs. 9.2j and 9.5e). Shafts and oblique burrow segments are rare, short, and tend to occur on top of the branching points. Walls are smooth and unlined, and vertical retrusive spreite are locally present. There are several interpretations for the function of these structures (e.g., burrows produced by selective deposit-feeding decapods; open burrows built to act as traps for meiofauna, and/or to induce microbial growth, i.e., combined feeding strategies (fodinichnion/agrichnion). These burrows occur in shallow-marine (mainly stressed settings) and deep-marine environments (as doomed-pioneers), and are known from the Late Cretaceous (Buatois et al. 2009) to early Pliocene (Belaústegui et al. 2013).

Maiakarichnus consists of subspherical chambers, with or without a clay-rich lining, preserved in full relief, with numerous shafts radiating in an upward direction (mainly from the chamber upper hemisphere; Figs. 9.2h and 9.5f). Usually, this form intergrades or connects to *Ophiomorpha* or *Thalassinoides* tunnels. *Maiakarichnus* has been interpreted as callianassid brood structures (Curran 1976; Verde and Martinez 2004) or fossil pantries (Nesbitt 2006). This form occurs in marginal-marine to shallow-marine deposits and is known since the Miocene (Verde and Martinez 2004).

Parmaichnus refers to vertical to oblique tubular burrows, composed of a U-shaped upper part and a basal shaft (Fig. 9.2i). Distinctive swellings or turn-around chambers are present in the upper part of the burrow and are considered a diagnostic character for this ichnogenus. *Parmaichnus* is interpreted as the burrow of suspension- and filter-feeding decapods, with the presence of turning chambers being typical for modern upogebiid burrows (Pervesler and Uchman 2009). This trace fossil occurs in nearshore deposits from early Pleistocene to Recent (Pervesler and Uchman 2009).

Glyphichnus consists of arcuate, vertical, and probably U-shaped burrows with deeply incised bioglyphs in fan-like groups, subparallel to burrow length (Bromley and Goldring 1992; Fig. 9.2k); rarely, apertural necks have been observed (Goldring et al. 2002). These structures are interpreted as produced by suspension-feeding decapods. The presence of apertural necks is common in structures used for suspension feeding and serves to inhibit intruders. This ichnogenus occurs in firm substrates in both shallow- and deep-marine settings from the late Mesozoic to Recent (Goldring et al. 2002; Wetzel et al. 2008).

Coenobichnus comprises asymmetrical trackways having left tracks larger than the right tracks, both being crescent-shaped, with the interior of the crescent pointing toward the interior of the trackway. This ichnogenus has been attributed to land hermit crabs (Walker et al. 2003). *Coenobichnus* occurs in coastal dune settings, from the Oligocene to Recent (Walker et al. 2003; Zonneveld et al. 2012).

Foersterichnus is a trackway comprising straight, or slightly curving, paired rows of elongate to tear-shaped impressions, parallel or subparallel to its long axis. This ichnogenus has been attributed to brachyurans and is only known from Cretaceous shallow-marine deposits (Pirrie et al. 2004).

As stated previously, burrow systems produced by decapods are among the most important components of post-Paleozoic shallow-marine ichnofaunas, reflecting the dominance of the Modern Evolutionary Fauna. In a study documenting the trace-fossil record of decapod-like gallery systems, Carmona et al. (2004) constructed a database of all occurrences through the Phanerozoic to analyze changes in abundance and ichnodiversity. During the Paleozoic, there are, in general, a low number of "decapod-like" burrow systems, and the identity of their tracemakers is uncertain, most likely reflecting behavioral convergence by groups other than decapod crustaceans. The scenario changed significantly with increase in the number of burrows attributed to decapods during the Mesozoic. This probably reflects an increasing pace of decapod radiation, as it is also indicated by the Mesozoic body-fossil record (Förster 1985; Schweitzer and Feldmann 2015; Klompmaker et al. 2015).

However, Triassic trace-fossil first occurrences are only slightly higher than those recorded in the late Paleozoic (Carmona et al. 2004). This is also confirmed by the body-fossil record, which indicates that decapod diversity was low in the Triassic (Klompmaker et al. 2013; Schweitzer and Feldmann 2015). In any case, there were changes in decapod ichnodiversity with *Thalassinoides* and *Ophiomorpha* being the most common ichnotaxa, along with *Gyrolithes* (resembling modern records) and *Pholeus* added to the list. *Spongeliomorpha* was also well established in shallow-marine environments. This suggests the overall expansion of behavioral modes through the Triassic.

During the Jurassic, decapod trace-fossil occurrences show a slight increase with respect to previous periods (Carmona et al. 2004). This is clearly related to the appearance of the body fossils of callianassids in the Late Jurassic (Glaessner 1969; Förster 1985; Schweitzer and Feldmann 2015). Interestingly, the basic ethological program recorded by these dwelling systems seems not to have changed significantly since the Jurassic.

The abundance of decapod trace-fossil forms underwent a major increase toward the end of the Mesozoic (Carmona et al. 2004). Crustacean dominance in the marine realm during the Cretaceous is indicated by the great diversity of body fossils, as well as by the abundance of decapod burrowing activity recorded in shallow-marine deposits. A decapod origin is supported by the preservation of claws within some of these burrows (e.g., Mángano and Buatois 1991; Swen et al. 2001) and by the presence of diagnostic features, such as pelleted walls, bioglyphs reflecting the use of hard appendage parts, and enlargements at burrow turnaround points. Decapod excavations are particularly abundant in middle- and lower-shoreface clastic environments, as well as in shallow-marine carbonate settings. The increase in the number of decapod trace-fossil occurrences accelerated by the end-Cretaceous, including addition of the oldest examples of *Sinusichnus* in Cretaceous deposits (Buatois et al. 2009).

Interestingly, Klompmaker et al. (2013) found that during the Mesozoic there was a long-term shift in diversity of the different crustacean groups based on the body-fossil record, with dominance of lobsters and shrimps during the Paleozoic and Triassic, whereas during the Jurassic onward, anomurans and brachyurans underwent rapid diversification. In particular, their study showed that the Late Jurassic decapod radiation was associated with the expansion of reef ecosystems, with a high percentage of generic origination of reef-dwelling brachyurans and anomurans (Klompmaker et al. 2013). This is in agreement with the trace-fossil record, confirming that the Mesozoic was a highly important time in the evolution of decapods (Schweitzer and Feldmann 2015).

During the Paleogene, the numbers of individual decapod trace fossils appear to be considerably reduced compared with that found in similar environmental settings in the Cretaceous (Carmona et al. 2004). This could be related to the end-Cretaceous mass extinction. However, the effect of this extinction on decapods (mostly of the Southern Hemisphere) was probably not so severe (Feldmann and Schweitzer 2006). In the same vein, Swen et al. (2001) analyzed the demise of the subfamily Protocallianassinae and the rise of other subfamilies (among them Callianassinae) in nearshore deposits, which occurred below the K–Pg boundary. They postulated that the demise of Protocallianassinae and the rise of Callianassinae were related to the worldwide emergence of seagrasses at the end of the Cretaceous and to the strong competition that took place globally in shallow-marine settings. These authors also thought that seagrasses may have favored the rise of families dominated by detritus-feeding shrimp (such as *Corallianassa*) over those of suspension feeders (e.g., *Protocallianassa*). The abundance of individual decapod trace fossils during the Eocene is apparently higher than for the other epochs of the Paleogene. The Eocene was a time of evolutionary radiation for decapods, and this appears to be reflected in the trace-fossil record.

Finally, during the Neogene, the abundance of decapod trace fossils underwent another major increase, probably reaching the highest level of the entire Phanerozoic (Carmona et al. 2004). Body-fossil data conform to the Neogene trace-fossil record, which shows primacy of decapod burrows in shallow-marine environments, with *Maiakarichnus* occurring for the first time in the Miocene. Interestingly, the summary study of Schweitzer (2001) indicated that the Miocene was a time of high origination rates within the decapod fauna, with first appearance of the modern genera that dominate the present seas.

Decapod burrows are widespread in modern coastal settings, being preferentially distributed in tropical and temperate shallow-marine and marginal-marine settings. The similarity between the modern callianassid burrows formed by *Sergio mirim* in the lower foreshore of Cassino Beach (Rio Grande do Sul State, southernmost Brazil) and *Ophiomorpha nodosa* specimens preserved in Pleistocene deposits of the Chuí Formation (Gibert et al. 2006), which represent an ancient beach line on the Rio Grande do Sul Coastal Plain, suggests that these faunas were not impacted by Quaternary glaciation, at least in the Southern Hemisphere. The presence of large *Ophiomorpha* specimens in Pleistocene shallow-marine deposits from Pehuen-Có, Argentina, further supports this interpretation (Mouzo et al. 1989).

9.2.1.2 Mollusks

Mollusks have a long evolutionary history and include several groups, with gastropods and bivalves being the most numerous, diverse, and common bioturbators from the early Paleozoic onward. The development of key external features, such as the shell, foot, and radula, helped mollusks acquire diverse ecological preferences. This section focuses on trace fossils attributed to gastropods and bivalves.

Gastropods and Polyplacophorans

Locomotion and feeding structures produced by gastropods and chitons can be observed in modern settings. Almost all gastropods and chitons use their foot during locomotion. Typically, the sole of the foot is flat and broad, ciliated and with abundant secretory glands, allowing gastropods to move over a variety of substrates (Ruppert et al. 2004). These glands produce mucus that forms a mucus trail. Most gastropods living on stable substrates move by pedal waves with the aid of the mucus trail (glide crawling, Schäfer 1962, 1972; see also Buatois and Mángano 2011). Gastropods are mostly microphagous browsers that feed on microscopic algae and scrape the substrate with their radula (a flexible longitudinal ribbon having rows of small and transverse chitinous teeth; Ruppert et al. 2004). The combined actions of the foot and radula generate distinctive patterns on the substrate, which have also been recognized in the fossil record, although some uncertainty persists regarding the attribution of these structures to gastropods. For example, the Cambrian ichnogenus *Climactichnites* is interpreted as having been produced by an elongate, dorso-ventrally flattened organism with a soft foot, which may have been a primitive gastropod, although other possibilities exist (Abel 1935; Getty and Hagadorn 2008, 2009; see Chap. 3). In modern intertidal environments, structures slightly similar to this trace fossil can be found, although their preservation potential is very low (except in settings with microbial mats; Carmona et al. 2010).

Other trace fossils (e.g., *Psammichnites*) have been interpreted as locomotion structures of gastropods, but other producers cannot be discarded (see discussions in Mángano et al. 2002a). In any case, neither *Climactichnites* nor *Psammichnites* are recorded in post-Paleozoic rocks, probably due to increased levels of bioturbation and obliteration of shallow-tier traces or extinction of their producers. The much simpler trail *Archaeonassa*, ranging from the Cambrian to the Recent, has been attributed to gastropods as well (Fenton and Fenton 1937), but there is no agreement in this regard (Buckman 1994; Yochelson and Fedonkin 1997). Therefore, the fossil record of bioturbation structures produced by gastropods remains uncertain.

Bivalves

Along with gastropods, bivalves constitute an important and extremely diverse molluscan class, with species living in both marine and freshwater environments. Within this group, a pronounced post-Paleozoic increase in infaunal representatives, also exhibited by several other major groups (e.g., echinoids), is widely recognized (Stanley 1970). The evolutionary diversification of most bivalve shells is related to different styles of burrowing in soft sediment and of boring in hard substrates, which provide escape from predators (Stanley 1970; Seilacher 1998). This tendency is not only reflected by the hard part anatomy, but also by the soft parts of bivalves, which show corresponding trends in the development of a lateral flat burrowing foot, fused mantle edges, and pallial siphons (Stanley 1970; Seilacher 1998; Kelley and Hansen 2003; Ruppert et al. 2004 and references therein). The replacement of epifaunal and semi-infaunal taxa by infaunal forms from the Cretaceous onward is well recognized (Vermeij 1977, 1987).

In contrast to crustacean ichnotaxa, which for the most part are represented by dwelling structures, the ichnogenera most commonly assigned to bivalve tracemakers comprise various ethologies (Fig. 9.6a–i), such as locomotion (*Protovirgularia, Ptychoplasma, Oravaichnium*), resting/dwelling (*Lockeia*), dwelling (*Solemyatuba*), feeding (*Lophoctenium, Saronichnus*), equilibrium (*Siphonichnus, Scalichnus*), and a complex combination of behaviors (*Hillichnus*), all in soft sediments (Figs. 9.7a–d and 9.8a–h). The dwelling ichnogenus *Gastrochaenolites* may occur in both hard and firm substrates (Fig. 9.8h) and will be addressed under bioerosion.

Protovirgularia comprises horizontal to inclined structures characterized by the presence of V-shaped or U-shaped sediment pads transverse to a longitudinal axis (Figs. 9.6a and 9.7a–d). This ichnogenus has been interpreted as formed by locomotion of protobranch bivalves, moving through the sediment by means of a split foot that employs a push-and-pull mechanism (Trueman 1966, 1975; Stanley 1970; Seilacher and Seilacher 1994; Mángano et al. 1998). In addition, Seilacher and Seilacher (1994) suggested that *Protovirgularia* can also be produced by scaphopods (another molluscan group with a cleft-foot), especially if the structures are not related to the resting trace *Lockeia* (Mángano et al. 1998). This trace fossil, recorded in marginal-, shallow-, and deep-marine environments, ranges from Ordovician to Recent (Seilacher and Seilacher 1994; Uchman 1998).

Ptychoplasma consists of irregularly meandering, looping, winding or straight, discontinuous or continuous, hypichnial crests having an amygdaloid, carinate, or blocky cross-section, with poorly developed or absent chevronate structure. This ichnogenus has been interpreted as a locomotion trace of wedge-foot bivalves (Pieńkowski and Uchman 2009; Uchman et al. 2011). Recorded from non-marine, marginal-, shallow-, and deep-marine environments, this ichnogenus ranges from Ordovician to Recent (Rodríguez-Tovar et al. 2014).

Oravaichnium consists of irregularly meandering, looping or winding, continuous, hypichnial crests having a box-like (non-carinate) cross-section. As with *Ptychoplasma*, this ichnogenus is regarded as a locomotion trace of wedge-foot bivalves (Uchman et al. 2011). In contrast to *Ptychoplasma*, however, *Oravaichnium* is less understood, having been recorded only from Eocene deep-marine deposits (Plička and Uhrová 1990; Uchman et al. 2011).

Lockeia commonly comprises oval- to almond-shaped structures, typically tapering at one end and being more rounded on the opposite end (Mángano et al. 1998; Figs. 9.6a and 9.8a). *Lockeia* is interpreted as a resting structure of bivalves, although

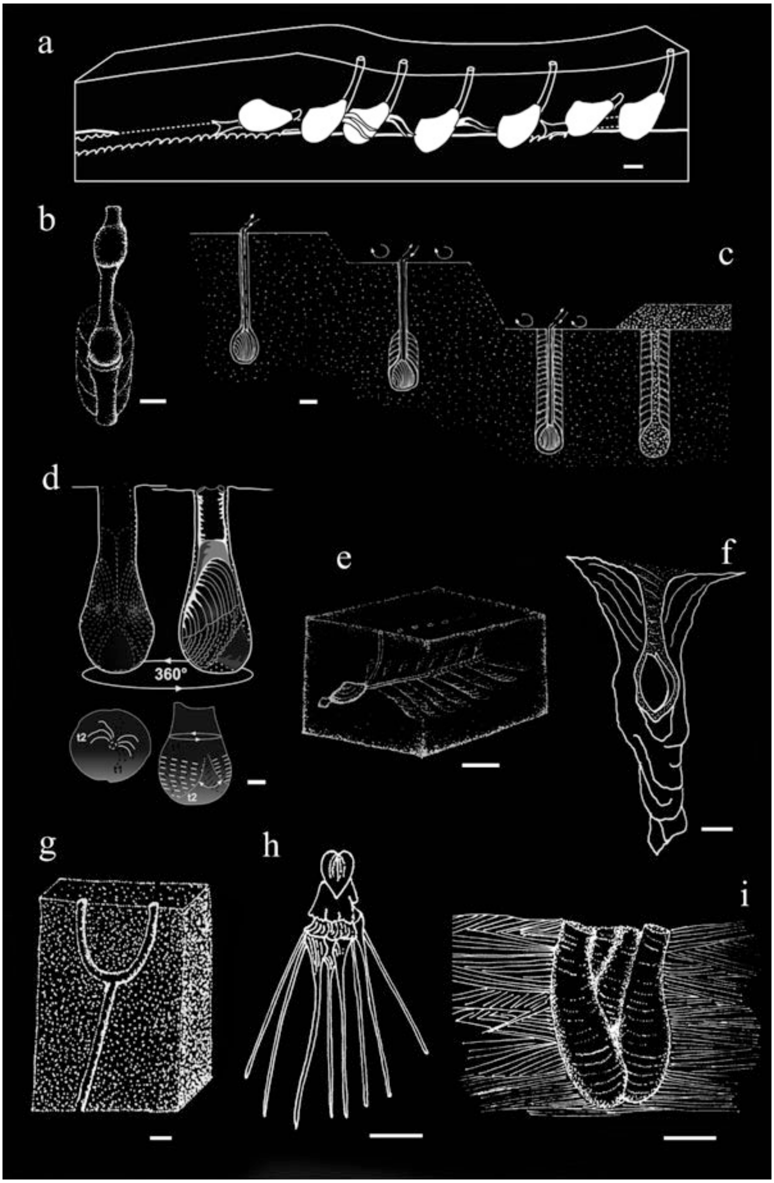

Fig. 9.6 Schematic reconstructions of bivalve-produced ichnogenera. (**a**) Reconstruction of the locomotion activity of a cleft-foot bivalve, producing *Protovirgularia* and *Lockeia* (modified from Ekdale and Bromley 2001a), *scale bar* is 5 cm; (**b**) Reconstruction of *Ptychoplasma* (redrawn from Uchman et al. 2011), *scale bar* is 1 cm; (**c**) Interpretation of *Siphonichnus* (modified from Stanistreet et al. 1980), *scale bar* is 5 cm; (**d**) Schematic representation of the pholadids during excavation and production of *Gastrochaenolites* (see Carmona et al. 2007), *scale bar* is 2 cm; (**e**) Interpretation of the complex behavior of a deposit-feeding bivalve illustrated by *Hillichnus* (modified from Bromley et al. 2003), *scale bar* is 5 cm; (**f**) Reconstruction of Scalichnus (modified from Hanken et al. 2001), *scale bar* is 5 cm; (**g**) Reconstruction of *Solemyatuba* (based on Seilacher 1990a), *scale bar* is 5 cm; (**h**) Reconstruction of *Saronichnus* (modified from Pervesler and Zuschin 2004), *scale bar* is 5 cm; (**i**) Reconstruction of *Teredolites* (based on Bromley et al. 1984), *scale bar* is 5 cm

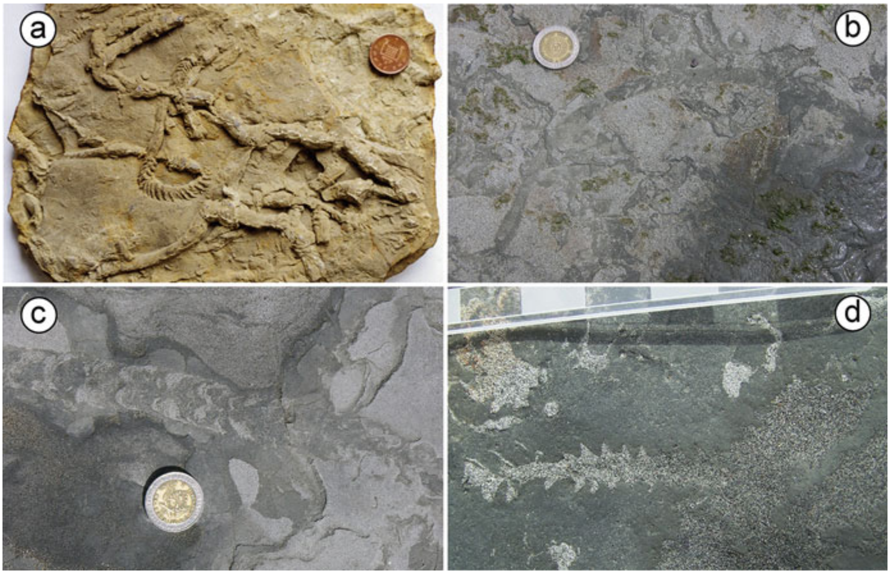

Fig. 9.7 Preservational variants of *Protovirgularia* in Mesozoic–Cenozoic shallow-marine deposits. (**a**) Forest Marble Formation, Jurassic, England, coin is 1.65 cm; (**b–d**) Chenque Formation, Lower Miocene, Argentina. Coins in (**b**) and (**c**) are 2.2 cm

some specimens can represent semipermanent domiciles (Seilacher 1953; Rindsberg 1994; Mángano et al. 1998). This ichnogenus has been reported from marginal-, shallow-, and deep-marine settings since the late Cambrian/Early Ordovician (Mángano et al. 2002b and references therein). In contrast to most bivalve ichnotaxa*,* *Lockeia* is also known from freshwater settings.

Solemyatuba consists of endichnial, vertically oriented, U-shaped burrows, elliptical in cross-section and with a lower extension tube in one of its ichnospecies (Seilacher 1990a; Mángano and Buatois 2003; Figs. 9.6g and 9.8d). *Solemyatuba* has been interpreted as the dwelling trace of a farming bivalve (Seilacher 1990a). This form can be found in shallow-marine deposits since the Ordovician (Seilacher 1990a; Mángano and Buatois 2003).

Lophoctenium is not generally assigned to the activity of bivalves. However, Ekdale and Bromley (2001a) interpreted Carboniferous specimens of this trace fossil as a feeding structure produced by the repetitive lateral probing of the labial palps of a protobranch along an organic-rich sediment deposit. This structure consists of coarse horizontal spreite formed by a series of closely spaced, curved ridges (Ekdale and Bromley 2001a). In particular, the specimen studied by these authors represents a compound trace fossil with three different ichnotaxa in combination (*Protovirgularia*, *Lockeia,* and "*Lophoctenium*"; see Ekdale and Bromley 2001a).

Saronichnus consists of a system of vertical or inclined tubular to blade-shaped probes diverging from a central area of broom- or star-like form (Pervesler and Zuschin 2004; Figs. 9.6h and 9.8f). This ichnotaxon has been found in direct connection with *Thyasira* shells, indicating formation by lucinoid bivalves. It is most likely a

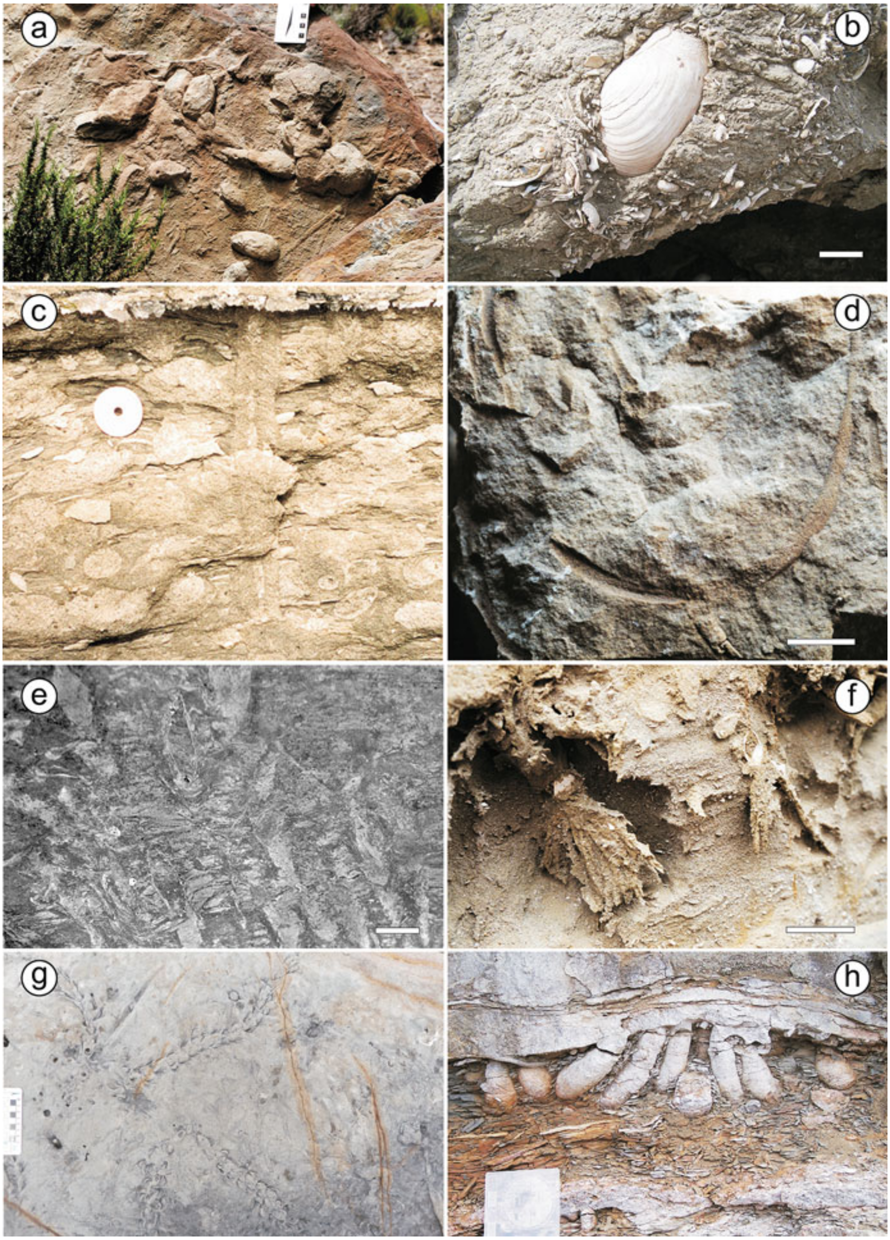

Fig. 9.8 Various bivalve ichnotaxa in Mesozoic–Cenozoic shallow-marine deposits. (**a**) Several specimens of *Lockeia siliquaria*, Mulichinco Formation, Cretaceous, Argentina; (**b**) *Scalichnus phiale*, Monte León Formation, Lower Miocene, Argentina, scale bar is 5 cm; (**c**) *Siphonichnus eccacensis*, Chenque Formation, Lower Miocene, Argentina, coin is 1.8 cm; (**d**) *Solemyatuba ypsilon*, Rhaetian Sandstone, Olgahain, Upper Triassic, southern Germany, scale bar is 1 cm; (**e**) Equilibrium traces of byssate bivalves, scale bar is 4 cm; (**f**) *Saronichnus abeli*, Grund Formation, Miocene, Austria, photograph courtesy of Peter Pervesler; (**g**) *Hillichnus lobosensis*, Carmelo Formation, Paleocene, Point Lobos, California, United States, photograph courtesy of Nic Minter; (**h**) *Gastrochaenolites* isp., Río Turbio Formation, Eocene, Argentina

feeding structure produced as a result of a chemosymbiotic life strategy. At present, it has only been recorded from Pleistocene shallow-marine strata (Pervesler and Zuschin 2004).

Siphonichnus comprises vertical structures containing a backfill of concave-downward menisci (Stanistreet et al. 1980; Figs. 9.6c and 9.8c). The laminae forming the backfill are cut through centrally by a vertical tube, filled with pale, massive sediment. The authors of this ichnogenus postulated that siphon length of a given bivalve tracemaker should be equal to the length of backfill laminae. *Siphonichnus* occurs since the Carboniferous in marginal- to shallow-marine settings (Stanistreet et al. 1980; Carmona et al. 2008; see also discussion in Zonneveld and Gingras 2013 and Knaust 2015).

Scalichnus includes large, vertically oriented, bottle-shaped structures, formed during retrusive and protrusive movements of the bivalve *Panopea* (Hanken et al. 2001; Figs. 9.6f and 9.8b). *Scalichnus* is regarded as an equilibrichnial trace fossil having a general sack-like morphology and a thick lining. This structure is common in Cenozoic marginal- to shallow-marine settings (Hanken et al. 2001; Nara and Kondo 2012; see also discussion in Zonneveld and Gingras 2013).

Hillichnus was defined to include morphologically complex structures interpreted as the work of subsurface deposit-feeding tellinacean bivalves (Bromley et al. 2003; Figs. 9.6e and 9.8g). This structure comprises several parts or levels: a segmented component with a basal tube within, from which lateral feather-like structures arise, alternating on either side, and vertical sand- and mud-lined tubes that also rise from the basal structure. According to the ichnogenus authors, the movement of the bivalve's inhalant siphon produced the feather-like structures on either side of the basal tube, and the siphonal excursions to the sediment surface produced the vertical tubes. The length of these tubes suggests that feeding activity of these bivalves occurred well below the oxygenated sediment layer, probably 20 cm or more beneath the surface, suggesting that in addition to deposit feeding, chemosymbiosis may have taken place. *Hillichnus* is known from the Cretaceous and Paleogene, in both shallow- and deep-marine environments (Bromley et al. 2003; Pazos and Fernández 2010).

Finally, it is possible that other ichnotaxa may have been produced by bivalves, but tracemaker origins cannot always be confirmed. An example would be *Paradictyodora*, which comprises vertical spreite structures that consist of subvertical folded laminae produced by the migration of a subvertical J-shaped tube (Olivero et al. 2004). This structure has been interpreted as the feeding trace of worms or tellinid bivalves (D'Alessandro and Fürsich 2005; Serpagli et al. 2008). This ichnogenus occurs from Late Cretaceous to Pleistocene (Olivero et al. 2004; D'Alessandro and Fürsich 2005).

Although bivalves were key players during the MMR, the trace-fossil record shows that some of the most representative ichnotaxa, such as *Protovirgularia* and *Lockeia*, have been present since the early Paleozoic, albeit becoming particularly abundant since the late Paleozoic. However, other bivalve ichnotaxa (e.g., *Hillichnus*) seem to be directly associated with the MMR, whereas the stratigraphic ranges of other ichnotaxa (e.g., *Scalichnus*, *Saronichnus*) are still poorly known due to sparse occurrence. *Hillichnus* reflects a level of behavioral complexity unknown in older bivalve-produced ichnotaxa (Bromley et al. 2003). Particularly, the proposed producers of this ichnogenus, the tellinid bivalves, originated in inner shelf environments during the Middle Triassic and then commenced significant radiation (Jablonski and Bottjer 1990). Interestingly, it seems that the earliest tellinaceans were suspension feeders, whereas deposit-feeding tellinids appeared during the Early Cretaceous (Bottjer and Jablonski 1988). Although lucinids originated in the Silurian, they experienced an evolutionary radiation near the end of the Cretaceous, coincident with the appearance of seagrasses and mangroves (Stanley 2014). It has been hypothesized that lucinids may have exploited the dysaerobic sediments below roots and rhizomes, acquiring sulfides for their endosymbiotic bacteria (Stanley 2014). *Saronichnus*, the only ichnogenus attributed confidently to lucinids, is only known from its type locality, so using ichnologic data to track evolutionary trends is still not possible.

9.2.1.3 Echinoderms

The Phylum Echinodermata is one of the most important and characteristic components of modern-marine benthic communities (Smith 1984). Echinoderms comprise very diverse marine groups, such as sea stars, brittle stars, sea urchins, sand dollars, sea cucumbers, and sea lilies, with the majority being bottom dwellers (Ruppert et al. 2004).

The Class Echinoidea consists of diverse and successful groups comprising approximately 950 living species (Smith 1984; Ruppert et al. 2004). Echinoids adapted to live in a variety of marine environments and present different life habits (Smith 1984). This part of the chapter focuses mostly on irregular echinoids, whose stratigraphic range covers the Early Jurassic to Holocene, with approximately 410 genera (Parma 2008).

Irregular echinoids are detritus- or deposit-feeding organisms that ingest material selected by their podia. This particulate material is covered by mucus and then moved to the mouth. Some irregular echinoid species burrow deeply into the substrate and build a vertical channel to provide oxygenated water from the sediment surface. They also construct sanitary channels or drains to remove fecal material mixed with seawater. Within irregular echinoids, the spatangoid heart urchins constitute the most diverse group in modern oceans, being found in all latitudes and at all depths, and contributing significantly to collective bioturbation of the surrounding sediments (Villier and Navarro 2004). In addition, the infaunal activities of these organisms stimulate bacterial production within the substrate via transport of organic matter to deeper sediment layers (Osinga et al. 1997). In turn, deep-burrowing irregular echinoids can induce a back-flow of organic matter in the form of dissolved nutrients returned to the sea (Lohrer et al. 2004).

The abundance of spatangoids increased rapidly during the Cretaceous and has remained stable since then, although other groups of irregular echinoids show a concurrent decline in diversity. This has been interpreted as due to the acquisition of

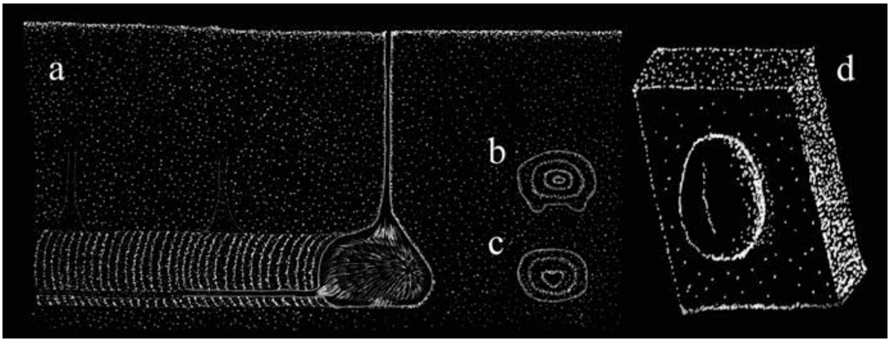

Fig. 9.9 Schematic reconstructions of trace fossils produced by irregular echinoids. (**a**) Reconstruction of the locomotion activity of *Echinocardium cordatum* producing *Scolicia*, scale is 1 cm; (**b**) Cross-sectional view of *Scolicia*; (**c**) Cross section view of *Bichordites*; (**d**) Basal view of *Cardioichnus* (based on Smith and Crimes 1983), scale is 1 cm. (**a–c**) modified from Bromley (1996)

a burrowing life mode, which allowed spatangoids to access new food resources and avoid predation (Smith 1984; Villier and Navarro 2004). Three ichnogenera (e.g., *Bichordites, Scolicia*, and *Cardioichnus*) are attributed to the activity of irregular echinoids (Figs. 9.9a–d and 9.10a–e; see Belaústegui et al. 2015a for a review).

Scolicia comprises horizontal to inclined trace fossils characterized by the presence of menisci (Figs. 9.9a–b and 9.10a–b). In cross-section and in hypichnial preservation, two parallel canals, functioning as drains for used respiratory water, are observed at the base of these structures. This ichnogenus ranges from the Jurassic onward (Uchman 1995).

Bichordites also consists of meniscate, horizontal structures, but with only one middle channel crossing the menisci (Figs. 9.9c and 9.10c–d). *Bichordites* ranges from the Eocene onward (Bernardi et al. 2010; Demírcan and Uchman 2012; Villegas-Martín et al. 2014).

Cardioichnus consists of heart-shaped structures having an axial depression (Figs. 9.9d and 9.10e). It is interpreted as the resting trace of irregular echinoids (Smith and Crimes 1983) and usually is found in association with locomotion traces. This ichnotaxon ranges from the Late Cretaceous onward (Smith and Crimes 1983).

In modern environments, two principal groups of irregular echinoids are known to excavate sediment: the *Spatangus* group, which produces meniscate structures with two basal drain canals (modern analogues for *Scolicia*), and the *Echinocardium* group, which produces structures with only one canal, resembling the ichnogenus *Bichordites* (Bromley and Asgaard 1975; Kanazawa 1995). Although Smith and Crimes (1983) postulated that irregular echinoids fully developed their capacity to excavate during the Early Cretaceous, when the *Spatangus* group first appeared, ichnologic evidence (i.e., the presence of *Scolicia* in Jurassic strata) suggests an earlier origin.

During the Paleozoic, epifaunal echinoderm taxa (mostly suspension- and detritus-feeders) were abundant (Dornbos 2008; Schneider 2008). Several reasons have been

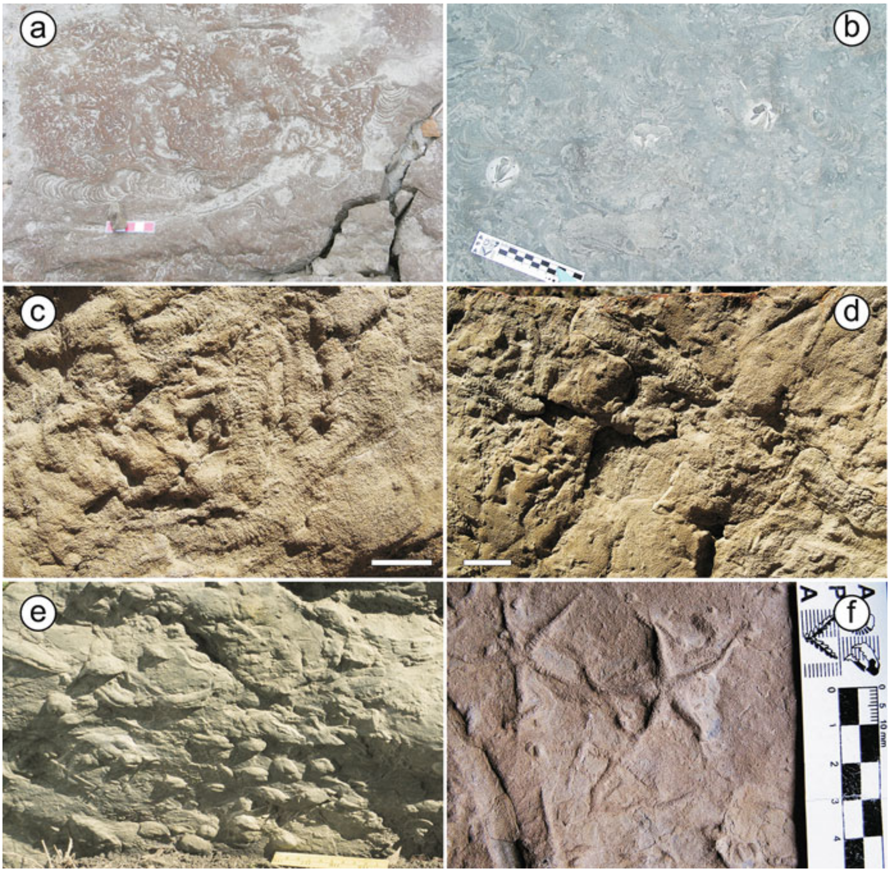

Fig. 9.10 Trace fossils produced by irregular echinoids. (**a**) *Scolicia* isp., López de Bertodano Formation, Upper Cretaceous, Antarctica; (**b**) *Scolicia* isp. with their producers, Chenque Formation, Lower Miocene, Argentina; (**c–d**) *Bichordites kuzunensis,* Mezardere Formation, Early Oligocene, Turkey, scale bar is 1 cm; (**e**) *Cardioichnus* isp., Upper Marine Molasse, Lower Miocene, Switzerland; (**f**) *Asteriacites lumbricalis*, Neill Klinter Formation, Lower Jurassic, Greenland

proposed for this abundance: high productivity of the seas during the early Paleozoic, low abundance of deep-infaunal organisms, and the absence of efficient predators (Sprinkle and Kier 1987; Parma 2008). This situation changed dramatically after the Paleozoic, when echinoderms developed infaunal detritus-feeding and predation strategies (Sprinkle and Kier 1987). Obviously, this change is also reflected in the trace-fossil record. Interestingly, Smith (2005) analyzed the growth and form of Paleozoic and post-Paleozoic echinoids and recognized that there was a distinct variation in the nature of disparity between these two groups, with an important diversification of shapes in those from post-Paleozoic times (see also Hopkins and Smith 2015). In particular, he found that there was a significant evolutionary innovation for echinoids with regard to specification of the final positions of plates during early stages of ontogeny. This early fixation of plate position favored the appearance of other evolutionary innovations, especially in the Atelostomata (e.g., spatangoids) and Clypeasteroida clades (Hopkins and Smith 2015). For example, the early fixation of plates allowed diverse regions of the test to differentiate both in structure and function. This involved also the morphological and functional differentiation of spines, especially for the spatangoids during the Cretaceous and Cenozoic, which poses important implications for acquisition of the ability to burrow. The early fixation of plate position also allowed for development of bands of spines called fascioles, which serve to create water currents and mucus streams. Fascioles are particularly important for burrowing in spatangoids, and their appearance permitted this group to diversify ecologically (Smith 2005). In addition to these innovations, the presence of an intestinal caecum enclosing sulfide-oxidizing bacteria in some spatangoid species allows them to burrow deeply within the substrate, well below the redox boundary, to ingest sulfide-rich and anoxic sediment (Bromley et al. 1995). Therefore, echinoids are able to avoid predation and reduce competition both for food and space, occupying a deep tier within the substrate (Bromley et al. 1995).

There are other trace fossils interpreted as produced by echinoderms. Among them, the most common is the resting trace *Asteriacites* (Fig. 9.10f–h), interpreted as produced by asterozoans (both asteroids and ophiuroids, but more commonly the latter; Seilacher 1953; Mángano et al. 1999). Although it has been suggested that *Asteriacites* is a *nomen dubium* (Schlirf 2012), the rediscovery of the type material justifies keeping the original name (Knaust & Neumann 2016; see also Gurav et al. 2014). *Asteriacites* is present in marginal- to shallow-marine settings since the Cambrian (Mikuláš 1992a), being particularly abundant in the Triassic and Jurassic (e.g., Dam 1990a; Wilson and Rigby 2000). There are also records from deep-marine facies (Crimes and Crossley 1991).

Some other ichnotaxa are also attributed to asterozoans, namely, *Pentichnus*, *Arcichnus*, and *Ophioichnus*. *Pentichnus* is a plug-shaped structure with pentameral symmetry interpreted as a dwelling burrow of ophiuroids. This ichnotaxon has been described from the Carboniferous (Maerz et al. 1976; Seilacher 1983, 1990b; Rindsberg 1994; Mángano et al. 2002b). *Arcichnus* is interpreted as the trackway of ophiuroids, and consists of a series of horseshoe-shaped impressions produced by the anterior arms. This trace fossil was described from the Devonian (Sutcliffe 1997). *Ophioichnus* consists of imprints interpreted as produced by the arms of ophiuroids and has been recorded in the Early Cretaceous (Bell 2004). Recently, incipient *Ophioichnus* were recognized on the modern sea floor (Schatz et al. 2013). Synonymization of *Ophioichnus* with *Biformites* has been recently suggested (Knaust and Neumann 2016).

The ichnologic record of holothurids is restricted to the ichnogenus *Artichnus*, which consists of a wide, J-shaped structure with a narrow, upward tapering shaft and the distal end tapering to a blind termination (Zhang et al. 2008). An irregular spreite structure surrounds the burrow lumen. This ichnogenus is known since the Eocene (Zhang et al. 2008; Ayranci and Dashtgard 2013; Ayranci et al. 2014; Belaústegui and Domènech 2014). A comparison with modern structures suggests that potential holothurid trace fossils may occur in Carboniferous rocks (Smilek and Hembree 2012). In fact, burrows attributed to holothurians have been recorded in the early Permian (Netto 1994; 2000). Further work is needed to assess the relationship between *Artichnus* and the previously defined ichnogenus *Naviculichnium* (Książkiewicz 1977) in order to evaluate more completely the record of trace fossils generated by holothurians.

In sum, the trace-fossil record matches closely body-fossil information, as indicated by the stratigraphic ranges of ichnotaxa attributed to irregular echinoids, such as *Scolicia*, *Bichordites,* and *Cardioichnus*, which are typical structures of the Modern Evolutionary Fauna. In contrast, structures commonly attributed to ophiuroids have a much longer stratigraphic range (*Asteriacites*, *Arcichnus*) or are still poorly known (*Ophioichnus*). Further occurrences of structures produced by holothurids in the fossil record are needed in order to establish potential trends.

9.2.1.4 Worms

Many ichnogenera have been attributed to the activity of "worms," without clear distinction regarding which group of worms might have been responsible. In fact, worm-like animals constitute a particularly important group of bioturbators in marine environments, including principally vermiform nemerteans, polychaetes, and hemichordates, all groups that are diverse and abundant. According to Seilacher (2007), when worms are mentioned, the term serves to designate "all long, soft and usually cylindrical animals belonging to many different phyla," which have evolved a peristaltic mode of locomotion for life in soft substrates, but other locomotion strategies may be employed, such as undulation and bolting (Schäfer 1972; Buatois and Mángano 2011). The objective of this section is to discuss the most common trace fossils attributed to worm-like organisms, while relating them to the evolutionary history of some of their likely producers wherever possible.

Polychaetes are annelids having a pair of parapodia and associated chaetae in each body segment. Most polychaetes (e.g., terebellids, maldanids, glycerids, ophelids) are burrowers, although some bore into shells and rocks, secrete tubes, move over surfaces, and even swim (Ruppert et al. 2004). Nutrition habits of polychaetes are closely related to their mode of life; deposit feeders are mostly burrowers and sedentary worms living in burrows/tubes; suspension feeders are sedentary organisms living in tubes in the sediment or are attached to organic or inorganic hard substrates; and scavengers, carnivores, and herbivores are typically errant worms (although some live in tubes or are active burrowers) (Ruppert et al. 2004). Groups with ichnologic importance include members of the clades Scolecida and Palpata (Gingras et al. 2008). Scolecids are deposit-feeding burrowers, similar to the presumed ancestor of annelids, without head appendages, and palpates have head appendages and more diversified life habits (Ruppert et al. 2004). In particular, ophelids (scolecids) include burrowers with an eversible bulbous pharynx with which they ingest sediment in high-energy areas such as the foreshore, producing *Macaronichnus*-like structures (Clifton and Thompson 1978; Ruppert et al. 2004).

Nemerteans include several species of long, slender worms resembling annelids, although lacking their segmentation. They have a characteristic proboscis apparatus with which they capture prey and burrow (Ruppert et al. 2004). Species that burrow (e.g., *Carinoma*) commonly have a muscular body wall that they use to produce peristaltic movement (Ruppert et al. 2004).

Echiurans (or spoon worms) comprise coelomate marine organisms that lack segmentation. Echiurans have two main body regions: an anterior cylindrical part, called the prostomium or proboscis, and a trunk, which commonly has three-layered musculature used to produce peristaltic movements to ventilate their burrows. Most echiurans are deposit-feeders, although some are suspension-feeders. Many species live in U-shaped burrows built in sand and mud in shallow-marine settings, although some occupy deep-marine sediments (Ruppert et al. 2004).

Sipunculids are a group of worms sharing some characters with echiurans (e.g., both lack segmentation). These organisms are suspension- or deposit-feeders, collecting their food with ciliated tentacles present in the oral disc. Sipunculids are bottom-dwelling organisms, with most living in shallow-marine settings, where they burrow into the sediment or bore into coralline rocks or wood (Ruppert et al. 2004). Although the fossil record of this group is sparse, Huang et al. (2004) reported three species from the early Cambrian.

Priapulids are benthic marine worms characterized by an extendable, eversible proboscis (i.e., introvert). These organisms excavate using a push-and-pull mechanism, with the trunk acting as a penetration anchor and the introvert as a terminal anchor. They live in sandy and muddy sediments in shallow- and deep-marine settings (Ruppert et al. 2004). Based on their fossil record, priapulids were important components of Cambrian marine communities (Huang et al. 2007), and it has been convincingly argued that priapulids may have been the producers of *Treptichnus pedum* (Vannier et al. 2010).

Enteropneusts are benthic worms that have a body divided into three regions: proboscis (protosome), collar (mesosome), and trunk (metasome), and thus are tricoelomate animals. Generally, they use their anterior region to burrow by retrograde peristaltic contractions, with most being deposit-feeders (Ruppert et al. 2004). They mostly live in shallow-marine environments, and their fossil record extends back to the Cambrian (Caron et al. 2013).

Trace fossils attributed to worms are diverse and comprise structures that are morphologically simple, such as vertical or U-shaped burrows, to those that are more complex, displaying sophisticated spreiten (Fig. 9.11a-i). In this section, a brief description of most of the ichnogenera attributed to “worms” is alphabetically presented.

Ancorichnus comprises a cylindrical meniscate burrow fill surrounded by a structureless tubular mantle (Heinberg 1974; Dam 1990a). This ichnogenus has been interpreted as a locomotion trace (repichnion) of a soft-bodied organism (Heinberg 1974), most likely a worm. Dam (1990a) noted transitions with *Jamesonichnites*, suggesting that *Ancorichnus* represents the axial burrow from which *Jamesonichnites* probes were made. *Ancorichnus* occurs in shallow-marine environments and ranges from the Jurassic to the Cretaceous (Heinberg 1974); older and younger records require critical re-evaluation (e.g., Singh et al. 2010).

Arachnostega consists of irregular, elongate, and net-like burrows in sediment fills of shells and visible on the surfaces of internal molds. This ichnotaxon is attributed to errant polychaetes, but crustaceans cannot be ruled out as producers. Bertling (1992) considered the diameter and course of the burrows to reflect an opportunistic polychaete larval infestation in recently sediment-filled bivalve borings. *Arachnostega* is known since the Cambrian (Rodrigues et al. 2005), although its presence is more common from the Jurassic onward in shallow-marine settings.

Arenicolites is a vertical U-tube without spreite. It is interpreted as a dwelling structure. Although it has been attributed to worm-like organisms such as polychaetes (Goldring 1962; Fürsich 1974); crustaceans (Goldring 1962) and holothurians (Seilacher 1990a; Bromley 1996) have been suggested as well. *Arenicolites* is present in a broad variety of shallow- to deep-marine and even continental environments, being most common in nearshore high-energy settings since the Cambrian (Mángano and Buatois 2014).

Asterosoma consists of elongate, bulbous segments having a terminal or eccentrical, laminated fill; segments are oriented (sub)horizontally and are arranged around a central vertical, somewhat twisted axis (Schlirf 2000; Fig. 9.11a). This ichnotaxon is a feeding trace produced by deposit or detritus feeders. Its intergradation with *Rosselia* suggests terebellid polychaetes as possible producers, but some authors (e.g., Neto de Carvalho and Rodrigues 2007) have proposed crustaceans as well. *Asterosoma* occurs most commonly in shallow-marine settings since the Cambrian (Mángano and Buatois 2014).

Balanoglossites consists of connected, U-shaped burrows that occur in shallow-marine environments, especially intertidal settings and carbonate ramps (Knaust 1998 and references therein; Fig. 9.11b). This trace fossil is interpreted as the domicile of enteropneusts or polychaetes (Mägdefrau 1932; Kaźmierczak and Pszczōłkowski 1969). Although this ichnogenus occurs since the Ordovician (Knaust and Dronov 2013), it mostly has been recorded since the Triassic (Knaust 2004, 2010; Carmona et al. 2008; Desai and Saklani 2012; Knaust and Costamagna 2012).

Bornichnus comprises clusters of small, lined, contorted, branched tubes (Bromley and Uchman 2003). These authors interpreted *Bornichnus* as an open burrow probably produced by farming organisms and noted that similar systems are produced by capitellid polychaetes in modern deposits. *Bornichnus* has only been reported from its type locality in the Lower to Middle Jurassic of Denmark (Bromley and Uchman 2003).

Chondrites comprise a tree-like system of tunnels that branch downward, with the angle of branching commonly less than 45° (Fig. 9.11c). The color of the sediment fills is invariably different from the host-rock color. This ichnotaxon has been interpreted as the burrow of infaunal detritus feeders or chemosymbiotic organisms (Fu 1991). Although worms, such as sipunculids and polychaetes, produce similar structures today, bivalves cannot be completely ruled out (Kotake 1991 and references therein). This ichnogenus is known since the Ordovician, and it is a facies-crossing form, from offshore to abyssal environments (Mángano et al. 2002b and references therein).

Cylindrichnus consists of broad U- or bow-shaped, concentrically laminated burrows (Fig. 9.11d). According to Belaústegui and de Gibert (2013), the morphologic characteristics of this ichnogenus display important similarities with burrows of some terebellid polychaetes. The ichnogenus *Cylindrichnus* occurs since the Cambrian (Mángano and Buatois 2014), and Belaústegui and de Gibert (2013) reported that *Cylindrichnus concentricus* ichnofabrics occur commonly in Mesozoic and Cenozoic offshore to shoreface settings.

Curvolithus comprises ribbon-like, flattened, endostratal trace fossils (Fig. 9.11e). Three rounded lobes are present on the upper surface (Buatois et al. 1998).

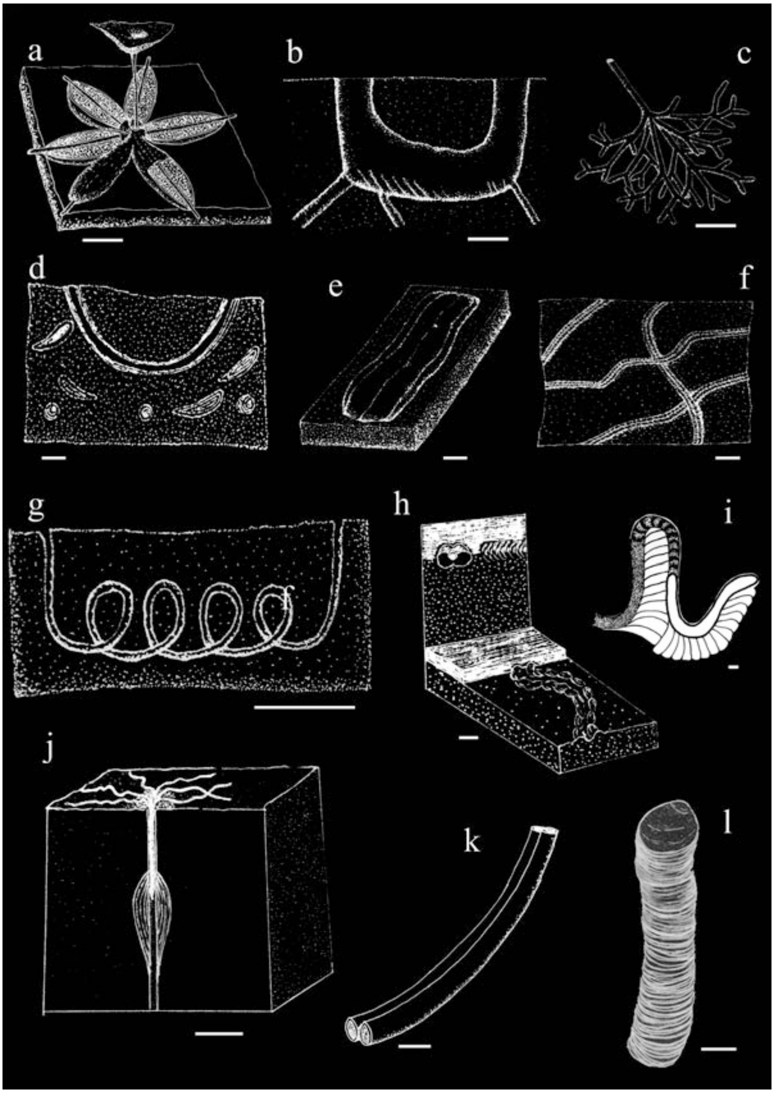

Fig. 9.11 Ichnogenera produced by worms. (**a**) *Asterosoma*, scale bar is 5 cm; (**b**) *Balanoglossites*, scale bar is 5 cm; (**c**) *Chondrites*, scale bar is 1 cm; (**d**) *Cylindrichnus* (modified from Belaústegui and de Gibert 2009), scale bar is 1 cm; (**e**) *Curvolithus*, scale bar is 1 cm; (**f**) *Gyrochorte*, scale bar is 1 cm; (**g**) *Helicodromites*, scale bar is 10 cm; (**h**) *Nereites* (modified from Seilacher 2007), scale bar is 1 cm; (**i**) *Phycosiphon* (modified from Bromley 1996), scale bar is 0.2 cm; (**j**) *Rosselia* (modified from Nara 1995), scale bar is 8 cm; (**k**) *Schaubcylindrichnus*, scale bar is 1 cm; (**l**) *Teichichnus* (transverse vertical section, modified from Nara 1995), scale bar is 1 cm

This ichnogenus is interpreted as the locomotion trace of infaunal predators, such as flatworms or nemerteans, but gastropods cannot be completely ruled out as producers (Buatois et al. 1998, see also Knaust 2010). It is known since the Cambrian (Mángano and Buatois 2014).

Diplocraterion is a U-shaped, vertical burrow with protrusive (common) or retrusive (seldom) spreite. Openings to the seafloor are commonly funnel-shaped. *Diplocraterion* is interpreted as a dwelling structure and an equilibrium structure (Goldring 1962; Cornish 1986; Ekdale and Lewis 1991; Bromley 1996). Polychaetes have been suggested as tracemakers (Arkell 1939), although crustaceans have been indicated as well (Bromley 1996). *Diplocraterion* occurs in a wide variety of shallow- to deep-marine and even continental environments. However, it is more common in nearshore high-energy settings and is known since the Cambrian (Mángano and Buatois 2014).

Euflabella is a morphologically complex ichnogenus that comprises burrows with single or multiple spreite bodies arranged in linear or radial patterns (Olivero and López-Cabrera 2013). This trace fossil is interpreted as most likely produced by an elongated worm-like organism and has been recognized only in Upper Cretaceous and Paleogene shallow-marine settings (Olivero and López-Cabrera 2013).

Gyrochorte consists of curved to meandering, vertically penetrating burrows, with a bilobate epichnial ridge and an underlying hypichnial groove, both with transverse striae (de Gibert and Ekdale 2002; Fig. 9.11f). This ichnogenus is interpreted as produced by detritus-feeding worms, most likely annelids (de Gibert and Benner 2002). It is known since the Early Ordovician, although most recorded occurrences are from the Jurassic (de Gibert and Benner 2002 and references therein).

Haentzschelinia is a vertical, radial spreite trace, having a central shaft (Fürsich and Bromley 1985). This structure is interpreted as produced by worm-like organisms with a proboscis used for reworking the sediment from a central shaft (Fürsich and Bromley 1985; de Gibert et al. 1995; Uchman and Pervesler 2007). Such structures have been commonly referred to as *Dactyloidites*, but this name should be reserved for more simple radial forms particularly common in early Paleozoic deposits (see Belaústegui et al. 2015b). Although it has been mentioned from the Triassic (Beatty et al. 2008), the oldest illustrated occurrences have been documented in the Jurassic (Agirrezabala and de Gibert 2004).

Helicodromites comprises horizontal spiral burrows, with pale fill contrasting with the host rock (Fig. 9.11g). These trace fossils are interpreted as feeding burrows constructed by vermiform organisms (probably capitellid polychaetes or enteropneusts; Poschmann 2015). *Helicodromites* is common in both deep- and shallow-marine deposits, especially in low-energy settings (Baldwin and McCave 1999). It occurs from the Devonian onward (Baldwin and McCave 1999; Poschmann 2015).

Jamesonichnites consists of cylindrical tunnels with meniscate infill and well-defined surrounding mantle (Dam 1990a). According to this author, *Jamesonichnites* is transitional with *Ancorichnus* and it represents a feeding trace (fodinichnion) of a soft-bodied organism. However, its possible occurrence in transition with *Hillichnus* (Pazos and Fernández 2010) would be consistent with a bivalve producer. It is present in shallow-marine settings, ranging from the Jurassic (Dam 1990a; Desai and Saklani 2014) perhaps to the Cretaceous (Pazos and Fernández 2010).

Korymbichnus is similar to *Arachnostega*, although it is distinguished by filiform, dichotomous branches that fan out distally (Damborenea and Manceñido 1996). This structure is interpreted as produced by small deposit-feeding polychaetes that fed at the interface between a shell and its internal mold. *Korymbichnus* is known only from within mollusks molds from the Middle Jurassic of the Neuquén Basin, Argentina (Damborenea and Manceñido 1996).

Lapispira consists of double helicoidal, concentrically arranged burrows with coiling axes perpendicular to the bedding plane (Lanés et al. 2007; Pagani et al. 2012). This ichnogenus is interpreted as a feeding burrow, but its producer is uncertain, with worms, such as polychaetes and enteropneusts, but also thalassinidean crustaceans, as the most likely candidates (Lanés et al. 2007). It is only known from Early Jurassic shallow-marine settings. Another possible recording of *Lapispira* has been documented from the Miocene. It was attributed to crustaceans and most likely represents a new ichnotaxon (de Gibert et al. 2012).

Macaronichnus is a mostly horizontal to sub-horizontal trace fossil with a fill characteristically lighter than the host rock. It tends to occur in high densities. Modern polychaetes (opheliids) produce structures similar to this ichnogenus by ingesting sand to consume bacteria and organic material attached to the grains and excreting the clean sand that fills the core of the burrow (Pemberton et al. 2001). This form is commonly present in upper-shoreface and foreshore deposits (Pemberton et al. 2001; Seike 2009) and occurs since the Permian (Quiroz et al. 2010).

Nereites is a predominantly horizontal, winding to meandering trace fossil with a central tunnel filled with relatively dark sediment and lateral lobes of reworked, paler sediment (Fig. 9.11h). Interpreted as the structure of vermiform deposit-feeders, probably enteropneusts (Uchman 1995 and references therein), *Nereites* is commonly reported in both shallow- and deep-marine environments since the Cambrian (Mángano and Buatois 2014).

Palaeophycus is a straight to slightly curved, inclined to horizontal burrow, with smooth, ornamented, or annulated walls and with infill identical to the host rock. This ichnogenus has been interpreted as the dwelling burrow of a predaceous or suspension-feeding organism. Glycerid and nereid polychaetes form similar structures in modern environments (Pemberton and Frey 1982), but *Palaeophycus* is a very simple structure that in fact can be produced by many different groups of phylogenetically unrelated organisms. It is a eurybathic trace fossil recorded from shallow-marine, deep-marine, brackish, and continental paleoenvironments since the Ediacaran (Mángano et al. 2002b and references therein).

Patagonichnus comprises a morphologically variable and complex burrow system consisting of vertically and horizontally branched, lined tubes, with cylindrically laminated structures surrounding the main tubes (Olivero and López-Cabrera 2005). These authors suggested that *Patagonichnus* was most likely produced by polychaetes, such as maldanids and capitellids. This ichnogenus is known since the Miocene (Olivero and López-Cabrera 2005).

Phoebichnus comprises a central shaft consisting of stacked disc-shaped layers from which several radial burrows emerged; these radial burrows display a lamination inclined toward the shaft and an annulated mantle with annuli concave toward the shaft (Bromley and Asgaard 1972; Dam 1990a; Evans and McIlroy 2016). *Phoebichnus* is a feeding trace (fodinichnion) of a worm-like organism (Bromley and Asgaard 1972). However, a crustacean producer has been suggested recently (Evans and McIlroy 2016). This ichnogenus is particularly common in shallow-marine settings, ranging from the Jurassic to the Pleistocene (Bromley and Asgaard 1972; Kotake 2003).

Phycosiphon is a spreite trace fossil formed by recurving U-lobes in bedding planes and having a dark core and a pale halo. This ichnogenus has been interpreted as a feeding structure of vermiform organisms, probably polychaetes (Wetzel and Bromley 1994), and it occurs in shallow- and deep-marine settings since the Ordovician (Mángano et al. 2002b and references therein).

Planolites is an unlined, straight to slightly curved, smooth trace fossil, with striae or annulations, being predominantly horizontal and with an infill contrasting in texture with the host rock. It is interpreted as a feeding trace of deposit-feeder organisms, probably polychaetes (Pemberton and Frey 1982). Documented as a eurybathic trace fossil recorded in shallow-marine, deep-marine, brackish-water, and continental paleoenvironments, *Planolites* is known since the Cambrian (Mángano and Buatois 2014).

Polykladichnus comprises vertical to steeply oblique tubes, lined or unlined, with single or multiple U or Y shapes. The tubes are usually connected to the surface, and slight enlargements can be seen at junctions. Probable producers for marine *Polykladichnus* are polychaetes (Schlirf and Uchman 2005) and nemerteans (Knaust 2010), although cerianthid anemones (Schlirf and Uchman 2005) have been suggested as well. This ichnogenus is known since the Devonian (Schlirf and Uchman 2005).

Rosselia is a vertical to inclined funnel-shaped burrow with a central tube filled with sandy sediment and surrounded by concentric muddy laminae (Fig. 9.11j). Specimens commonly exhibit erosional truncations. *Rosselia* is interpreted as the dwelling structure of deposit-feeders, such as terebellid or trichobranchid polychaetes (Nara 1995). This ichnotaxon is common in shallow-marine environments, with normal-marine or brackish-water conditions, although it has also been reported from deep-marine environments in a few cases (Mángano et al. 2002b and references therein). *Rosselia* is known since the Cambrian (Jensen 1997).

Schaubcylindrichnus consists of oblique to horizontal bundles of congruent, lined, circular, and pale-colored tubes (Fig. 9.11k). Some specimens show cross-cutting relationships between successive tubes. This ichnogenus is usually interpreted as a dwelling structure produced by tubicolous deposit-feeders, similar to modern maldanid polychaetes (Pemberton et al. 2001). Löwemark and Hong (2006) considered the *Schaubcylindrichnus* tracemaker to be a suspension-feeding organism with the ability to construct closely spaced tubes sequentially within the sediment. This ichnogenus occurs in shoreface and upper-offshore sediments deposited under normal salinity conditions (Pemberton et al. 2001). Although known from the Carboniferous, it is much more common in post-Paleozoic rocks (Buckman 1997; Löwemark and Hong 2006; Löwemark and Nara 2013).

Skolithos is a simple, vertical burrow that can be lined or unlined. In marine environments, it is interpreted as the domicile of vermiform organisms (e.g., phoronids and/or polychaetes; Schlirf and Uchman 2005). *Skolithos* occurs across a broad range of shallow- to deep-marine and even continental environments, being most common in nearshore high-energy settings since the Cambrian (Howard and Frey 1975; Mángano and Buatois 2014).

Taenidium is a cylindrical and unlined, sinuous trace fossil, with fill that consists of meniscate segments alternately composed of fine- and coarse-grained sediment. This ichnogenus is interpreted as a grazing or feeding structure produced by vermiform, deposit-feeding invertebrates that fed while moving through the sediment (Keighley and Pickerill 1994). It occurs since the Cambrian in various marine environments (e.g., marginal-marine, shallow- and deep-marine) and also in continental settings (Buatois et al. 2007; Netto 2007).

Teichichnus is a horizontal to slightly inclined, unlined, simple structure, with retrusive spreite (Fig. 9.11l). It is interpreted as the feeding structure of deposit-feeding organisms, with each spreite formed during sediment mining, or an equilibrium structure with the spreite being in response to sea floor aggradation (Seilacher 1955; Corner and Fjalstad 1993). Probable tracemakers are polychaetes and sipunculan worms, but some arthropods may produce similar structures (Mángano et al. 2002b and references therein). This is a eurybathic form, being common in marginal-, shallow-, and deep-marine environments since the Cambrian (Mángano and Buatois 2014).

Zoophycos is a complex trace fossil with a wide range of morphological variability (Olivero and Gaillard 2007; Fig. 9.11i). This ichnogenus ranges from simple and isolated lobes with spreite to commonly large and very complex structures with spiral morphology (Bromley and Hanken 2003). It is known since the Cambrian (Olivero 2003). Various ethologic models have been invoked to explain the origin of this structure, including strip mining, detritus feeding, refuse-dump, food cache, and gardening (Bromley 1991; Löwemark 2015). Morphologic analysis suggests it is the work of sipunculid or echiuran worms (Wetzel and Werner 1981; Kotake 1992; Olivero and Gaillard 2007). Olivero and Gaillard (2007) noted that the oldest *Zoophycos* are usually unlobed, in contrast to more recent forms that show well developed lobes (see also Seilacher 1986; Bottjer et al. 1988) (see Sect. 9.6).

Considering the evolutionary history of the above-mentioned groups of worms, most of the major clades appeared during the early Paleozoic, although their body-fossil record is patchy due to their low preservation potential. For example, unquestionable polychaetes had certainly appeared by the middle Cambrian (Glasby et al. 2000). Fauchald (1984) suggested that by the end of the Paleozoic, most of the polychaete orders were already present, with groups such as opheliids (Scolecida) recorded since the Devonian (Thompson 1979). Interestingly, some groups of polychaetes became extinct by the end of the Paleozoic, and many groups recognized today appeared during the Triassic (Glasby et al. 2000). In this regard, Vermeij (1987) observed that lugworms (Arenicolidae), which intensely bioturbate sediments by excavating very deep burrows in modern settings, are known from the Triassic onward. Similarly, Ippolitov (2010) studied the diversification patterns of serpulids (calcareous tube-dwelling polychaetes) during the Mesozoic, recording an important increase in the total biodiversity of this group during the Middle to Late Jurassic. Knaust (2010) documented exceptionally preserved soft-bodied organisms together with their trace fossils in a Middle Triassic mud flat. He recorded structures produced by flatworms, nemerteans, nematodes, annelids, arthropods, and mollusks, and concluded that these different taxa were already established in the early Mesozoic (Knaust 2010).

Although the vast majority of the ichnotaxa attributed to worm-like organisms is known since the early Paleozoic (e.g., *Planolites*, *Palaeophycus*, *Cylindrichnus*), other more complex forms seem to have resulted from behavioral innovations associated with the MMR (e.g., *Bornichnus*, *Euflabella*, *Haentzschelinia*, *Lapispira*, *Patagonichnus, Phoebichnus*). Also, some ichnotaxa, albeit known from the Paleozoic, are much more common in post-Paleozoic rocks (e.g., *Macaronichnus*, *Schaubcylindrichnus*). In addition, some ichnogenera are represented by a few ichnospecies in the Paleozoic and then experienced marked increase in morphologic variability, resulting in diversifications at ichnospecific rank. In addition, post-Paleozoic ichnospecies tend to display deeper-tier positions and are morphologically more complex than Paleozoic ones. Good examples include *Asterosoma* and *Teichichnus*. The ichnospecies *A. radiciformis*, *A. ludwigae*, and *A. coxii* are known since the Devonian-Carboniferous, but the Jurassic shows the addition of *A. surlyki*, *A. striata*, and an unnamed ichnospecies referred to by Seilacher (2007) as Tatzelwurm (for discussion on these forms see Chamberlain 1971; Schlirf 2000; Bromley and Uchman 2003, and Seilacher 2007). The ichnospecies *Teichichnus rectus, T. nodosus, T. flexuosus*, and (probably) *T. zigzag* originated in the Paleozoic, whereas *T. sigmoidalis*, *T. spiralis*, and *T. patens* have their earliest representatives in the Mesozoic (for further discussion of these ichnospecies, see Schlirf 2000 and Seilacher 2007).

9.2.2 The Main Groups of Bioeroders

Bioerosion was central to the MMR (Vermeij 1977; Bertling 1999; Perry and Bertling 2000; Taylor and Wilson 2003; Bromley 2004; Wilson 2007). Of particular significance is the role of sponges, gastropods, bivalves, chitons, echinoids, and worms as bioeroders (Wilson 2007). Bryozoans and crustaceans were also important bioerosion players in the MMR. Brachiopods, which typically produce etching structures, were already established bioeroders in the Paleozoic and, therefore, are not treated here. Algae, fungi, and foraminiferans, and cyanobacteria significantly contribute to microbioerosion (Glaub and Vogel 2004; Bromley 2004; Taylor et al. 2015), but the majority of their ichnogenera have a Paleozoic origin (Glaub and Vogel 2004; Bromley 2004). Vertebrates, such as fish and sharks, also were important bioeroders during the MMR, as recorded by bite marks. However, in most cases, these traces have not received ichnotaxonomic treatment. As with burrows, the degree of precision in attribution of individual ichnotaxa to specific bioeroders is variable, with endolithic algae, cyanobacteria, and bryozoans typically leaving distinctive fingerprints and worm-generated structures having a higher level of uncertainty (Bromley 2004). In this section, the most important bioerosion structures produced by these groups of organisms are described (Table 9.2).

Table 9.2 Common bioerosion ichnogenera in shallow-marine post-Paleozoic deposits (see main text for references)

Ichnogenera	Stratigraphic range	Potential producers	Ethology	Trophic type
Belichnus	Oligocene–Recent	Stomatopods	Praedichnia	Predation
Caulostrepsis	Devonian–Recent	Spionid (polydorid) polychaetes	Domichnia	Suspension feeding/predation
Cavernula	Ordovician–Recent	Algae	Domichnia	Photoautotrophy
Centrichnus	Cretaceous–Recent	Anomiid bivalves, balanid cirripeds	Fixichnia	Suspension feeding
Circolites	Jurassic–Recent	Regular echinoids	Domichnia	Grazing
Entobia	Devonian–Recent	Sponges (mostly clionaids)	Domichnia	Suspension feeding
Finichnus	Cretaceous–Recent	Cheilostome bryozoans	Fixichnia	Suspension feeding
Gastrochaenolites	Ordovician–Recent	Bivalves	Domichnia	Suspension feeding
Gnathichnus	Triassic–Recent	Regular echinoids	Pascichnia	Grazing
Helicotaphrichnus	Eocene–Recent	Spionid polychaetes	Domichnia	Commensalism
Meandropolydora	Jurassic–Cretaceous	Spionid polychaetes	Domichnia	Suspension feeding
Oichnus	Ediacaran–Recent	Gastropods (also octopods)	Praedichnia	Predation
Palaeosabella	Ordovician–Recent	Sipunculids and polychaetes	Domichnia	Commensalism
Pennatichnus	Miocene–Recent	Ctenostome bryozoans	Domichnia	Suspension feeding
Petroxestes	Ordovician-Miocene	Mytilid bivalves	Domichnia	Suspension feeding
Radulichnus	Jurassic–Recent	Gastropods and polyplacophorans	Pascichnia	Herbivory
Renichnus	Cretaceous–Recent	Vermetid gastropods	Fixichnia	Suspension feeding
Rhopalia	Carboniferous–Recent	Algae	Domichnia	Photoautotrophy
Rogerella	Devonian–Recent	Acrothoracican cirripeds	Domichnia	Suspension feeding
Ropalonaria	Ordovician–Recent	Ctenostome bryozoans	Domichnia	Suspension feeding
Saccomorpha	Carboniferous–Recent	Fungi or algae	Domichnia	
Spirichnus	Jurassic	Worms	Domichnia	
Stellichnus	Pliocene	Ctenostome bryozoans	Domichnia	Suspension feeding
Talpina	Devonian–Recent	Phoronid pseudocolonies	Domichnia	
Teredolites	Jurassic–Recent	Wood-boring bivalves	Fodinichnia	Herbivory (wood consumption)
Trypanites	Cambrian–Recent	Polychaetes and sipunculids	Domichnia	Suspension feeding/predation

9.2.2.1 Sponges

Sponge borings typically consist of anastomosing channel networks generally forming rounded chambers and commonly displaying diagnostic bioglyphs on the walls (Bromley 1992, 2004). The most common boring produced by sponges is *Entobia*, although other ichnotaxa (e.g., *Clionolithes*, *Clionoides*, *Cicatricula*) have been attributed to the activity of sponges, albeit with variable degrees of certainty (Taylor and Wilson 2003; Bromley 2004; Wilson 2007).

Entobia consists of multi-apertured and multi-chambered borings (Fig. 9.12b, d). It is mostly produced by clionaid sponges, although other groups of modern endolithic sponges, such as those in the Family Adociidae, produce similar structures (Bromley 2004). Traditionally, *Entobia* was thought to range from the Jurassic to Recent (Taylor and Wilson 2003; Bromley 2004), occurring in both shallow- and deep-marine settings, although displaying higher ichnospecies richness in the former (Bromley and D'Alessandro 1990). However, subsequent taxonomic revisions by Tapanila (2006) regarded the Devonian boring *Topsentopsis* as a junior synonym

Fig. 9.12 Bioerosion structures associated with the MMR. (**a**) Cliff conglomerate clast containing deep *Gastrochaenolites* isp., Middle Miocene, Skotniki Quarry, Holy Cross Mountains, Poland; (**b**) *Entobia cracoviensis*, a large chambered sponge boring formed in a Late Cretaceous abrasion platform cut into Upper Jurassic limestone. Upper Cretaceous, Bonarka Quarry, Cracow, Poland; (**c**) *Teredolites clavatus*, Horseshoe Canyon Formation, Upper Cretaceous, near Drumheller, Canada, scale bar is 2 cm; (**d**) *Gastrochaenolites* isp. and *Entobia* isp. preserved as casts on a shell, Rio Negro Formation, Miocene-Pliocene, Argentina

of *Entobia*. Therefore, the ichnospecies *Entobia devonica* is an early representative of this ichnogenus, which reached a peak in ichnospecific diversity as a result of the MMR.

9.2.2.2 Mollusks

Mollusks are well suited for the exploitation of hard substrates, producing both dwelling and grazing structures. The focus here is on bioerosion structures attributed to gastropods and bivalves, although chitons are also known to produce grazing raspings and can collectively be a major source of bioerosion (Bromley et al. 1990; Radley 2010).

Gastropods

Gastropods typically produced predatory borings, such as *Oichnus* (Wisshak et al. 2015) and radulation marks, primarily assigned to *Radulichnus* (Taylor and Wilson 2003; Bromley 2004; Wilson 2007). In addition, they may produce structures that are intermediate between borings and surface scars, representing fixation/anchoring traces or Fixichnia (de Gibert et al. 2004), as illustrated by the ichnogenus *Renichnus*. Gastropods also produce a wide variety of etched and rasped pits and scars on shells, but such marks have not yet received ichnotaxonomic treatment (Bromley 2004; Walker 2007). An extensive analysis of predatory gastropods and their associated structures, most of them still unnamed, is provided by Walker (2007).

Oichnus comprises circular or subcircular borings generated during predation by gastropods (but also octopods; Bromley 1981, 1993; Nielsen and Nielsen 2001; Taylor and Wilson 2003; Wilson 2007; Wisshak et al. 2015). This ichnotaxon is known from the Ediacaran to Recent (Hua et al. 2003; Taylor and Wilson 2003), occurring in both shallow- and deep-marine settings (Bromley 2005).

Radulichnus consists of a series of parallel sets of straight to curving scrape marks produced by the radula of gastropods and chitons (Taylor and Wilson 2003). This ichnogenus is known in shallow-marine settings since the Jurassic (Voigt 1977; Kase et al. 1998).

Renichnus consists of etchings comprising a series of kidney-shaped depressions produced by vermetid gastropods spiraling at an angle to the substrate surface (Mayoral 1987a). It is known in shallow-marine settings from the Pliocene to the Recent (Mayoral 1987a).

Bivalves

As well as being major bioturbators during the MMR, bivalves were also important bioeroders. They produced dwelling structures not only in hardgrounds but also in woodgrounds, as recorded by the ichnogenera *Gastrochaenolites* and *Teredolites*, respectively.

Gastrochaenolites comprises clavate or drop-like trace fossils that are circular to heart-shaped in cross-section, with a narrowed, neck-like upper part in most ichnospecies (Kelly and Bromley 1984; Figs. 9.6d, 9.12a, d). It is interpreted as a dwelling structure produced by suspension-feeding bivalves that commonly bore into rockgrounds, hardgrounds, and corals of shallow-marine environments (especially intertidal to shallow subtidal environments), although they also can occur in firm substrates (Kelly and Bromley 1984; Carmona et al. 2006, 2008). This ichnogenus has been recorded in deposits ranging from the Ordovician to Recent (Pemberton and Frey 1985; Ekdale and Bromley 2001b), but the earliest example confidently attributed to bivalves is from the late Carboniferous (Wilson and Palmer 1998; Taylor and Wilson 2003).

Teredolites consists of straight to clavate-shaped, gregarious, closely spaced borings in wood (Kelly and Bromley 1984; Figs. 9.6i and 9.12c). It is a dwelling structure produced by wood-boring bivalves (Kelly 1988). This ichnogenus ranges from the Jurassic to Recent (Villegas-Martín et al. 2012) and has been described from marginal-marine coal seams and woodgrounds, as well as from transported logs in shallow- and deep-marine environments (Bromley et al. 1984; Buatois and Mángano 1992; Savrda and King 1993).

In addition, the ichnogenus *Petroxestes*, a boring with elongate outline and rounded base, known from the Ordovician (Wilson and Palmer 1988) and the Silurian (Tapanila and Cooper 2002), has been attributed to mytilids. This ichnogenus represents an early example of bivalve bioerosion, significantly predating the MMR and having been recorded also in the Cretaceous (Jagt et al. 2009) and Miocene (Pickerill et al. 2001). The ichnospecies *Centrichnus eccentricus*, an Upper Cretaceous to Recent ichnotaxon, consists of etching scars produced by anomiid bivalves (Bromley 1999).

9.2.2.3 Echinoids

Echinoids also produce bioerosion structures, known from Mesozoic and Cenozoic shells and hardgrounds. Most of these structures consist of a pattern of five radiating grooves that are interpreted as tooth scratches produced by regular echinoids (Bromley 1975).

Gnathichnus is a penta-radiate scrape mark produced by regular echinoids (Bromley 1975, 2004; Taylor and Wilson 2003; Wilson 2007). *Gnathichnus* likely reflects development of the jaw apparatus of regular echinoids (Bromley 1975). It is known from the Triassic to Recent (Bromley 1975; Michalík 1977), occurring in both shallow- and deep-marine settings (Bromley 2005).

Circolites comprises hemispherical pits that have been attributed to regular echinoids (Mikuláš 1992b; Bromley 2004). This ichnogenus ranges from the Jurassic to Recent, occurring in shallow-marine settings (de Gibert et al. 1998a; Bromley 2004).

Ericichnus consists of series of deep and sinuous grooves and has been attributed to regular echinoids (Santos et al. 2015). It is known from a rocky shoreline of the Miocene (Santos et al. 2015).

9.2.2.4 Worms

Several bioerosion structures have been assigned to the activity of "worms," especially borings attributed to polychaetes and sipunculids (Tapanila and Hutchings 2012). They include a wide variety of morphologies from simple borings to branching and spiraled structures. Some of these structures are known since the Paleozoic (e.g., *Caulostrepsis*, *Palaeosabella*, *Trypanites*), whereas others appear to be a product of the MMR (e.g., *Maeandropolydora*) and others appear even later (e.g., *Helicotaphrichnus*). A number of ichnotaxa (e.g., *Lapispecus, Ramosulcichnus*) may be associated with the MMR, but they are only known from their type localities, precluding further inferences; these structures are not discussed here. In addition, the status of some worm ichnotaxa is a matter of debate (Taylor and Wilson 2003; Bromley 2004; Wilson 2007). Finally, some of the ichnotaxa (e.g., *Caulosptrepsis*, *Talpina*) that have their first occurrence in the Paleozoic but only achieve common occurrence from the Mesozoic onward (Bromley 2004; Wilson 2007).

Trypanites consists of unbranched, cylindrical borings (Mägdefrau 1932). Examples from the Ordovician contain scolecodonts within, suggesting that the producers were polychaetes (Kobluk and Nemcsok 1982). Also, short and fat *Trypanites* are known to be made today by sipunculids (Bromley 1978). *Trypanites* occurs since the Cambrian, typically in shallow-marine environments (Taylor and Wilson 2003).

Maeandropolydora consists of sinuous to contorted galleries, having two or more apertures (Voigt 1965; Bromley and D'Alessandro 1983; Taylor and Wilson 2003) and was probably produced by spionid polychaetes (Santos et al. 2003a). It is known since the Cretaceous (Taylor and Wilson 2003), occurring in both shallow- and deep-marine settings (Bromley 2005).

Caulostrepsis consists of a vertical gallery slightly bent to a U-shaped tube, constituting an overall pouch- or ear-shaped structure, which can be even more complex by the development of lobes (Bromley and D'Alessandro 1983). It has been attributed to the activity of spionid (polydorid) polychaetes and is known since the Devonian (Taylor and Wilson 2003), occurring in both shallow- and deep-marine settings (Bromley 2005).

Palaeosabella comprises long, tubular borings that expand distally (Bromley 2004). This structure is attributed to sipunculids, which make similar bioerosion structures today (Rice 1969). *Palaeosabella* has been regarded as a junior synonym of *Clionoides* (Furlong and McRoberts 2014). However, *Palaeosabella* is mostly an unbranched boring, whereas *Clionoides* is branched, forming complex three-dimensional networks (Wilson 2007). This ichnotaxon is known since the Ordovician (Bromley 2004), occurring in both shallow- and deep-marine settings (Bromley 2005).

Talpina consists of curved and branching tunnels produced by phoronid pseudocolonies (Voigt 1972, 1978). It ranges from the Devonian to Recent (Rodrigues and Gutschick 1970), occurring in both shallow- and deep-marine settings (Bromley 2005).

Helicotaphrichnus is a helicoidal boring made in the columella of gastropod shells occupied by hermit crabs (Kern et al. 1974). This ichnogenus is attributed to spionid worms living in a commensal relationship with hermit crabs (Walker 1992). It occurs in shallow-marine settings and ranges from the Eocene to the Recent (Walker 1992).

Spirichnus is a cylindrical spiral boring that branches at regular intervals (Fürsich et al. 1994). Although attributed to worms (Bromley 2004), no further details regarding its affinities are known. It has only been recorded in Jurassic shallow-marine settings (Fürsich et al. 1994; Bertling and Insalaco 1998).

Cunctichnus is a cylindrical boring with tapering side branches that occurs on shells (Fürsich et al. 1994; Donovan et al. 2015). It has been attributed to sipunculids (Fürsich et al. 1994). *Cunctichnus* is present in shallow-marine settings and ranges from the Jurassic to the Cretaceous (Donovan et al. 2015). However, doubts persist regarding its taxonomic validity, and some authors have argued in favor of synonymization with *Vermiforichnus*, which is known since the Devonian (Taylor and Wilson 2003).

9.2.2.5 Bryozoans

Bryozoans are important bioeroders, although taxonomic issues (e.g., the fact that some bryozoan biotaxa are erected based on their borings) complicate further evaluation of their significance as players during the MMR (Bromley 2004; Wilson 2007). *Finichnus* (a senior synonym of *Leptichnus*; Taylor et al. 2013), arguably the most widespread bryozoan ichnotaxon linked to the MMR, comprises surficial etchings produced by cheilostome bryozoans (Taylor et al. 1999; Rosso 2008). It ranges from the Cretaceous to Recent. *Stellichnus* and *Pennatichnus* have been attributed to ctenostome bryozoans, but these forms have only been reported from the Pliocene (Mayoral 1987b, 1988; Mayoral and Reguant 1995). *Ropalonaria*, ramifying tunnels that may have been produced by ctenostome bryozoans, is known since the Ordovician, although some of its ichnospecies may have originated during the late Mesozoic (Taylor and Wilson 2003; Bromley 2004).

9.2.2.6 Crustaceans

Crustaceans, major bioturbators of the MMR, are also important bioeroders. Bioerosion structures are produced by acrothoracican and ascothoracican cirripeds, brachyuran crabs, stomatopods, and thalassinideans (Seilacher 1969; Radwański 1977; Walker 1992; Taylor and Wilson 2003; Bromley 2004). Verrucid cirripeds produce etching scars (Bromley and Martinell 1991). These are represented by the ichnospecies *Centrichnus concentricus*, which is known from the Miocene to Recent (Radwański 1977; Bromley and Martinell 1991). *Rogerella*, a pouch-shaped boring produced by acrothoracican barnacles, is known from the Devonian, but is definitely more abundant since the Mesozoic (Taylor and Wilson 2003; Bromley 2004). Ascothoracican borings are known since the Cretaceous, but have not received proper ichnotaxonomic treatment (Bromley 2004). Shell chipping and peeling are commonly performed by decapod crustaceans, particularly brachyuran crabs (Alexander and Dietl 2003). Although chipping and peeling have been known to occur prior to the MMR, these activities are particularly common since the late Mesozoic and are an innovation of the MMR (Huntley and Kowalewski 2007). Some of the resulting structures have been recently included in the new ichnogenus *Caedichnus* (Stafford et al. 2015). Brachyuran crabs experienced a rapid diversification during the Late Jurassic (Klompmaker et al. 2013). Branching borings in corals produced by thalassinideans are common, but have not received ichnotaxonomic treatment yet (Bromley 2004). *Belichnus*, representing predatory holes produced by blows struck by stomatopods, is known since the Oligocene (David 1997). However, the finding that similar structures may be produced by sea gulls provides a cautionary note (Cadée and de Wolf 2013)

9.2.2.7 Algae

Endolithic, photoautotrophic organisms, such as algae, are responsible for a wide variety of microbioerosion ichnotaxa, but most of them are known since the Paleozoic (Bromley 2004; Glaub and Vogel 2004; Wisshak 2012). One exception is *Eurygonum*, interpreted as produced by chlorophytes, which is known since the Triassic (Wisshak et al 2005).

9.2.2.8 Fungi

A few microbioerosion ichnotaxa have been attributed to fungi. In particular, the ichnogenera *Saccomorpha* and *Orthogonum* seem to be relatively abundant (Schmidt 1992; Wisshak 2012). Although the possibility of an algal producer cannot be disregarded for *Saccomorpha* (Glaub and Vogel 2004), recent detailed analysis reinforces the idea of a fungal origin (Golubic et al. 2014). In any case, the earliest representatives of these ichnogenera are Ordovician, whereas some ichnospecies (e.g., *S. sphaerula*) seem to have originated in the Cenozoic (Wisshak 2012).

9.2.2.9 Foraminifera

Foraminifera are known to produce borings of various morphologies, such as horseshoe-shapes or rosettes (Bromley 2004; Bromley et al. 2007). Rosetted and fan-shaped microbioerosion structures have been included in the Ichnofamily Dendrinidae by Bromley et al. (2007). Of these, the ichnogenus *Semidendrina* has been attributed to foraminifera and ranges in age from the Carboniferous to the

Recent (Bromley et al. 2007). However, this ichnogenus is most likely a junior synonym of *Nododendrina* (M. Wisshak, written communication 2015). At present, any connection between bioeroding foraminiferans and the MMR is unclear.

9.3 Ichnofaunal Composition, Infaunalization, and Tiering Structure: Patterns Developed During the Mesozoic Marine Revolution

The MMR strongly shaped the nature of animal–substrate interactions in the post-Paleozoic world. Because trace fossils provide direct evidence of colonization of infaunal ecospace, they represent useful tools to evaluate the degree of infaunalization and complexity of tiering structure manifested during the MMR. In this regard, comparing tiering structure and ichnoguilds through the Mesozoic and Cenozoic may help to answer the question of whether or not the exploitation of deep infaunal ecospace that characterizes the MMR was an abrupt or a protracted event (Thayer 1983; Bambach 1983). Within the bioturbated zone of soft sediments, two different intervals are distinguished. The mixed layer occurs just beneath the sediment surface and has a homogeneous appearance, whereas distinct burrows (trace fossils) are formed within the transitional layer that lies below (Berger et al. 1979). Benthic faunas from marginal-marine, brackish-water environments are affected by a number of stress factors (e.g., dilution of normal-marine salinities) and, therefore, their ichnologic record may reflect departures from that of the archetypal, fully marine ichnofaunas (Pemberton and Wightman 1992; MacEachern and Pemberton 1994; MacEachern et al. 2007; Buatois and Mángano 2011) and will be addressed elsewhere (see Sect. 9.5). In this section, the focus is on innovations involving trace-making organisms and trace fossils that took place in open, shallow- and normal-marine environments.

The timing of the MMR is a controversial issue. Central to this evolutionary breakthrough is the replacement of brachiopod-dominated faunas to those dominated by mollusks, which involved a change from primarily sedentary, epifaunal suspension feeding to mobile suspension feeding and deposit feeding, with increased predation (Wagner et al. 2006; Leighton et al. 2013). Certainly, this faunal turnover started by the late Paleozoic when many groups of bivalves and gastropods, which were previously dominant in nearshore settings, moved seaward to become part of mixed brachiopod-mollusk communities in offshore environments (Sepkoski and Miller 1985; Jablonski and Bottjer 1990; Olszewski and Patzkowsky 2001). However, other major players in the MMR, such as decapod crustaceans and irregular echinoids, became dominant or appeared for the first time during the Jurassic. From the perspective of bioerosion structures, an increase in diversity for macroborings occurred by the Devonian (Wilson 2007). Some bioerosion ichnotaxa that appeared for the first time by the middle Paleozoic, such as *Rogerella*, *Caulostrepsis,* and *Talpina*, became dominant later in the Phanerozoic (Bromley 2004; Wilson

2007). Signor and Brett (1984) noted that a rapid radiation of durophagous predators also took place during the Devonian, and they considered this diversification event as a precursor of the MMR. However, the middle Paleozoic diversification of bioeroders seems to be a distinct episode, whose link with the subsequent MMR is tenuous at best.

9.3.1 The Triassic: Setting the Stage for the Mesozoic Marine Revolution

The Triassic seems to represent a pivotal point in the ecology of shallow-marine environments, being bracketed by two major mass extinctions. Unsurprisingly, ichnologic information from the Triassic is biased toward the aftermath of the end-Permian mass extinction and subsequent marine fauna recovery (see Chap. 7). To a lesser extent, other ichnologic studies have focused on the end-Triassic mass extinction (see Chap. 8). Ichnofaunas from the lowermost Triassic, reflecting benthic conditions during the immediate post-extinction aftermath, are typically monospecific and consist of trace-fossil specimens that are smaller than normal and attributed to opportunistic tracemaker organisms. During the rest of the Early Triassic, there is evidence of recovery, as suggested by an increase in ichnodiversity, burrow size, and depth of bioturbation (Twitchett and Barras 2004; see Chap. 7).

From an ichnologic perspective, some of the most thoroughly studied Middle to Upper Triassic units are the Muschelkalk and Keuper of Europe (e.g., Pérez-López 1997; Knaust 1998, 2002, 2007, 2008; Knaust and Costamagna 2012; Chrząstek 2013). These studies offer a glimpse of animal–substrate interactions between the two mass extinction events and, therefore, need to be treated in detail. In particular, a comprehensive study by Knaust (2007) provided detailed documentation of the ichnology of Muschelkalk carbonates in Germany. Forty ichnospecies (and 24 ichnogenera) were identified and described, pointing to a high-diversity community. This is particularly remarkable given the restricted environmental conditions that controlled deposition of the Muschelkalk carbonates. Both bioturbation and bioerosion structures are present. The former are dominated by trace fossils produced by decapod crustaceans (e.g., *Pholeus*, *Rhizocorallium*, *Thalassinoides*), worm-like organisms (possibly *Balanoglossites*, *Arachnostega*, and *Zoophycos*), actinarians (*Bergaueria*), and bivalves (*Lockeia*, *Protovirgularia*), among other groups. The presence of trace fossils interpreted as being produced by meiobenthos also was indicated (*Cochlichnus*, *Helminthopsis*, *Helminthoidichnites*). Among the bioerosion structures (*Caulostrepsis*, *Maeandropolydora*, *Palaeosabella*, *Trypanites*), polychaetes or sipunculans are the most likely tracemakers, although bivalve borings (*Gastrochaenolites*) also have been recognized.

Tiering structure remained quite simple, but it is unclear if this was due to evolutionary or environmental constraints. A remarkably similar ichnofauna to that of the Muschelkalk in Germany has been recently documented for coeval strata in Poland, which is thought to have been deposited in a shallow, storm-affected carbonate ramp setting that is located within the same basin, but closer to the gateway to the Tethys Ocean (Chrząstek 2013). The Polish ichnofauna consists of *Archaeonassa*, *Balanoglossites*, *Gastrochaenolites*, *Lockeia*, *Palaeophycus, Planolites*, *Protovirgularia*, *Rhizocorallium, Skolithos*, *Thalassinoides*, and *Trypanites* (Chrząstek 2013). A similar ichnofauna to those of Germany and Poland, albeit with lower diversities, also has been recorded from Middle to Upper Triassic carbonates of Sardinia (Knaust and Costamagna 2012).

With respect to Triassic shallow-marine clastics, a detailed study on the ichnology of a transgressive–regressive deltaic succession of the Bravaisberget Formation in Svalbard (Mørk and Bromley 2008) provided valuable information to compare with the emerging picture based on carbonate ichnology. The tiering structure consists essentially of three levels: a shallow tier dominated by *Taenidium* and *Rhizocorallium*, a middle tier consisting of *Thalassinoides*, and a deeper tier represented by *Chondrites*, which may occur as reburrowing of *Thalassinoides* fills; *Polykladichnus* seems to have been associated with a late colonization event. Overall ichnodiversity levels are moderate, and the tiering structure is quite simple. As in the case of the Muschelkalk, discriminating between environmental constraints (e.g., salinity dilution, oxygen fluctuations) and evolutionary factors is not straightforward. The fact that the tiers are interpreted as representing a succession of community replacements caused by an unstable environmental regime, rather than a single stable community (Mørk and Bromley 2008), supports the former possibility.

Despite some caveats, the emerging picture for the end-Triassic mass extinction is also one of decreasing ichnodiversity, degree of bioturbation, and burrow size (see Chap. 8). For example, the lower "Pre-*Planorbis* Beds" (uppermost Triassic) of the Blue Lias Formation record low ichnotaxonomic diversity, low bioturbation intensity, small burrow diameters, and an absence of deep-tier bioturbation, reflecting the impact of the end-Triassic mass extinction (Barras and Twitchett 2007).

With regard to bioerosion, the bioeroders typical of modern reefs, such as endolithic bivalves or clionaid sponges, were uncommon to absent prior to the Late Triassic (Bertling 1999). By the Late Triassic, boring bivalves exhibited increased size and abundance, accompanied by an increased importance of sponges (Perry and Bertling 2000; Tapanila and Hutchings 2012). Although the Triassic witnessed the appearance of some ichnotaxa (e.g., *Gnathichnus*) that were destined to become dominant later, these ichnotaxa were relatively uncommon prior to the onset of the MMR (Taylor and Wilson 2003; Bromley 2004).

Regarding microborings, although earlier studies suggested an early Mesozoic radiation (Glaub and Vogel 2004), the subsequent finding of a superbly preserved Carboniferous ichnocoenosis indicates that Carboniferous microendolith communities were "modern" in aspect (Wisshak et al. 2006). In fact, Mesozoic ichnodiversity levels are similar to those of the Carboniferous (Wisshak et al. 2006).

Many Paleozoic predators became extinct by the end of the Permian, with few groups surviving; however, some predators rebounded rapidly after the end-Permian mass extinction (Walker and Brett 2002). According to these authors, during the Middle Triassic, a number of new predator guilds appeared; these include lobsters having appendages indicative of durophagy. However, an increase in diversity of predator decapods took place later in the Late Cretaceous (Schweitzer and Feldmann 2010). Also, some durophagous marine reptiles, boney fish, and sharks may have been active predators since the Triassic (Cuny and Benton 1999; Neenan et al. 2013; Brachaniec et al. 2015). In contrast, the sparse record of shell boreholes may indicate that drilling predation was limited during the Triassic (Kowalewski et al. 1998; Walker and Brett 2002). Also, the overall frequency of shell repair is quite low during the Triassic (Vermeij et al. 1981; Walker and Brett 2002; Alexander and Dietl 2003).

Overall, sparse ichnologic information from the Triassic precludes generalizations. However, data from the Muschelkalk seem to suggest that by the Middle Triassic, full recovery from the end-Permian mass extinction had taken place in equatorial carbonate settings, particularly with respect to diversity levels (Knaust 2007), although refugia may have been present (Wetzel et al. 2007). Nonetheless, Triassic ichnofaunas show limited infaunalization and relatively simple tiering structure, particularly in clastic environments (e.g., Mørk and Bromley 2008). Accordingly, the evidence from bioturbation and macrobioerosion structures reviewed here seem to suggest that the Triassic is better regarded as a prelude to the MMR, rather than part of this evolutionary breakthrough. However, ichnologic information indicates that a few of the key players of this major evolutionary event, particularly decapod crustaceans, were already dominant in carbonate settings by the Middle to Late Triassic.

9.3.2 The Jurassic: Onset of the Mesozoic Marine Revolution

Recovery from the end-Triassic mass extinction is characterized by a gradual increase in burrow size and the reappearance of deep-tier trace fossils, suggesting the return to “normal” environmental conditions by the end of the Hettangian (see Chap. 8; Barras and Twitchett 2007). In fact, an 8 % increase in global ichnodiversity has been recorded in marine environments for the Early Jurassic (see Chap. 16). The Lower to Middle Jurassic Plover Formation of the northwest Australia shelf is a critical stratigraphic unit for assessing the degree of infaunalization and tiering complexity at the onset of the MMR because it contains intensely bioturbated marine deposits (Buatois et al. 2013; Burns et al. 2013). In particular, shelf, offshore, and shoreface deposits of Sinemurian to Aalenian age reveal quite complex tiering patterns along the depositional profile (Fig. 9.13). For example, upper-offshore mudstones of this unit are typically intensely bioturbated (BI 5–6), with some intervals locally showing moderate levels of reworking (BI 3–4). The upper-offshore ichnofauna consists of very shallow-tier *Planolites montanus,* shallow-tier *Asterosoma* isp., mid-tier *Thalassinoides* isp., *Palaeophycus tubularis*, *P. heberti*, *Cylindrichnus concentricus*, *Rosselia socialis*, *Schaubcylindrichnus*

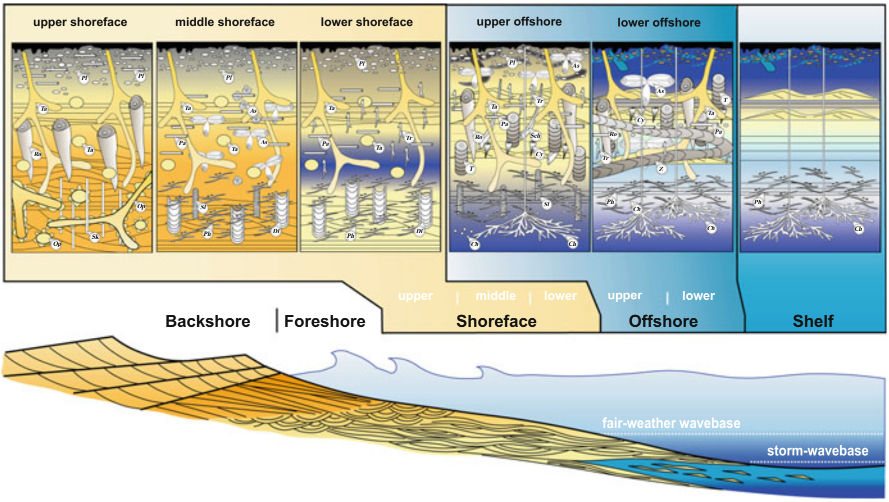

Fig. 9.13 Tiering structure along the depositional profile of a Lower to Middle Jurassic wave-dominated shallow-marine platform, Plover Formation of the northwest Australia shelf

coronus, Teichichnus rectus, and *Siphonichnus eccacensis*, and deep-tier *Chondrites* isp. and *Phycosiphon incertum* (Fig. 9.14a–f). From an ichnoguild perspective, seven are recognized: the *Planolites* ichnoguild (vagile, deposit-feeding, very shallow tier), the *Asterosoma* ichnoguild (semi-vagile, deposit-feeding, shallow tier), the *Cylindrichnus-Rosselia* ichnoguild (semi-vagile, deposit- to detritus-feeding, mid-tier), the *Palaeophycus-Schaubcylindrichnus* ichnoguild (vagile, suspension- to deposit-feeding, mid-tier), the *Teichichnus* ichnoguild (vagile, deposit-feeding, mid-tier), the *Siphonichnus* ichnoguild (permanent, suspension-feeding, mid-tier), and the *Phycosiphon-Chondrites* ichnoguild (vagile, deposit-feeding to chemosymbiont, deep-tier).

The Sinemurian-Toarcian Neill Klinter Formation of Greenland is another important unit to evaluate the onset of the MMR. Although no tiering analysis is available from this unit, ichnologic studies by Dam (1990a, b) showed relatively high-diversity assemblages in upper-offshore deposits, including dwelling (*Arenicolites* isp., *Diplocraterion parallelum, Ophiomorpha nodosa, Palaeophycus* isp., *Thalassinoides* isp.), locomotion (*Cruziana* isp., *Curvolithus simplex, Gyrochorte comosa*), and feeding (*Planolites beverleyensis, Rhizocorallium irregulare, Taenidium serpentinum*) structures. Similar ichnofaunas are known in shallow-marine storm-affected deposits of the Lower to Middle Jurassic Bardas Blancas Formation of Argentina (Bressan and Palma 2009).

Middle Jurassic shallow-marine ichnofaunas are particularly abundant in India, where a number of studies have been made (e.g., Chiplonkar and Badve 1970; Chiplonkar and Ghare 1975; Badve and Ghare 1978; Badve 1987; Fürsich 1998; Sudan et al. 2000; Patel et al. 2008, 2014; Desai et al. 2008; Srivastava et al. 2010;

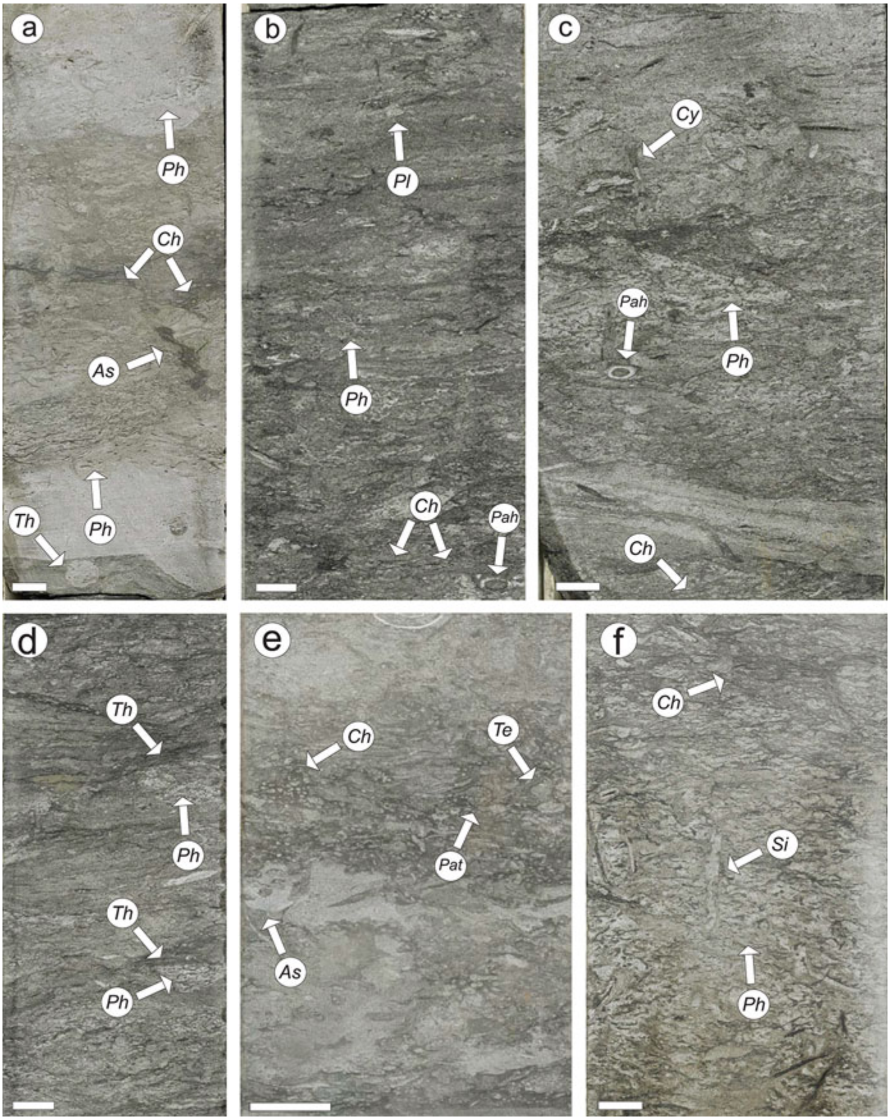

Fig. 9.14 Ichnofaunas from upper-offshore deposits of the Lower to Middle Jurassic Plover Formation of the northwest Australia shelf. (**a**) Shallow-tier *Asterosoma* isp. (*As*), mid-tier *Thalassinoides* isp. (*Th*), and deep-tier *Chondrites* isp. (*Ch*) and *Phycosiphon incertum (Ph)*; (**b**) very shallow-tier *Planolites montanus* (*Pl*)*,* mid-tier *Palaeophycus heberti* (*Pah*), and deep-tier *Chondrites* isp. (*Ch*) and *Phycosiphon incertum (Ph)*; (**c**) mid-tier *Palaeophycus heberti* (*Pah*) and *Cylindrichnus concentricus (Cy*), and deep-tier *Chondrites* isp. (*Ch*) and *Phycosiphon incertum (Ph)*; (**d**) mid-tier *Thalassinoides* isp. (*Th*) reworked by deep-tier *Phycosiphon incertum (Ph)*; (**e**) Shallow-tier *Asterosoma* isp. (*As*), mid-tier *Palaeophycus heberti* (*Pah*) and *Teichichnus rectus*, and deep-tier *Chondrites* isp.; (**f**) mid-tier *Siphonichnus eccacensis* (*Si*), and deep-tier *Chondrites* isp. (*Ch*) and *Phycosiphon incertum (Ph)*. All scale bars are 1 cm

Joseph et al 2012; Gurav et al. 2014). With the exception of Desai et al. (2008), these studies have focused on the broader characteristics of these ichnofaunas, rather than tiering analysis. In any case, the available ichnologic information indicates high diversity levels in fully marine environments, suggesting a continuation of the trends displayed in the Early Jurassic. High-diversity levels also have been noted for the Middle Jurassic Vardekløft Formation of Greenland (Heinberg and Birkelund 1984; Fig. 9.15a–d). Relatively diverse ichnofaunas are also known from the deltaic deposits of the Middle Jurassic Lajas Formation of Argentina (McIlroy 2007 and Fig. 9.16a–d herein). In particular, offshore deposits were intensely bioturbated, but lack of lithologic contrast prevented recognition of discrete trace fossils (McIlroy 2007). These deposits pass upward into delta-front deposits containing various ichnotaxa. The ichnogenus *Haentzschelinia* (Fig. 9.16c) is present in some of these deposits together with crustacean burrows (*Ophiomorpha*, *Thalassinoides*), among other forms, such as *Asteriacites* (Fig. 9.16a), *Phycosiphon* (Fig. 9.16b), and *Rhizocorallium* (Fig. 9.16d) (McIlroy 2007; Canale et al. 2015). Although the unit has been interpreted as having been deposited in a tide-dominated delta (McIlroy 2007), recent observations indicate a greater fluvial dominance than previously recognized (Canale et al. 2015).

Another Middle Jurassic unit interpreted as having formed in a tide-dominated delta is the Ile Formation of offshore Norway (McIlroy 2004). Moderate ichnodiver-

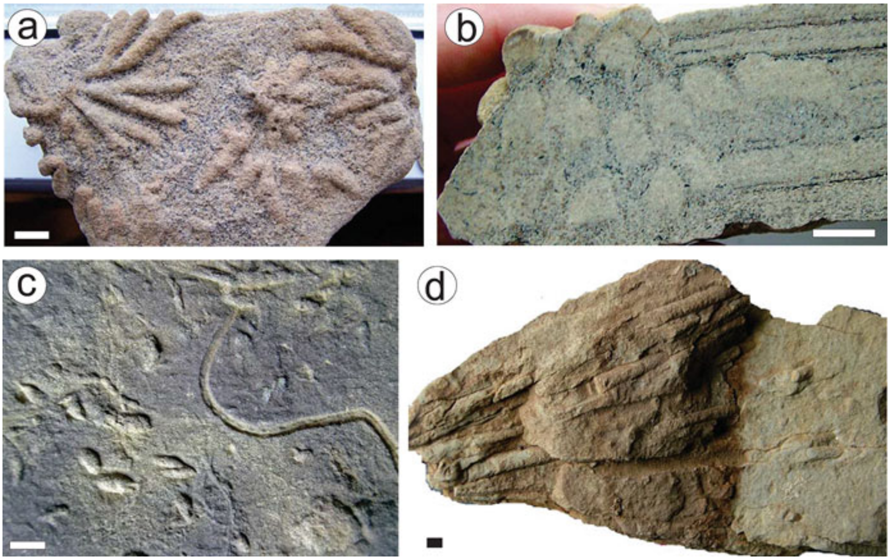

Fig. 9.15 Characteristic trace fossils from Lower to Middle Jurassic shallow-marine deposits of Greenland. (**a**) *Haentzschelinia ottoi* in bedding-plane view, unknown unit; (**b**) *Haentzschelinia ottoi* in cross-section view, unknown unit; (**c**) *Gyrochorte comosa* and *Lockeia amygdaloides*, Middle Jurassic, Vardekløft Formation, Jameson Land; (**d**) *Phoebichnus trochoides*, Lower Jurassic, Neill Klinter Formation, Jameson Land. All scale bars are 1 cm

Fig. 9.16 Characteristic trace fossils from the Middle Jurassic Lajas Formation of Argentina. (**a**) *Asteriacites lumbricalis* in cross section view, scale bar is 1 cm; (**b**) *Phycosiphon incertum* in cross-section view, scale bar is 1 cm; (**c**) *Haentzschelinia ottoi* in bedding-plane view; (**d**) *Rhizocorallium* isp. in bedding-plane view

sity was recorded in the associated offshore facies, where *Phycosiphon*, *Phoebichnus*, *Schaubcylindrichnus*, *Palaeophycus,* and *Thalassinoides* are present. *Gyrochorte*, otherwise a common ichnogenus in the Jurassic, is only abundant in the mouth-bar facies, whereas archetypal crustacean burrows, such as *Thalassinoides* and *Ophiomorpha,* occur in a wider spectrum of subenvironments (McIlroy 2004).

Available information indicates that by the Early to Middle Jurassic, shallow-marine settings were host to diverse infaunal communities displaying complex tiering patterns. Tiering and ichnoguild analysis reveals colonization of shallow-, mid-, and deep-tiers by detritus, deposit and suspension feeders, as well as predators and chemosymbionts. However, ichnodiversity per tier may be regarded as moderate. Intensity of bioturbation commonly was conducive to total reworking of fine-grained sediments, indicating the presence of efficient bioturbators.

The trends established during the Early to Middle Jurassic continued into the Late Jurassic. Burrowing innovations are reflected by the appearance of crab burrows, as recorded by the earliest occurrences of *Psilonichnus* (Fürsich 1981) and *Macanopsis* (Neto de Carvalho et al. 2010) in coastal deposits of Portugal. From an ichnofacies perspective, this represents the appearance of the *Psilonichnus* Ichnofacies, which characterizes transitional settings, typically backshore areas, washover fans, coastal dunes, and supratidal flats (Frey and Pemberton 1987; Curran and White 1991; Buatois and Mángano 2011).

Upper Jurassic fully marine ichnofaunas have been documented in detail from the North Sea (Fig. 9.17a–g). Typical elements of these Upper Jurassic deposits are *Ophiomorpha*, *Skolithos*, *Diplocraterion* (Fig. 9.17g), *Cylindrichnus*, *Schaubcylindrichnus*, *Siphonichnus*, *Palaeophycus*, *Planolites*, *Asterosoma* (Fig. 9.17a–b), *Phoebichnus* (Fig. 9.17c–e), *Teichichnus* (Fig. 9.17f), *Phycosiphon,* and *Chondrites* (Martin and Pollard 1996; Goldring et al. 1991, 2005; Baniak et al. 2014). In particular, the Fulmar Formation of England contains intensely bioturbated ichnofabrics that have been the focus of a number of studies (Taylor and Gawthorpe 1993; Martin and Pollard 1996; Goldring et al. 1991, 2005). Pervasively bioturbated Upper Jurassic shallow-marine deposits also have been recently described from the Ula Formation of Norway (Baniak et al. 2014). In particular, the offshore deposits of the Fulmar and Ula formations are remarkably similar to those described from Lower Jurassic counterparts. For example, the ichnotaxonomic composition of the upper-offshore deposits of the Ula Formation is almost identical to that of the upper-offshore deposits of the Lower to Middle Jurassic Plover Formation previously described. Although no information on tiering structure has been provided for the Ula Formation, the available illustrations seem to indicate a four-tier structure resembling that of the Plover Formation. A similar picture emerges from deposits in the Fulmar Formation (e.g., Martin and Pollard 1996). Ichnologic comparison of similar offshore deposits through the Jurassic indicates that the main evolutionary innovations in these fully marine siliciclastic settings took place in the Early Jurassic and persisted for the remainder of the period and, as will be described, continued into the Cretaceous.

Jurassic nearshore sands were host to mid- to deep-tier infaunal communities (e.g., Heinberg and Birkelund 1984; Dam 1990b; Buatois et al. 2013; Burns et al. 2013; Baniak et al. 2014). Crustacean burrows, such as *Ophiomorpha*, become dominant particularly in middle- to upper-shoreface settings. In fact, *Ophiomorpha* replaced *Skolithos* as the dominant component of the *Skolithos* ichnofacies in post-Paleozoic strata (Droser and Bottjer 1993). The Sinemurian-Toarcian Neill Klinter Formation of East Greenland contains extensive *Ophiomorpha* systems in strongly storm-affected lower-shoreface deposits (Dam 1990b). This occurrence reveals that an *Ophiomorpha* ichnoguild was already present in high-energy nearshore settings by the Early Jurassic, revealing the establishment of a deep-tier malacostracan guild. In addition to *Ophiomorpha*, relatively high-energy nearshore deposits are characterized by deep-tier *Diplocraterion habichi*, which may reach up to 1 m below the sediment-water interface. Because these structures can occur with high densities, *Diplocraterion habichi* ichnofabrics may be regarded as a post-Paleozoic equivalent of *Skolithos* pipe rock. Under slightly lower-energy conditions, most typically in the lower shoreface, other ichnotaxa, such as *Rosselia*, *Teichichnus*, *Asterosoma,* and *Rhizocorallium*, may become common as well (Ager and Walace 1970; Schlirf 2000, 2003).

Also, by the Jurassic, oxygen-depleted ichnofaunas of modern aspect appear to have become well established (Savrda and Bottjer 1989; Wignall 1991; Etter 1995;

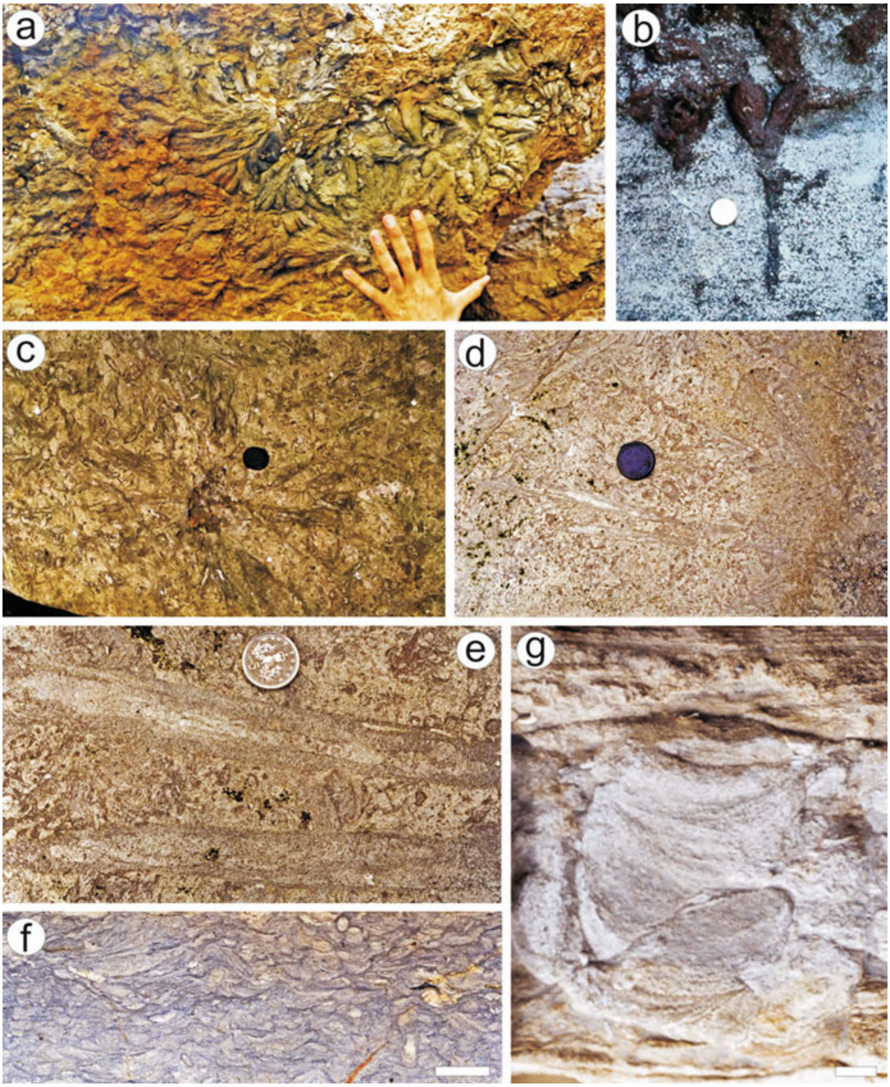

Fig. 9.17 Characteristic trace fossils from Lower to Middle Jurassic shallow-marine deposits of the Yorkshire coast, northeast England**.** (**a**) *Asterosoma* isp. in bedding-plane view, Middle Jurassic, Hundale Sandstone Member, Scarborough Formation, Hundale Point; (**b**) *Asterosoma* isp. in cross-section view, Middle Jurassic, Hundale Sandstone Member, Scarborough Formation, Hundale Point; (**c**) *Phoebichnus trochoides*, Middle Jurassic, Helwath Beck Member, Scarborough Formation, Cloughton Bay; (**d**) *Phoebichnus trochoides*, Lower Jurassic, Blea Wyke Sandstone, Blea Wyke Point; (**e**) Close-up of one of the radial branches shown in (d) to illustrate complex backfilling; (**f**) *Teichichnus rectus*, Middle Jurassic, Gristhorpe Member, Scarborough Formation, Yon's Nab; (**g**) *Diplocraterion parallelum*, Lower Jurassic, Staithes Sandstone Formation, Staithes Harbour. Scale bars are 1 cm, lens cap diameter is 5.5 cm, and coin is 1.8 cm

Monaco 1994, 1995; Komatsu et al. 2001; Olóriz and Rodríguez-Tovar 2002; Uchman et al. 2003; Leonowicz 2012; Šimo and Tomašových 2013). Study of these ichnofaunas has been favored by past occurrences of various anoxic events, which have been particularly widespread in the European portion of the Tethys. Essentially, all the basic aspects of the model of oxygen-related ichnocoenoses (ORI) put forward by Savrda and Bottjer (1986, 1987, 1991) in their seminal papers were in place by the Jurassic. These include a decrease in ichnodiversity, burrow diameter, and burrowing depth in concert with decreasing oxygen content. According to this model, structures emplaced in deep tiers in oxygenated sediments tend to move upward as a response to the upward migration of the redox discontinuity under dysoxic conditions. *Chondrites* generally has been regarded as the trace-fossil form most tolerant to lowered oxygen content of bottom waters, showing diminished size and shallow-tier positions under extreme oxygen depletion (Bromley and Ekdale 1984a).

Shallow-marine carbonate ichnofabrics tend to be dominated by crustacean burrows, such as *Thalassinoides* (Fig. 9.18a–b) and *Ophiomorpha* (Monaco and Garassino 2001; Monaco and Giannetti 2002; Giannetti and Monaco 2004; Goldring et al. 2005; Neto de Carvalho et al. 2010). The latter commonly form nodular limestones, a fabric in which crustacean burrows serve as nuclei for $CaCO_3$ precipitation (Fürsich 1972; Fig. 9.18a). Other ichnogenera common in Jurassic shallow-marine carbonates include *Rhizocorallium* (Fig. 9.18c–d), *Diplocraterion* (Fig. 9.18e), *Phymatoderma* (Fig. 9.18f), *Chondrites* (Fig. 9.18g), and *Cylindrichnus* (Fürsich 1974, 1975; Monaco et al. 1996; Monaco 2002; Goldring et al. 2005; García-Ramos et al. 2011; Rodríguez-Tovar et al. 2012). As in the case of clastic settings, trace-fossil assemblages in shallow-marine carbonates tend to reflect an energy gradient along the depositional profile, with dwelling structures commonly, but not exclusively, produced by suspension feeders (e.g., *Diplocraterion*, *Arenicolites*, *Ophiomorpha*) occupying high-energy proximal areas, monospecific suites of *Teichichnus* in protected lagoonal deposits, and a wider variety of ethologies and trophic types (e.g., *Rhizocorallium*, *Chondrites*, *Planolites*, *Thalassinoides, Cylindrichnus*) present in distal, low-energy shelf deposits, as documented in Upper Jurassic carbonates of England and France (Fürsich 1974, 1975).

Similar studies in the Upper Jurassic of Saudi Arabia also show comparable proximal-distal trends in an unrestricted carbonate shelf, displaying high ichnodiversities in distalmost mudstone facies (Goldring et al. 2005). These authors noted the dominance of deep-tier *Cylindrichnus* typically cross-cutting shallow- to mid-tier ichnotaxa, such as *Planolites*, *Rhizocorallium,* and *Chondrites*. In fact, Goldring et al. (2005) noted a close correspondence between ichnofaunas from siliciclastics of the Upper Jurassic Fulmar Formation of the North Sea and carbonates from the roughly coeval Jubaila Formation of Saudi Arabia. The tiering structure of infaunal communities in storm-affected carbonate platforms has been documented in the Jurassic of Italy by Monaco et al. (1996) and Monaco (2002), who identified four tiers: a shallow-tier *Thalassinoides*, a shallow-tier *Planolites-Palaeophycus*, a

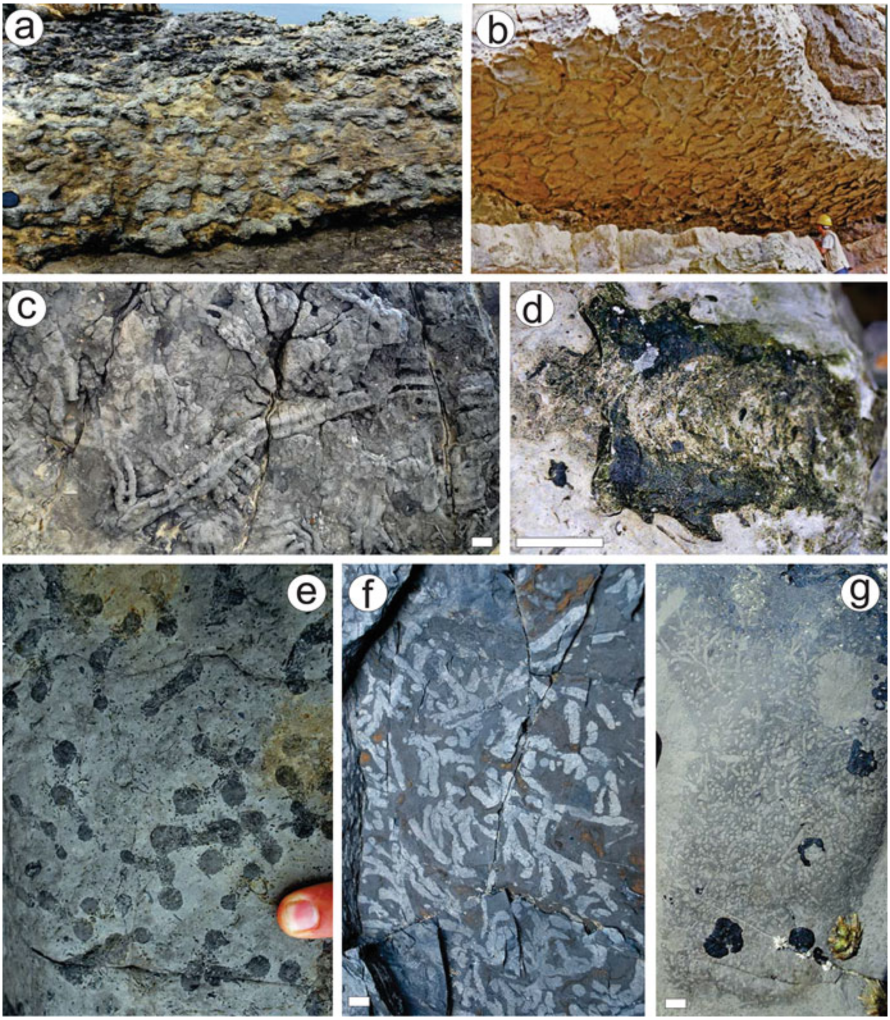

Fig. 9.18 Characteristic trace fossils from Jurassic carbonates. (**a**) *Thalassinoides* nodular limestone, Upper Jurassic, Coralline Oolite Formation, Carr Naze, England, lens cap diameter is 5.5 cm; (**b**) Extensive networks of *Thalassinoides suevicus*, Upper Jurassic, Coralline Oolite Formation, Carr Naze; (**c**) *Rhizocorallium jenense jenense*, Lower Jurassic, Buerres Member, Rodiles Formation, Punta Rodiles, Asturias, northern Spain, scale bar is 1 cm; (**d**) *Rhizocorallium jenense spinosus*, Lower Jurassic, Buerres Member, Rodiles Formation, Punta Rodiles, Asturias, northern Spain, scale bar is 1 cm; (**e**) *Diplocraterion parallelum* in bedding-plane view, Lower Jurassic, Buerres Member, Rodiles Formation, Punta Rodiles, Asturias, northern Spain; (**f**) *Phymatoderma* isp., Lower Jurassic, Rodiles Formation, Vega Beach, Asturias, northern Spain, scale bar is 1 cm; (**g**) *Chondrites* isp., Lower Jurassic, Rodiles Formation, Vega Beach, Asturias, northern Spain, scale bar is 1 cm

Fig. 9.19 *Rhizocorallium* isp. from a Jurassic carbonate firmground, Upper Jurassic, Rodiles Formation, El Puntal Cliffs, San Martín del Mar, Villaviciosa, Asturias, northern Spain. (**a**) General view of the surface with several superbly preserved specimens of *Rhizocorallium* isp., lens cap diameter is 5.5 cm; (**b**) Close-up of a specimen of *Rhizocorallium* isp. showing well-preserved bioglyphs, scale bar is 1 cm; (**c**) Close-up of specimens of *Rhizocorallium* isp. with sharp burrow boundaries

mid-tier *Helminthopsis,* and a deep-tier *Chondrites*. The ichnogenus *Rhizocorallium* is quite common in carbonate firmgrounds as illustrated by spectacular examples in the Jurassic of Asturias (García-Ramos et al. 2011; Rodríguez-Tovar et al. 2012; Fig. 9.19a–c).

In addition to infaunalization in soft substrates, ichnologic evidence suggests that the character and levels of bioerosion in hard substrates also showed significant changes by the Jurassic (Fürsich et al. 1994; Kowalewski et al. 1998; de Gibert et al. 1998a; Bertling 1999; Bromley 2004; Tapanila and Hutchings 2012). In particular,

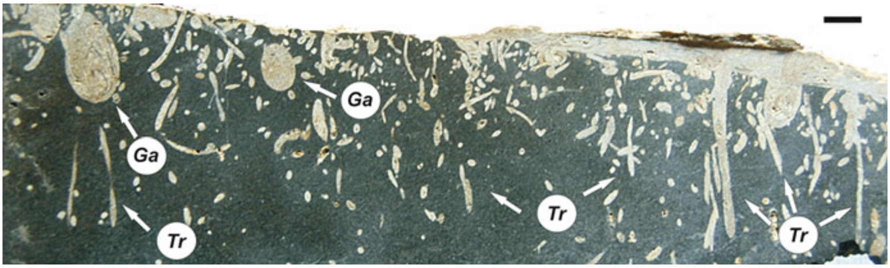

Fig. 9.20 *Gastrochaenolites* isp. and *Trypanites* isp. demarcating the carbonate hardground at the contact between the Middle Jurassic Upper Inferior Oolite and the underlying Carboniferous limestone, England. Scale bar is 1 cm

de Gibert et al. (1998a)) noted the sharp contrast between Paleozoic and post-Paleozoic (mostly from the Jurassic onward) bioerosion ichnofaunas, with the former being dominated by worm borings and the latter by bivalve and sponge borings. Middle Jurassic patch reefs from Israel have been extensively bioeroded by bivalves, worms, barnacles, and phoronids (Wilson et al. 2010). The documented ichnogenera include *Clionolithes* (produced by sponges or algae), *Gastrochaenolites* (bivalves; Fig. 9.20), *Oichnus* (likely a soft-bodied sclerobiont), *Rogerella* (acrothoracican barnacle), *Talpina* (phoronids), and *Trypanites* (worms; Fig. 9.20).

Fürsich et al. (1994) documented a high diversity of macroborings in an Upper Jurassic reef, noting that this is the oldest example where borers destroyed such a large part of the reef, removing up to 40 % of reef volume. Bertling (1999) indicated that the appearance of a modern macrobioeroding reef fauna took place by the Late Jurassic. However, a subsequent study by Perry and Bertling (2000) downplayed the importance of the Late Jurassic radiation of macroborers in favor of a more protracted process throughout the Jurassic. According to these authors, cirripeds, bivalves, and worms dominated in the Early Jurassic, with clionaid sponges becoming main players by the Middle Jurassic. The appearance of *Radulichnus* in the Jurassic is particularly important because gastropods and chitons may have contributed significantly to grazing disturbance in shallow-marine settings, leading to the post-Triassic decline of articulate brachiopods and their retreat to deep-water and/or cryptic refugia (Radley 2010).

A Jurassic diversification of macroborers was certainly not restricted to reefs, but can be extended to hard substrates in other settings, such as mollusk shells and limestone rockgrounds, which supported a bioeroding fauna of modern aspect, including polychaetes, sponges, and bivalves (Taylor and Wilson 2003; Goldring et al. 2005). Despite these changes, Tapanila (2008) noted that, with the exception of echinoids, no new classes of organisms adopted an endolithic strategy during the MMR. From an ichnofacies perspective, the Jurassic marks the appearance of the *Gnathichnus* ichnofacies (de Gibert et al. 2007).

Woodgrounds were colonized for the first time by the Early Jurassic, as indicated by the first appearance of the ichnogenus *Teredolites*, which is produced by pholadacean bivalves (Villegas-Martín et al. 2012). This occurrence predates the first recorded appearance of pholadacean body fossils, documented from the Middle Jurassic (Haga and Kase 2011; Villegas-Martín et al. 2012). Innovations in microbioerosion were not apparent by the Jurassic (Glaub and Vogel 2004; Wisshak et al. 2006).

Increase in predation pressure is one of the most important features of the MMR. Although increased predation is reflected in the body-fossil record, the ichnologic record of predation provides key information for understanding the role of predators during this evolutionary breakthrough (Huntley and Kowalewski 2007). In particular, the roles of drilling predation, as reflected by bioerosion structures, typically including drill holes of the ichnogenus *Oichnus* (Müller 1977) in shells (e.g., Kowalewski et al. 1998, 1999; Harper et al. 1998, 1999; Walker and Brett 2002; Harper 2003) and of durophagous predation, as evidenced by shell-crushing structures (e.g., Harper 2003; Oji et al. 2003; Zatoń and Salamon 2008), have received considerable attention. In addition, fish bite marks in echinoid spines have been recently documented (Wilson et al. 2014). Evaluation of the role of drilling in the Jurassic has been controversial, essentially due to a patchy fossil record (Kowalewski et al. 1998, 1999; Harper et al. 1998, 1999). Although the 120 Myr gap in the presence of drill hole structures, ranging from the end of the Late Triassic to the beginning of the late Early Cretaceous, is starting to be filled with a few reports (see discussions in Kowalewski et al. 1998, 1999; Harper et al. 1998, 1999), available evidence seems to suggest that drilling was not a major selection pressure during the Jurassic (Harper 2003; Huntley and Kowalewski 2007).

In contrast, a number of animals capable of durophagous predation, including malacostracan crustaceans with crushing chelae and several vertebrates (e.g., marine crocodilians, ichthyosaurs, and plesiosaurs), appeared for the first time by the Jurassic (Walker and Brett 2002). The extent of durophagous predation by the Jurassic is still uncertain, but the presence of abundant shells displaying crushing structures most likely produced by predatory fish, probably selachians or teleosteans, in the Middle Jurassic of Poland points toward intense predation pressure, at least locally (Zatoń and Salamon 2008). Interestingly, grazing by gastropods, chitons, and regular echinoids may have been responsible for widespread dislodgement, removal, and consumption of sessile and cemented epifauna from hardgrounds. According to this view, grazing bioerosion was an important factor of escalation during the Jurassic (Radley 2010). This is consistent with the ideas of Vermeij (2008), who noted that the Early Jurassic was characterized by a remarkable increase in escalation-related innovations, with rapid diversification of clades displaying adaptative responses to predators.

Ichnologic data suggest that the rise to dominance of the Modern Evolutionary Fauna is clearly evidenced since the beginning of the Jurassic. Burrow systems attributed on actualistic grounds to malacostracan crustaceans are pervasive in shallow-marine carbonates and siliciclastics, including *Ophiomorpha*, *Thalassinoides*, and *Spongeliomorpha* (e.g., Dam 1990a, b; Monaco and Garassino 2001; Monaco and Giannetti 2002; Giannetti and Monaco 2004; Neto de Carvalho et al. 2010). *Rhizocorallium* is another ichnotaxon produced by crustaceans, at least in some cases, which has been extremely common since the Jurassic (see review in

Knaust 2013). Although present since the Cambrian, post-Paleozoic forms of *Rhizocorallium* record more sophisticated feeding strategies, including the presence of spine-shaped protuberances that may have served as caches or for farming (Rodríguez-Tovar et al. 2012; Fig. 9.18d).

The occurrence of *Scolicia* in shallow-marine deposits (e.g., Dam 1990a, b), albeit rare in comparison with younger deposits, reveals the impact of irregular echinoids. Bivalve trace fossils, such as *Protovirgularia*, although known since the early Paleozoic, are quite abundant since the Jurassic (e.g., Hallam 1970; Leonowicz 2008). Trace fossils attributed to worm-like organisms or unknown animals reflect the appearance of new behavioral programs. This is clearly evidenced by the ichnogenera *Haentzschelinia* (referred to as *Dactyloidites* in some studies, but see Belaústegui et al. 2015b) and *Phoebichnus* (Bromley and Asgaard 1972; Heinberg and Birkelund 1984; McIlroy 2004, 2007; Srivastava et al. 2010; Patel et al. 2014; Canale et al. 2015; Evans and McIlroy 2016). Other worm structures, such as *Gyrochorte*, although present in Paleozoic rocks, became particularly abundant in the Jurassic (e.g., Hallam 1970; Heinberg 1973; Heinberg and Birkelund 1984; Powell 1992; Sudan et al. 2000; de Gibert and Benner 2002; Leonowicz 2008; Bressan and Palma 2009; Patel et al. 2014). The ichnogenus *Curvolithus*, probably produced by flat worms, also seems to be particularly abundant in Jurassic shallow-marine deposits (Häntzschel and Reineck 1968; Heinberg 1973; Heinberg and Birkelund 1984; Buatois et al. 1998). Both *Gyrochorte* and *Curvolithus* may be regarded as part of a relatively widespread ichnoguild in the Jurassic, comprising vagile, shallow-tier detritus-feeder and predation structures. The spiral burrow *Lapispira*, a structure that may be attributed to either worms or crustaceans, is at present only known from Lower Jurassic shallow-marine deposits (Lanés et al. 2007; Pagani et al. 2012, but see de Gibert et al. 2012 for a possible Miocene occurrence).

Overall, Jurassic ichnofaunas reveal a compositional turnover with respect to older, particularly Paleozoic, ichnofaunas and give strong evidence for the rise to dominance of the Modern Evolutionary Fauna. Comparison of shallow-marine ichnofaunas through the Triassic-Jurassic suggests that this faunal turnover took place essentially by the Early Jurassic as indicated by bioturbation structures, with evidence of a more protracted process for macrobioeroders.

9.3.3 The Cretaceous: Continuation of Previous Trends

Cretaceous siliciclastic shallow-marine ichnofaunas are extremely well known and have been analyzed in detail in several studies. One area that has been explored in great detail is the Western Interior Seaway of North America (Howard and Frey 1984; Vossler and Pemberton 1988, 1989; Frey and Howard 1982, 1985, 1990; Frey 1990; MacEachern and Pemberton 1992; Pemberton et al. 1992; Saunders et al. 1994; Pemberton and MacEachern 1997; MacEachern et al. 1999). Although these studies emphasized ichnofacies applications in facies analysis and sequence stratigraphy, the data presented can be easily explored from an evolutionary perspective. As a whole, information from the Cretaceous of the Western Interior reveals the establishment of diverse climax communities in fully marine offshore settings. Ichnofaunas from these settings include a wide variety of ethologic types and feeding strategies, represented by a large number of ichnogenera, such as *Thalassinoides* (Fig. 9.21f), *Diplocraterion* (Fig. 9.21c), *Cylindrichnus*, *Protovirgularia* (Fig. 9.21l), *Schaubcylindrichnus* (Fig. 9.21g), *Gyrochorte* (Fig. 9.21h), *Curvolithus* (Fig. 9.21i), *Halopoa* (Fig. 9.21k), *Palaeophycus*, *Planolites*, *Teichichnus*, *Taenidium*, *Zoophycos*, *Helminthopsis*, *Phycosiphon*, *Nereites* (referred to as *Cosmorhaphe* in some of the original studies), *Phoebichnus*, *Scolicia, Bichordites* (Fig. 9.21j), *Chondrites*, *Rhizocorallium*, *Bergaueria*, *Asterosoma*, and *Rosselia* (Fig. 9.21d). Overall, no major departures are apparent from the trends established in the Jurassic for these settings.

Relatively high-energy nearshore deposits from Cretaceous sections elsewhere display ichnofaunas that are essentially identical to those of the Jurassic (e.g., Curran 1985; Martino and Curran 1990; Pollard et al. 1993; Nielsen et al. 1996; Weissbrod and Barthel 1998). Cretaceous nearshore sandstones are dominated by mid- to deep-tier dwelling burrows, typically of crustacean (e.g., *Ophiomorpha;* Fig. 9.21a) and worm (e.g., *Skolithos*) origin. Crustaceans encompass a wide variety of feeding strategies. Among other producers, although suspension-feeding strategies are dominant, other trophic types include detritus feeding (e.g., *Cylindrichnus*, *Rosselia*) and passive predation (*Conichnus, Bergaueria,* Fig. 9.21e). The ichnogenus *Macaronichnus* became particularly common in high-energy nearshore sands of Cretaceous deposits (see review by Quiroz et al. 2010; Fig. 9.21a).

From the perspective of infaunalization, Upper Cretaceous lower-offshore deposits of the Magallanes Formation of Patagonia, Argentina provide a glimpse into the complexity of tiering structures by the end of the Mesozoic. These deposits have been totally obliterated by bioturbation, mostly due to the activity of a deposit-feeding infauna (Buatois et al. 2011; Fig. 9.22a–d). The shallowest tier consists of an indistinct mottling (*Planolites*) representing background bioturbation in the water-saturated, soupy substrate of the mixed zone. Below are shallow-tier *Thalassinoides*, *Phycosiphon*, and *Zoophycos*. The mid-tier is represented by *Asterosoma*, *Planolites,* and "Terebellina" (= *Palaeophycus heberti*), whereas the deep tier is occupied by *Chondrites*, *Teichichnus,* and a second type of *Thalassinoides*. The well-defined morphology and sharp burrow margins of *Teichichnus,* in addition to the absence of other trace fossils cross-cutting this ichnotaxon, indicate emplacement deep in compacted sediment. Six ichnoguilds are recognized: the *Planolites* ichnoguild (vagile, deposit-feeding, very shallow tier), the *Thalassinoides* ichnoguild I (semi-vagile and vagile, shallow-tier deposit-feeder structures), the *Phycosiphon-Zoophycos* ichnoguild (vagile, deposit-feeding to chemosymbiont, shallow-tier), the *Asterosoma-Planolites*-"Terebellina" ichnoguild (semi-vagile, deposit-feeding, mid-tier), the *Teichichnus-Chondrites* ichnoguild (vagile, deposit-feeding to chemosymbiont, deep-tier), and the *Thalassinoides* ichnoguild II (semi-vagile and vagile, deep-tier deposit-feeder structures).

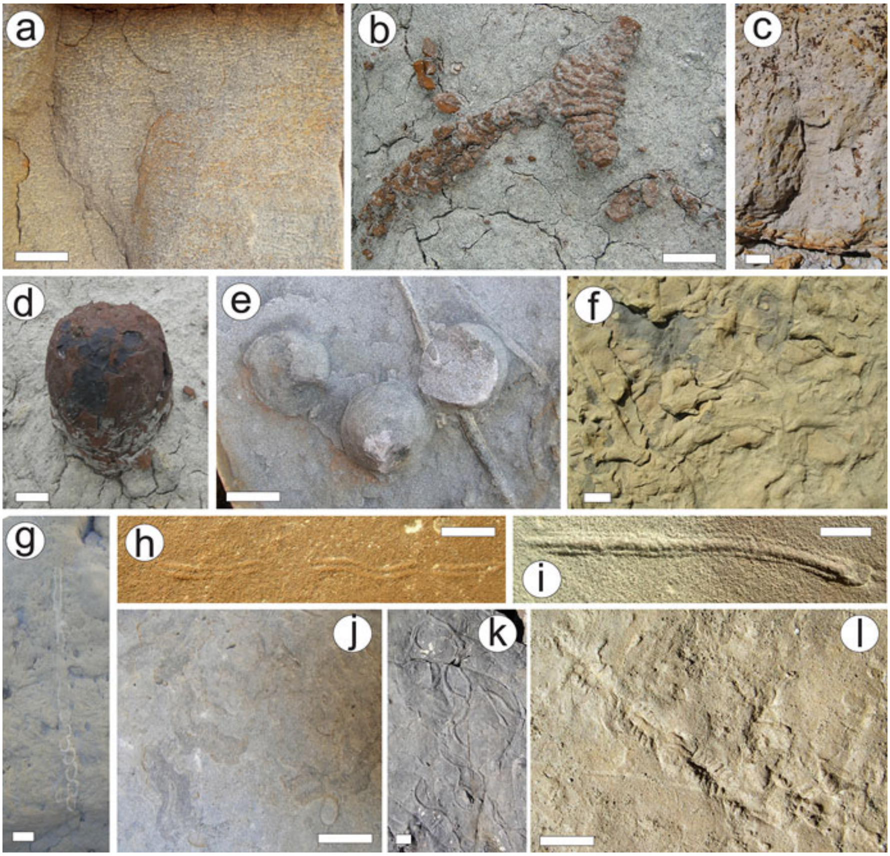

Fig. 9.21 Characteristic trace fossils from the Cretaceous Western Interior Seaway of North America. (**a**) *Macaronichnus segregatis*, Upper Cretaceous, Horseshoe Canyon Formation, near Drumheller, Alberta, Canada; (**b**) *Ophiomorpha irregulaire*, Upper Cretaceous, Horseshoe Canyon Formation, near Drumheller, Alberta, Canada; (**c**) *Diplocraterion parallelum*, Lower Cretaceous, Dakota Group, Alameda Avenue, Denver, Colorado, United States; (**d**) *Rosselia socialis*, Upper Cretaceous, Horseshoe Canyon Formation, near Drumheller, Alberta, Canada; (**e**) *Bergaueria* isp., Upper Cretaceous, Wapiabi Formation, Mount Yamnuska Quarry, Alberta, Canada; (**f**) *Thalassinoides suevicus*, Upper Cretaceous, Ferron Sandstone, Ivie Creek area, Utah, United States; (**g**) *Schaubcylindrichnus coronus*, Upper Cretaceous, Panther Tongue Member, Star Point Formation, Kenilworth Wash, Book Cliffs, Utah, United States; (**h**) *Gyrochorte comosa*, Upper Cretaceous, Kenilworth Member, Blackhawk Formation, near the southern entrance to Tusher Canyon, Book Cliffs, Utah, United States; (**i**) *Curvolithus simplex*, Upper Cretaceous, Kenilworth Member, Blackhawk Formation, near the southern entrance to Tusher Canyon, Book Cliffs, Utah, United States; (**j**) *Bichordites* isp., Upper Cretaceous, Panther Tongue Member, Star Point Formation, Kenilworth Wash, Book Cliffs, Utah, United States; (**k**) *Halopoa* isp., Upper Cretaceous, Ram Member, Cardium Formation, Seebe Dam, Alberta, Canada; (**l**) *Protovirgularia dichotoma*, Upper Cretaceous, Kenilworth Member, Blackhawk Formation, Hutch Mesa area, Book Cliffs, Utah, United States. Scale bars in (**g**, **h**, **i, j**, and **l**) are 1 cm, whereas those in (**a**, **b**, **c**, **d**, **e, f**), and (**k**) are 3 cm

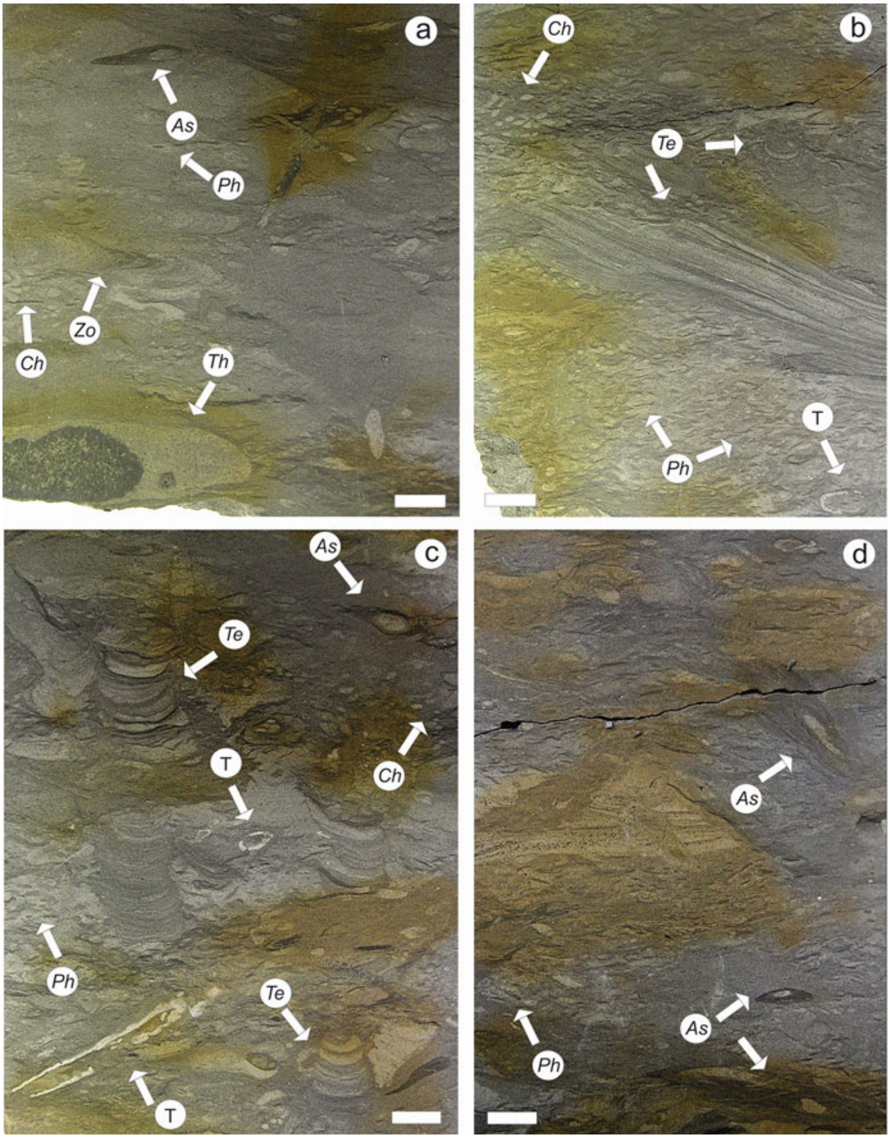

Fig. 9.22 Intensely bioturbated Upper Cretaceous lower-offshore deposits of the Magallanes Formation, Austral Basin, Patagonia, Argentina. (**a**) Shallow-tier *Phycosiphon* (*Ph*) and *Zoophycos* (*Zo*), mid-tier *Asterosoma* (*As*), and deep tier *Chondrites* (*Ch*) and *Thalassinoides* (*Th*); (**b**) Shallow-tier *Phycosiphon* (*Ph*), mid-tier "Terebellina" (T), and deep tier *Chondrites* (*Ch*) and *Teichichnus* (*Te*); (**c**) Shallow-tier *Phycosiphon* (*Ph*), mid-tier *Asterosoma* (*As*) and "Terebellina" (T), and deep tier *Chondrites* (*Ch*) and *Teichichnus* (*Te*); (**d**) Shallow-tier *Phycosiphon* (*Ph*) and mid-tier *Asterosoma* (*As*). Scale bars are 1 cm

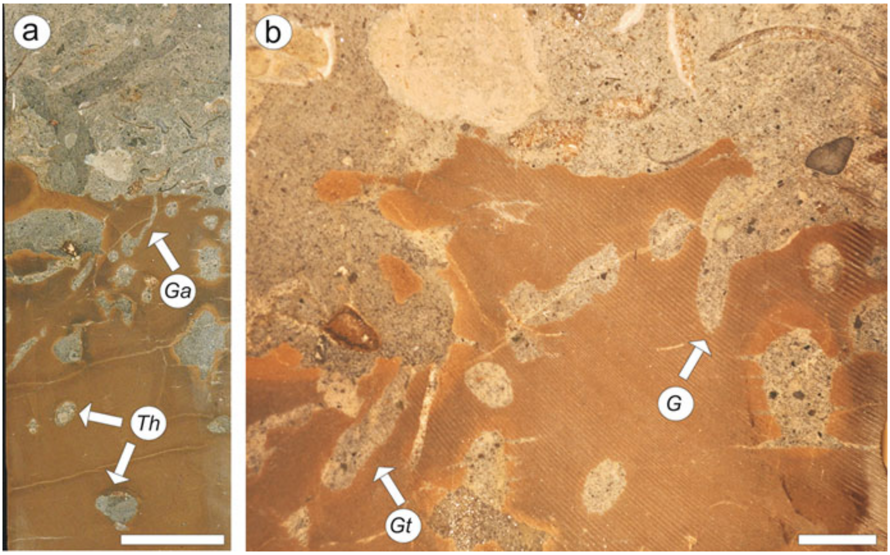

Fig. 9.23 A hardground surface demarcating the Intra-Valanginian Discontinuity (Lower Cretaceous) from the Neuquén Basin of Argentina. (**a**) Close-up showing *Thalassinoides* isp. (*Th*) penetrating well below the surface and *Gastrochaenolites* isp. (*Ga*) right below the discontinuity surface; (**b**) Close-up showing *Gastrochaenolites turbinatus* (*Gt*) and *Gastrochaenolites*? isp. (*G*). Note abundant intraclasts mantling the surface and unidentified borings. Scale bars are 1 cm

Information on Cretaceous oxygen-depleted ichnofaunas comes from the analysis of the Oceanic Anoxic Event 2 (OAE-2) during the Cenomanian–Turonian transition in Europe (Uchman et al. 2008; Rodríguez-Tovar et al. 2009a, b; Monaco et al. 2012; Uchman et al. 2013). These trace-fossil assemblages are virtually identical to those of the Jurassic. In fact, ichnofaunas of oxygen-depleted environments from the Cretaceous onward seem overall to be quite conservative, and no major changes have been recorded subsequent to the Jurassic.

As in the case of the Jurassic, Cretaceous shallow-marine carbonates tend to be dominated by crustacean burrows, particularly in high-energy nearshore grainstones (e.g., Spalletti et al. 2001a, b), but also in slightly distal and lower-energy packstones and wakestones (e.g., Mángano and Buatois 1994) and omission surfaces (e.g., Mángano and Buatois 1991; Schwarz and Buatois 2012; Fig. 9.23a–b). Other less common elements, most likely produced by worms, including *Schaubcylindrichnus* and *Phycodes*, tend to be present in more distal settings (e.g., Mángano and Buatois 1994).

It has been noted that in modern environments, a rapid response of the deep-marine benthic community is triggered by seasonal productivity, resulting in a pattern referred to as the "benthic–pelagic coupling" (Graf 1989). Calcareous nannofossils, diatoms, and dinoflagellates became the largest components of the phytoplankton during the Cretaceous (Katz et al. 2007). As a result, primary production increased dramatically

(Kotake 2014). There is significant ichnologic evidence supporting the establishment of a modern-style benthic–pelagic coupling during the Cretaceous (Kotake 2014; Izumi 2015). These include the permanent occupation of the same burrow by the *Zoophycos* producer as a response to high benthic-food conditions (Kotake 2014) and the synchronization of deposit-feeding strategies with coccolithophore bloom by the *Phymatoderma* animal (Izumi 2015). Therefore, ichnologic information underscores the fact that significant changes took place in marine ecosystems by the late Mesozoic.

Another dataset comes from chalk that has been extensively studied from an ichnologic perspective in Europe (e.g., Bromley 1967; Kennedy 1967, 1970, 1975; Fürsich et al. 1981; Bromley and Ekdale 1984b, 1986; Ekdale and Bromley 1984, 1991) and the United States (Frey 1970, 1972; Frey and Bromley 1985; Savrda 2014). During the Cretaceous, thick chalk deposits resulted from the accumulation of coccoliths on the seafloor, derived post-mortem from the flourishing populations of coccolithophores that dwelled in the marine photic zone above (Stanley et al. 2005). Such deposits provide an ideal medium for ichnofabric analysis due to their complete bioturbation as a result of very slow rates of sedimentation and full-marine conditions (Ekdale and Bromley 1991; Savrda 2012). Coccolithophorids first appeared in the Late Triassic and diversified rapidly during the Early Jurassic (Bown 2005), but it is not until the Cretaceous that this group became a major contributor to ocean sedimentation (Hay 2004). The average size of individual coccoliths increased with time, from Early Jurassic to Middle Cretaceous, and this size history parallels the diversity history of Mesozoic coccolithophorids (Aubry et al. 2005).

In particular, shelf chalk beds, which formed between water depths of 50 and 300 m (Scholle et al. 1983), provide a window to unique infaunal tiered communities in shallow-water settings (Figs. 9.24a–d and 9.25a–e). Crustacean burrow systems, such as those of *Thalassinoides*, are dominant in these deposits, with *Ophiomorpha* and *Gyrolithes* being less common (Ekdale and Bromley 1984). Feeding structures, such as *Chondrites*, *Phycosiphon*, *Zoophycos*, *Planolites,* and *Teichichnus*, are common as well (Ekdale and Bromley 1984). Concretionary flint in chalk typically represents silicified burrow systems, such as *Thalassinoides*, commonly allowing for three-dimensional preservation (Fig. 9.26a–b); Bromley and Ekdale 1984b). Another common structure in European chalks is the large burrow structure *Bathichnus paramoudrae*, which is typically encircled by ring-like paramoudra flint (Bromley and Ekdale 1984b).

From an ichnofabric perspective, chalk hosts extremely complex, tiered ichnocommunities as demonstrated by the detailed analysis of pelagic deposits from Denmark (Ekdale and Bromley 1991). As noted by these authors, degree of bioturbation in these deposits is so high that virtually every grain of sediment was processed by several animals, resulting in composite ichnofabrics recording the activity of multi-tiered infaunal communities. The shallowest tier corresponds to indistinct burrow mottling onto which as many as four ichnoguilds are typically overprinted. A complete overprinting sequence would include the *Planolites* ichnoguild (vagile, shallow-tier deposit-feeder structures), the *Thalassinoides* ichnoguild (semi-vagile and vagile, mid-tier deposit-feeder structures), the *Taenidium-Phycosiphon* ichnoguild (vagile, middle-to-deep-tier deposit-feeder structures), and the *Zoophycos*-

Fig. 9.24 Chalk trace fossils, Upper Cretaceous, West Melbury Chalk Formation, Beachy Head, southeast England. (**a**) General view of intensely bioturbated deposits overprinted by mid-tier *Thalassinoides paradoxicus*; (**b**) Close-up of *Thalassinoides paradoxicus*; (**c**) Close-up of *Thalassinoides paradoxicus* cross-cut by deep-tier *Chondrites* isp.; (**d**) General view of intensely bioturbated deposits overprinted by mid-tier *Thalassinoides paradoxicus*. Scale bars are 1 cm

Chondrites ichnoguild (non-vagile, deep-tier deposit-feeder or chemosymbiont structures). A similar tiering pattern has been recorded in chalk from Alabama (Frey and Bromley 1985). The tiering structure of the Alabama deposits consists of very shallow-tier, indistinct burrow mottling and three ichnoguilds, the *Thalassinoides* ichnoguild (semi-vagile and vagile, mid-tier deposit-feeder structures), the *Zoophycos-Taenidium* ichnoguild (vagile, middle-to-deep-tier deposit-feeder or farming structures), and the *Chondrites* ichnoguild (non-vagile, deep-tier deposit-feeder or chemosymbiont structures).

Common macroborers in the Cretaceous include acrothoracican barnacles, bivalves, clionaid sponges, polychaetes, and bryozoans (Taylor and Wilson 2003). In the specific case of macroborers in reef environments, information is patchy for the Early Cretaceous, but available data suggest a dominance of bivalves and worms over cirripedians (Perry and Bertling 2000; Tapanila and Hutchings 2012). Bivalve borings (*Gastrochaenolites*) were also common in Early Cretaceous hardgrounds (Schwarz and Buatois 2012; Fig. 9.23a–b). During the Late Cretaceous, borer sponges may have played a major role, particularly in rudist reefs, and to some extent also in coral reefs, together with worms and bivalves (Perry and Bertling 2000; Tapanila and Hutchings 2012). Rocky shorelines also were affected by significant bioerosion, with hardgrounds and carbonate rockgrounds displaying similar borer communities (Taylor and Wilson 2003). A wide diversity of bioerosion structures

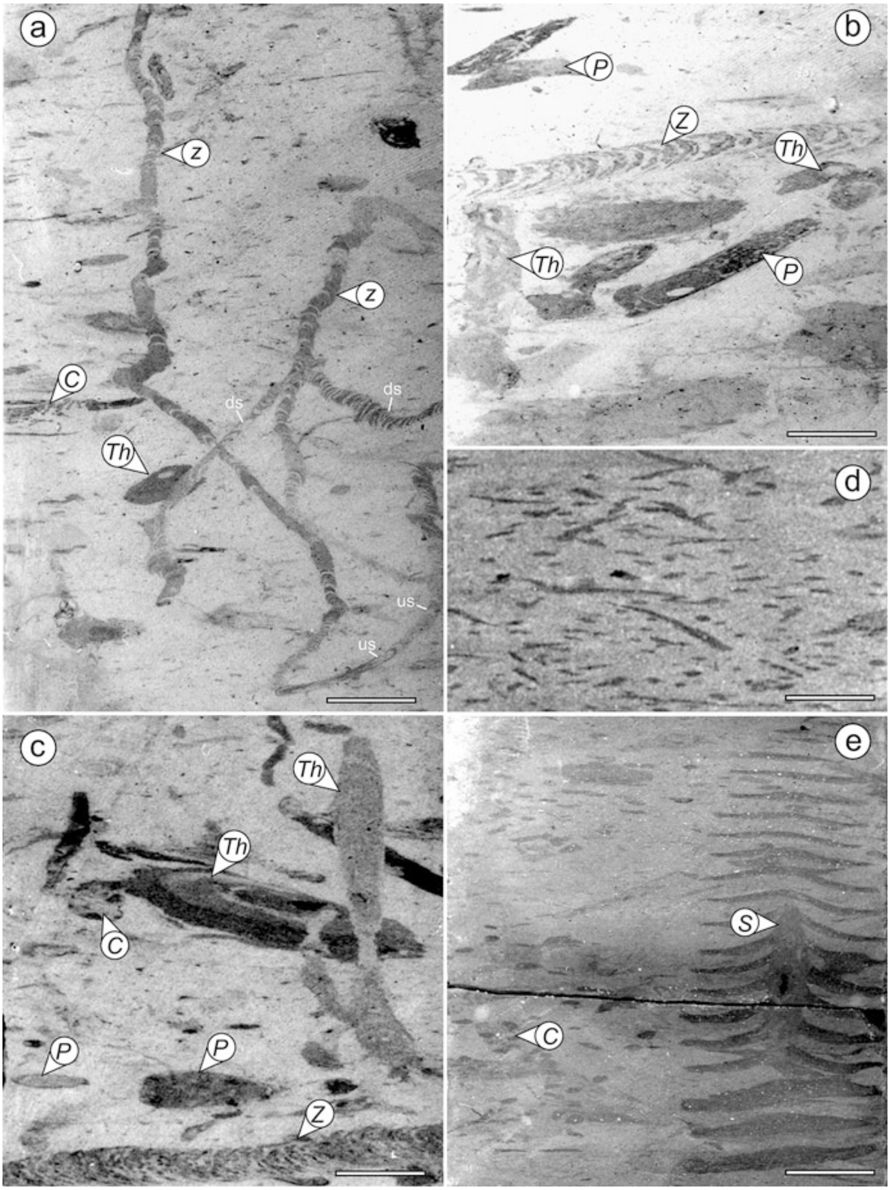

Fig. 9.25 Ichnofabrics and trace fossils in Eocene to Maestrichtian chalk cored at DSDP Site 605 (for details about the lithology see van Hinte et al. 1987; for details about the ichnology see Wetzel 1987). (**a**) Ichnofabric characterized by the vertical or steeply oriented spreite of *Zoophycos* isp. (*Z*) [note deviating spreite (ds) and even upward shifting ones (us)], *Thalassinoides* isp. (*Th*) some no longer identifiable burrows have been reworked by producers of *Chondrites* isp. (*C*); background sediment has been homogenized (core 19, section 4, 20–29 cm); (**b**) Complex ichnofabric composed of *Planolites* isp. (*P*), *Teichichnus* isp. (*T*), *Thalassinoides* isp. (*Th*), and *Zoophycos* isp. (Z); some burrows have been reworked by producers of *Chondrites* isp. (*C*) (core 21, section 1, 75–81 cm); (**c**) Complex ichnofabric composed of *Zoophycos* isp. (Z), *Teichichnus* isp. (*T*), and *Planolites* isp. (P) that both have been reworked by producers of *Chondrites* isp. (*C*), and *Thalassinoides* isp. (*Th*) (core 17, section 1, 21–29 cm); (**d**) Ichnofabric with dominant *Chondrites* isp. (core 41, section 6, 15–19 cm); (**e**) *Spirophyton*-like burrow (*S*) and some *Chondrites* isp. tubes (*C*) (core 50, section 3, 64–71 cm)

Fig. 9.26 Concretionary flint in chalk representing silicified *Thalassinoides* isp. (**a, b**) Upper Cretaceous specimens, Beachy Head, southeast England. All scale bars are 1 cm

was described from a Lower Cretaceous karst surface in the Czech Republic (Mikuláš 1992b). The assemblage included borings by sponges (various ichnospecies of *Entobia*), worms (*Trypanites*), acrothoracican barnacles (*Rogerella*), bivalves (*Gastrochaenolites*), and echinoids (*Circolites*). Non-carbonate rocky shorelines were characteristically of low diversity, as indicated by a monospecific suite of bivalve borings (*Gastrochaenolites*) penetrating slates (Buatois and Encinas 2011). Bioerosion in woodgrounds became much more common in the Cretaceous, as shown by widespread occurrences of the ichnogenus *Teredolites* (Taylor and Wilson 2003; Villegas-Martín et al. 2012). From a microbioerosion perspective, the Cretaceous seems to show only a very slight increase in the number of ichnospecies recorded (Wisshak et al. 2006).

Predation structures, drilling and, to a lesser extent, durophagous predation may have increased in intensity during the Cretaceous (Walker and Brett 2002; Harper 2003, 2006; Huntley and Kowalewski 2007). There is overwhelming paleontologic and ichnologic evidence that drilling predation underwent major evolutionary innovation in the Cretaceous (Kelley and Hansen 2003; Huntley and Kowalewski 2007). The earliest undisputed body-fossil record of muricid and naticid gastropods is from the Late Cretaceous (Merle and Pacaud 2002), although drill holes identical to those produced by these gastropods occur in the Early Cretaceous (Taylor et al. 1983) and even the Triassic (Fürsich and Jablonski 1984). The appearance of these gastropods undoubtedly increased predation pressures (Harper 2003, 2006). Octopod cephalopods may have been important predators, but no undisputed ichnologic evidence of Cretaceous drilling predation by these organisms has been documented (Walker and Brett 2002). With respect to durophagous predation, the appearance by the Cretaceous of many crustacean decapod families that are known to be active predators (e.g., Palinuridae) represented a major breakthrough (Harper 2003). In addition, many vertebrate predators were very active during the Cretaceous, with crocodilians, ichthyosaurs, and plesiosaurs being common in the Early Cretaceous and pliosaurids and mosasaurs as well during the Late Cretaceous (Walker and Brett 2002). Oji et al. (2003) noted that, although a number of durophagous decapod crustaceans (as well as teleost fish) were present by the Late Cretaceous, the scarcity of crushed shells suggests that durophagous predators did not play a major role in

Cretaceous ecosystems. However, their study is of very local scale, based on a number of units in Japan, which may explain the discrepancies with broader compilations, such as those by Vermeij et al. (1981) that noted a global peak in gastropod shell repair frequency in the Cretaceous.

Regarding burrowers, crustaceans, bivalves, and echinoderms were among the most important, signaling consolidation of the MMR in shallow-marine environments. Worm-like organisms also were undoubtedly key bioturbators in these settings. Opheliid polychaetes became common in high-energy foreshore to upper-shoreface sands, as evidenced by the abundance of *Macaronichnus,* particularly in mid- to high-latitude settings (Quiroz et al. 2010). Also, in high-latitude settings, complex spreiten burrows, namely, *Paradictyodora* and *Euflabella,* occurred for the first time (Olivero et al. 2004; Olivero and López-Cabrera 2013; Olivero and López-Cabrera 2014).

To summarize, from the perspective of animal–substrate interactions in shallow-marine siliciclastic settings, the Cretaceous represents a continuation of the trends established in the Jurassic. However, by the end of the Cretaceous, a modern-style benthic–pelagic coupling pattern was established and an important increase in global ichnodiversity (35 %) took place in marine environments (see Chap. 16). In carbonate settings, crustacean burrows are among the dominant forms. In the specific case of chalk, the explosion in coccolithophores provided a new substrate that allowed for the establishment of extremely complex tiering structures, unknown in older deposits. Diversification of microborers was limited, but macrobioerosion exhibited the increased activity of borers typical of modern communities (e.g., sponges, bivalves, gastropods).

9.3.4 The Paleogene: Rise of the Modern Evolutionary Fauna After End-Cretaceous Mass Extinction

The end-Cretaceous mass extinction (see Chap. 12) differentially impacted the various tracemakers involved in the MMR. Unfortunately, the present scarcity of papers documenting Paleogene shallow-marine ichnofaunas inhibits detailed recognition and reconstruction of patterns and trends.

The few available trace-fossil studies of shallow-marine clastic settings seem to display similarities with late Mesozoic ichnofaunas, although the sparse record prevents real evaluation of tiering structure. Crustacean burrows, such as *Thalassinoides*, continued to be elite trace fossils (sensu Bromley 1990) in the Paleogene, having been recorded in shallow-marine deposits as early as the early Paleocene (Danian; Rodríguez and Panza 2003). Overall, typical Mesozoic elements, such as *Thalassinoides*, *Ophiomorpha*, *Psilonichnus*, and *Rhizocorallium*, are dominant in shallow-marine areas during the entirety of the Paleogene (Belt et al. 1997; 2005; Myint 2001; Shelley and Lawton 2005; Uchman and Gaździcki 2006; Singh et al. 2008; Villegas-Martín et al. 2014). Other typical Mesozoic burrowers, such as irregular echinoderms and prosobranch bivalves, also are represented by their trace fossils in the Paleogene (Uchman and Gaździcki 2006; Demírcan and Uchman 2012;

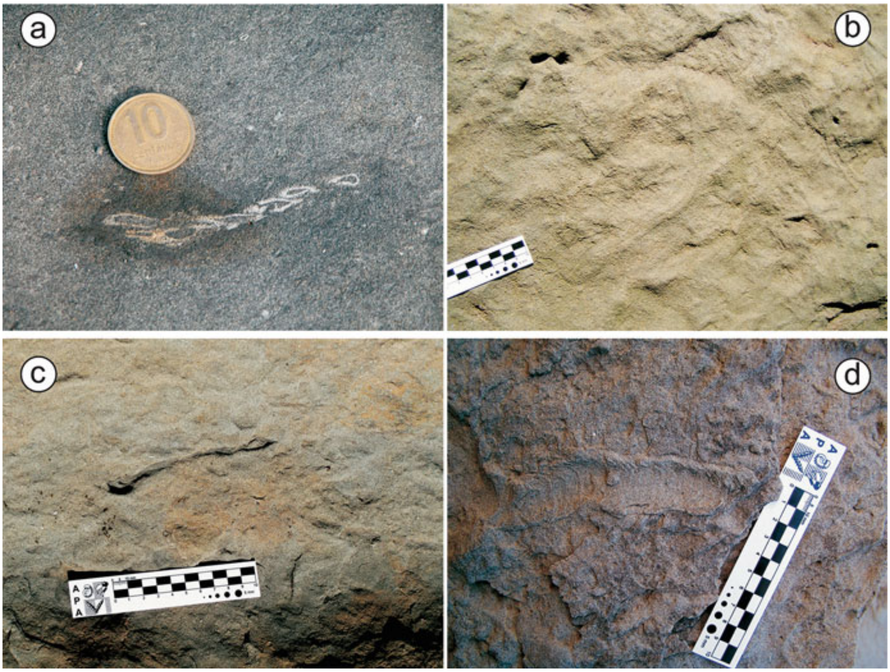

Fig. 9.27 Characteristic trace fossils from the Middle to Upper Eocene Leticia Formation, Patagonia, Argentina (**a**) *Schaubcylindrichnus* isp., cross-section view, coin is 1.8 cm; (**b**) *Gyrochorte* isp., bedding-plane view; (**c**) *Diplocraterion* isp., bedding-plane view; (**d**) *Scolicia* isp., bedding-plane view

Villegas-Martín et al. 2014). One of the most detailed analysis of Paleogene ichnofaunas is that of López-Cabrera et al. (2008), who documented a high-diversity ichnofauna from the upper Eocene of Tierra del Fuego, Argentina, comprising the ichnogenera *Diplocraterion*, *Schaubcylindrichnus*, *Palaeophycus*, *Planolites*, *Rosselia*, *Asterosoma*, *Rhizocorallium*, *Taenidium*, *Teichichnus*, *Tasselia*, *Curvolithus*, *Gyrochorte*, *Patagonichnus*, and *Paradictyodora* (Fig. 9.27a–d). This study showed that, at least by the middle Eocene, ichnodiversity levels were similar to those attained in the late Mesozoic. Of particular importance is the appearance of the ichnogenus *Patagonichnus*, a complex trace fossil attributed to gregarious polychaetes (see also Olivero and López-Cabrera 2005).

As in the case of Jurassic-Cretaceous examples, Paleogene nearshore sands are typically dominated by *Ophiomorpha* (Deville 1996), as well as by other vertical burrows, such as *Skolithos*, *Diplocraterion*, and *Arenicolites* (Zhou 1997; Shelley and Lawton 2005). Quiroz et al. (2010) noted that *Macaronichnus,* an ichnogenus common in nearshore sands of high- to mid-latitudes, is absent in Paleocene to lower Eocene deposits, a pattern that may reflect overall climatic conditions.

Evaluation of the macrobioerosion record is biased as a result of uneven stratigraphic distribution of host substrates, but reports include borings in reefs, rocky shorelines, clasts, and shells. In general, Perry and Bertling (2000) did not note any major change in style of macrobioerosion across the Cretaceous–Paleogene boundary. At present there are few examples of Paleocene and Eocene reef bioerosion, but the sea-level highstand and global oligotrophic conditions during the Oligocene contributed to extensive reef development (Perry and Bertling 2000). Bivalves were apparently the most important macrobioeroders in reefs during the Paleocene, with a subordinate presence of sponges, worms, and bryozoans (Babić and Zupanič 1981; Bernecker and Weidlich 1996; Schuster 1996). Sparse information from the Eocene also underscores the important role of bioeroding bivalves in reefs (Gaemers 1978). Advanced teleost fish, most significantly parrotfish, were important contributors to macrobioerosion in tropical settings since the Eocene because they have a sophisticated jaw mechanism for herbivory (Berg 1940; Steneck 1983). Perry and Bertling (2000) noted that the interpretation of Oligocene patterns is not straightforward, with European reefs having a meager macrobioerosion record, whereas those from the Caribbean display a high ichnodiversity.

In particular, patch and barrier reefs from Puerto Rico contain a wide variety of ichnotaxa, including *Trypanites* and *Uniglobites*, as well as several ichnospecies of *Entobia* and *Gastrochaenolites* (Edinger and Risk 1994). Overall, sponges dominated over bivalves and worms in these reefs. In addition to reefs, rocky shorelines were subject to significant bioerosion by clionaid sponges, bivalves, polychaete worms, and barnacles (Roniewicz 1970; Hanna and Al-Radwany 1993). Composite ichnofabrics typically developed in association with omission surfaces, including both burrows in softgrounds and firmgrounds and borings in hardgrounds, leading to complex patterns of cross-cutting relationships (Lewis and Ekdale 1992). Bioerosion by bivalves and polychaetes has been recorded in clasts as well (Babić and Zupanič 2000). Furthermore, bioerosion in shells was also common during the Cretaceous–Paleogene, particularly in the Eocene-Oligocene (Taylor and Wilson 2003). Examples include borings by acrothoracican barnacles (Abletz 1993), phoronids (Abletz 1994), and lithophagid bivalves (Krumm and Jones 1993; Krumm 1999). Nummulite tests breached by *Oichnus* have been documented from the Eocene (Sengupta and Nielsen 2009). In addition, nummulitids were used as materials to reinforce burrow walls, as illustrated by the ichnogenus *Nummipera* (Hölder 1989; Jach et al. 2011; our Fig. 9.28a–b). During the Oligocene, whale skeletons for

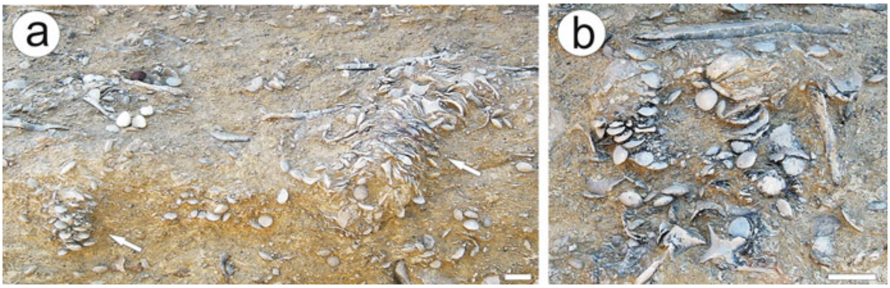

Fig. 9.28 The ichnogenus *Nummipera,* characterized by the presence of nummulite shells reinforcing burrow walls. Middle Eocene, Soğucak Limestone Formation, Uğurlu Beach, Gökçeada Island, western Turkey. (**a**) General view; (**b**) Close-up. Scale bars are 1 cm

the first time show evidence of bioerosion, most likely produced by the osteophagous worm *Osedax* (Boessenecker and Fordyce 2014).

Although there was a slight increase in the diversity of microborings in the Paleogene, a faunal turnover is apparent (Glaub and Vogel 2004). Change in the dominant macrobioeroding ichnotaxa took place by this time, with the appearance of new ichnospecies whose oldest record is Paleogene (Glaub and Vogel 2004; Wisshak 2012).

The great end-Cretaceous mass extinction differentially impacted some groups of predators. Many marine reptiles and the ammonites and belemnoids became extinct, but the majority of invertebrate and fish predatory groups survived (Walker and Brett 2002). Several predatory invertebrates (e.g., neogastropods, decapods) and vertebrates (e.g., teleost fish, neoselachian sharks, sea birds, marine mammals) diversified during the Paleogene. Although precise documentation of ichnologic trends through time is difficult to evaluate, there is general agreement that drilling predation increased during the Paleogene (Kelley and Hansen 2003; Huntley and Kowalewski 2007). Vermeij (1987) indicated that an episode of drilling escalation occurred between the Cretaceous and the Eocene, but the details of timing are uncertain due to uneven stratigraphic distribution of data, including a lack of information from the Paleocene.

A similar Cretaceous–Paleogene phase has been identified (Kowalewski et al. 1998). A decline of drilling frequencies across the Cretaceous–Paleogene boundary followed by a subsequent increase may have resulted from the end-Cretaceous mass extinction and subsequent recovery (Kelley and Hansen 1996, 2003). The record of octopod shell drilling is essentially restricted to the Cenozoic (Walker and Brett 2002). An Eocene radiation of crushing predator crustaceans, including the Portunidae, Cancridae, Calappiidea, Grapsidae, Partheopidae, and Majodae, may have contributed to an increase in predation pressures (Walker and Brett 2002; Harper 2003), although claw-like appendages, such as those in these groups, may have evolved first as defensive traits (Vermeij 1982). Stomatopod crustaceans, comprising both gonodactyloids and squilloids, became important predators in the Cenozoic, although only the former are durophagous predators, commonly preying on mollusks (Walker and Brett 2002). The earliest representatives of gonodactyloid stomatopods in the fossil record are Miocene (Hof and Briggs 1997; Hof 1998). However, the ballistic ichnogenus *Belichnus*, which consists of small puncture marks on mollusk shells (Geary et al. 1991; Pether 1995), has been recognized since the Oligocene (David 1997). Vertebrate predators also contributed to durophagy, including sea turtles as well as a number of marine mammals, the latter since the Eocene (Walker and Brett 2002). Interpretation of shell repair frequency is not straightforward, but Allmon et al. (1990) noted a drop in repair frequency for turritellid shells during the Paleocene and a rebound in the Eocene.

In short, Paleogene ichnofaunas from shallow-marine clastic settings are similar to those of the late Mesozoic. Macrobioerosion styles seem to have persisted across the Cretaceous–Paleogene boundary as well, although an increased role of sponge and fish bioerosion is noted later in the Paleogene. In addition, predation pressures, as reflected by both drilling and durophagy, likely increased during this interval (Kowalewski et al. 1998; Kelley and Hansen 2003; Huntley and Kowalewski 2007).

9.3.5 The Neogene: Establishment of Modern Marine Ecosystems

The Neogene records the establishment of modern-marine ecosystems. In comparison with the Paleogene, the ichnology of Neogene shallow-marine clastic deposits has been documented through a larger number of studies (e.g., Curran and Frey, 1977; Mayoral 1986; Ting et al. 1991; Martini et al 1995; Uchman and Krenmayr 1995, 2004; Pickerill et al. 1996, 1998; Hong 1997; de Gibert et al. 1998b, de Gibert et al. 2013; de Gibert and Martinell 1998; Mayoral et al. 1998, 2013; Muñiz and Mayoral 2001a; Buatois et al. 2003; Malpas et al. 2005; Campbell et al. 2006; Cantalamessa et al. 2007; Carmona et al. 2008, 2012; Pervesler et al. 2011; Lokho and Singh 2013).

Compositionally, Neogene shallow-marine ichnofaunas in clastic settings tend to display similar elements to their Paleogene counterparts. Crustacean burrows, such as *Thalassinoides*, *Ophiomorpha*, *Spongeliomorpha*, *Psilonichnus*, *Macanopsis*, *Gyrolithes,* and *Rhizocorallium*, continued to be common elements (e.g., Mayoral 1986; Ting et al. 1991; Martini et al. 1995; Uchman and Krenmayr 1995, 2004; Hong 1997; de Gibert et al. 1998b, 2013; Mayoral et al. 1998; Muñiz and Mayoral 2001a, b; Buatois et al. 2003; Carmona and Buatois 2003; Cantalamessa et al. 2007; Carmona et al. 2004, 2008, 2012; Malpas et al. 2005; Campbell et al. 2006; Pervesler et al. 2011; de Gibert et al. 2013). Both locomotion and resting trace fossils generated by irregular echinoids are common (e.g., Plaziat and Mahmoudi 1988; Colella and D'Alessandro 1988; Uchman and Krenmayr 1995, 2004; Mayoral and Muñiz 2001; Buatois et al. 2003; Carmona et al. 2008, 2012).

Bivalves are also key burrowers in Neogene shallow-marine sediments, as revealed by the abundance of the ichnogenera *Lockeia*, *Protovirgularia,* and *Siphonichnus* (e.g., Buatois et al. 2003; de Gibert and Domènech 2008; Carmona et al. 2008, 2010, 2012). Also added to this list should be two bivalve ichnogenera that seem to have occurred for the first time by the Neogene: the equilibrium structure *Scalichnus* (Hanken et al 2001; Carmona et al. 2008) and the feeding trace *Saronichnus* (Pervesler and Zuschin 2004). Equilibrium structures of terebellid polychaetes, included in the ichnogenus *Rosselia,* are also common, sometimes displaying a response to sedimentation pulses by formation of dense assemblages (Nara 1995, 1997, 2002; Campbell et al. 2006; Frieling 2007). The highly complex burrow system *Patagonichnus*, produced by gregarious polychaetes, displays sophisticated feeding patterns expressed by its various ichnospecies (Olivero and López-Cabrera 2005).

Neogene nearshore sands display similar ichnofaunas to those of other Early Jurassic–Paleogene deposits. Typical ichnogenera are *Ophiomorpha*, *Conichnus*, *Bergaueria*, *Skolithos*, *Arenicolites,* and *Diplocraterion* (e.g., Curran and Frey 1977; Mayoral 1986; Ting et al. 1991; Martini et al. 1995; Uchman and Krenmayr 1995; 2004; Hong 1997; de Gibert et al. 1998b; Mayoral et al. 1998; Muñiz and Mayoral 2001a,b; Buatois et al. 2003; Carmona and Buatois 2003; Cantalamessa et al. 2007; Carmona et al. 2004, 2008, 2012; Malpas et al. 2005; Pervesler et al. 2011). *Macaronichnus* became common again, with records from a number of high-energy settings (e.g., Uchman and Krenmayr 2004; Carmona et al. 2008; Quiroz et al. 2010).

Despite the overall similarities with Paleogene ichnofaunas, Neogene ichnofaunas display an increase in ichnodiversity (both alpha and global sensu Buatois and Mángano 2013; see Chap. 16) and a more complex pattern of infaunal tiering. Detailed analysis in lower Miocene lower-shoreface to offshore-transition deposits of Patagonia, Argentina (Fig. 9.29a–f) revealed the presence of six ichnoguilds and nine tiers (Buatois et al. 2003; Carmona et al. 2012). This extremely complex infaunal tiering structure includes a mottled texture (vagile, deposit feeders, very shallow-tier), the *Thalassinoides*-*Asterosoma*-*Rosselia* ichnoguild (semi-vagile,

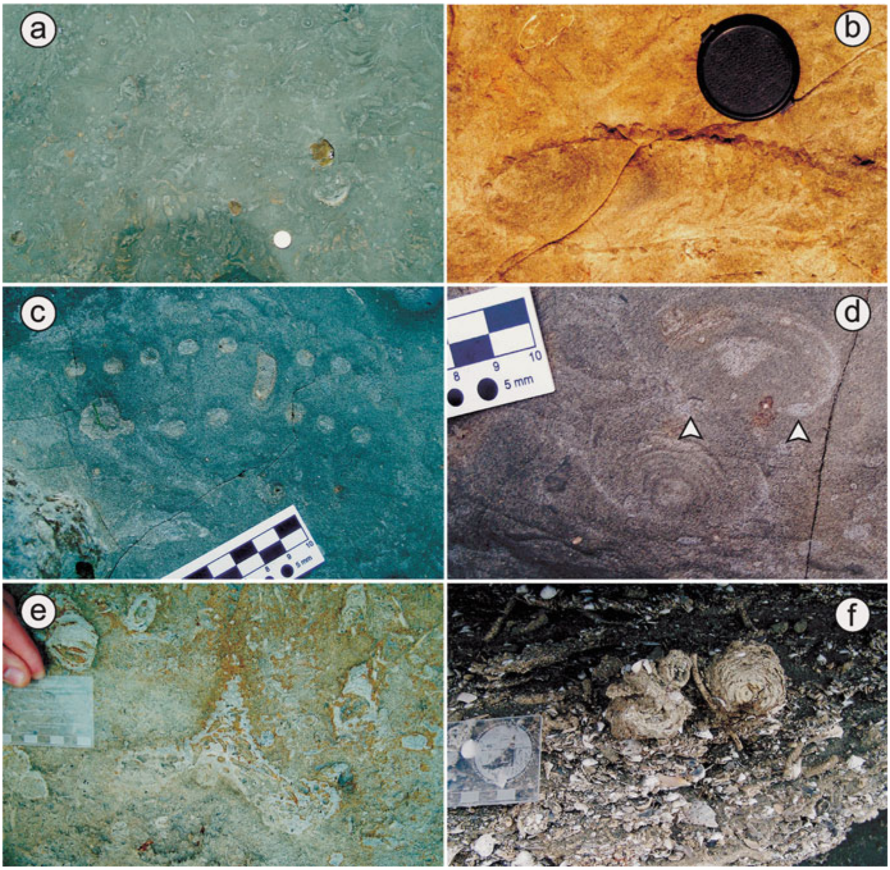

Fig. 9.29 Characteristic trace fossils from Lower Miocene shallow-marine deposits of Patagonia, Argentina. (**a**) *Scolicia* isp. and its producer, bedding-plane view, Chenque Formation, coin is 2.5 cm; (**b**) *Ophiomorpha* isp., bedding-plane view, Chenque Formation, lens cap diameter is 5.5 cm; (**c**) *Helicodromites* isp., bedding-plane view, Chenque Formation; (**d**) *Scolicia* isp., cross-section view, note the two drain channels at the base of the specimens (white arrows); (**e**) *Ophiomorpha nodosa*, cross-section view, Monte León Formation; (**f**) *Asterosoma* isp., cross-section view

deposit feeders, shallow-tier), the *Schaubcylindrichnus*-*Palaeophycus* ichnoguild (vagile, suspension and deposit feeders, middle-tier, the *Scolicia*-*Phycosiphon*-*Helicodromites*-*Teichichnus*-*Taenidium* ichnoguild (vagile, deposit feeders, middle-tier), the *Thalassinoides* ichnoguild (stationary, deposit feeders, deep-tier), and the *Chondrites* ichnoguild (stationary, deposit feeders or chemosymbionts, very deep-tier). This tiering structure reflects higher partitioning of the infaunal habitat and an increase in degree of complexity than that found in older ichnofaunas from siliciclastic settings. This is revealed not only by the number of ichnoguilds present, but particularly by the increased diversity within individual ichnoguilds.

Regarding carbonate settings, an extensive review of the character and importance of ichnology to the study of shallow-marine carbonates was made by Knaust et al. (2012). In a comprehensive study of the Bateig Limestone, Miocene of southeastern Spain, de Gibert and Goldring (2007) identified several ichnofabrics in a pelagic limestone, typically displaying intense bioturbation. The dominant ichnogenera are *Ophiomorpha*, *Bichordites,* and *Palaeophycus*, with subordinate presence of *Planolites*, *Skolithos,* and *Teichichnus*. Invariably, deeply emplaced biogenic structures cross-cut indistinct mottling. Crustacean burrows commonly form quite complex compound structures (de Gibert et al. 2012). More recently, Belaústegui and de Gibert (2013) noted the abundance of *Cylindrichnus*, which contributes to intensely bioturbated carbonate fabrics, and, in this case, represents an elite trace fossil (see also Goldring et al. 2002).

Detailed information on carbonate ichnofaunas also has been derived from Pleistocene–Holocene Bahamian-type carbonates (Curran 2007, and earlier papers cited therein). The ichnologic study of grainstones on San Salvador and other islands of the Bahamas Archipelago and the Miami Limestone of south Florida defined five ichnocoenoses within the *Skolithos* and *Psilonichnus* ichnofacies (Fig. 9.30a–g). *Ophiomorpha* is the dominant trace fossil in shallow subtidal grainstones whereas *Psilonichnus upsilon*, representing the burrows of the ghost crab, *Ocypode quadrata*, is common in beach backshore beds. Carbonate dune deposits (eolianites) also can exhibit a distinctive ichnocoenosis dominated by sometimes complex insect burrows (Curran and White 2001). Similar subtidal ichnofaunas have been recorded in the Pleistocene grainstones of the Cayman Islands (Pemberton and Jones 1988; Jones and Pemberton 1989; Metz 2011).

As is the case with bioturbation structures, macrobioerosion during the Neogene is essentially indistinguishable from that of the modern oceans. Modern reef bioerosion is dominated by grazing and, although the timing of this evolutionary innovation is not totally clear, the onset of widespread grazing may have occurred by the end of the Oligocene (Perry and Bertling 2000). Extensive information on

Fig. 9.30 (continued) shallow-subtidal grainstone, Upper Pleistocene, Cockburn Town Member, Grotto Beach Formation, Clifton Pier, New Providence, pen is 15 cm in length; (**f**) Specimen of a large, well-lithified *Ophiomorpha nodosa* shaft-terminus structure, Upper Pleistocene, Harry Cay, Little Exuma; (**g**) *Psilonichnus upsilon* in beach-backshore grainstone, Holocene, Hanna Bay Member, Rice Bay Formation, Moriah Harbour Cay, Little Exuma

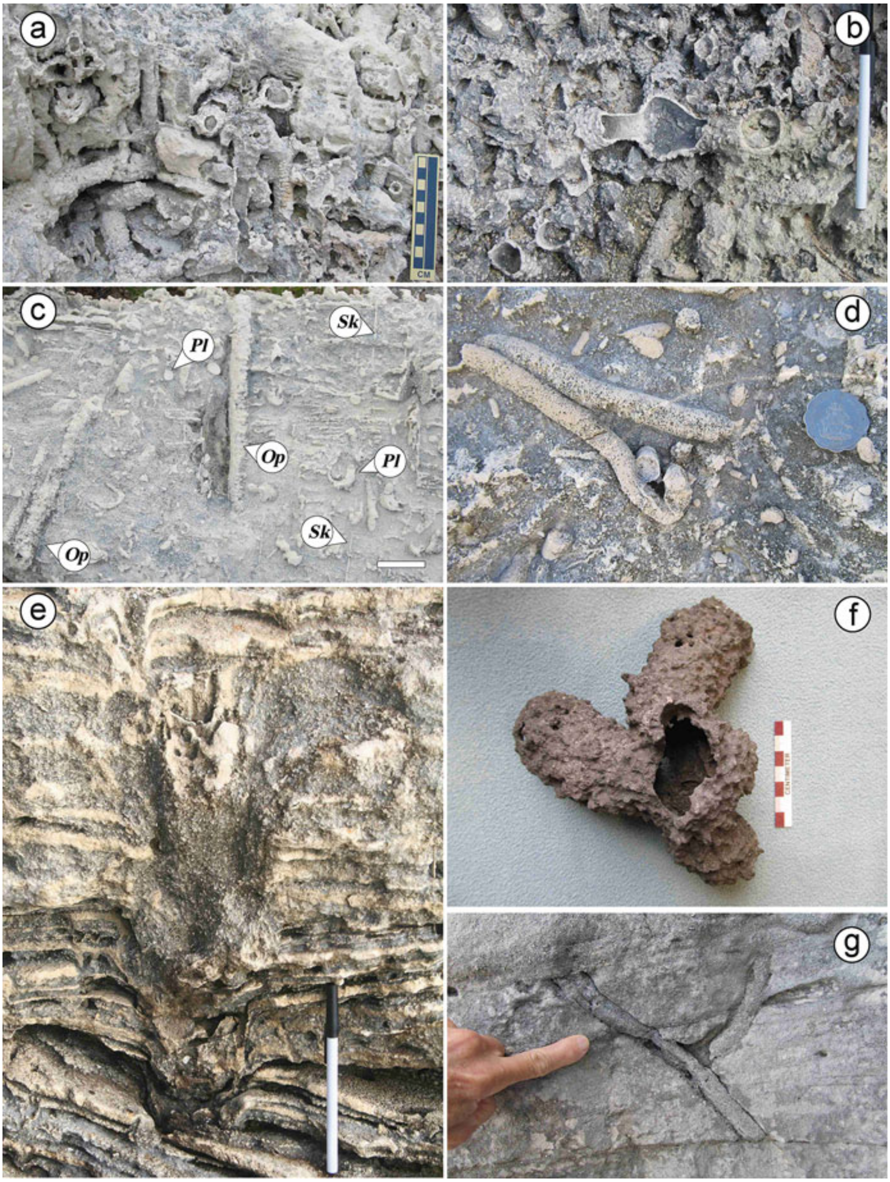

Fig. 9.30 Characteristic trace fossils from Pleistocene–Holocene Bahamian-type carbonates. (**a**) Closely-packed *Ophiomorpha nodosa* in shallow-subtidal, coral-rich grainstone, Upper Pleistocene, Cockburn Town Member, Grotto Beach Formation, Cockburn Town Fossil Coral Reef, San Salvador; (**b**) *Ophiomorpha nodosa* tunnels and shafts, bedding-plane view, same age and location as (**a**), pen is 15 cm in length: (**c**) Shallow-subtidal grainstone with abundant *Ophiomorpha nodosa* (Op), *Planolites* isp. (Pl), and *Skolithos linearis* (Sk), Upper Pleistocene, Cockburn Town Member, Grotto Beach Formation, Harry Cay, Little Exuma, scale bar is 2.5 cm; (**d**) Well-lithified *Planolites*, same age and location as (**c**); coin is 1.8 cm; (**e**) *Conichnus conicus*, a structure commonly attributed to the resting and upward-movement activity of sea anemones, in

macrobioerosion comes from the study of rocky shorelines, which are abundantly preserved in Miocene-Pliocene deposits. Clionaid sponges, echinoids, bivalves, gastropods, polychaete worms, and barnacles are the dominant members of the bioerosion community in hardgrounds and carbonate rocky shorelines, as documented in a large number of studies (e.g., Radwański 1970, 1977; Bromley and Asgaard 1993a, b; Mikulás and Pek 1995; Martinell and Domènech 1995; D'Alessandro and Massari 1997; de Gibert and Martinell 1998; Domènech et al. 2001; Bromley et al. 2009; Caracuel et al. 2011; Demírcan 2012; Pineda-Salgado et al. 2015). Typical ichnogenera include *Entobia*, *Gastrochaenolites*, *Maeandropolydora*, *Centrichnus*, *Caulostrepsis*, *Trypanites*, *Gnathichnus*, *Conchotrema*, *Oichnus*, *Phrixichnus*, *Radulichnus*, *Renichnus*, and *Rogerella*.

Shells and clasts are also host to a wide variety of bioerosion structures (e.g., Martinell and Domènech 1995; Kim and Heo 1997; de Gibert and Martinell 1998; Doyle et al. 1998; Pickerill and Donovan 1998; Farinati and Zavala 2002; Santos et al. 2003a, b, 2005, 2011). Detailed studies by Bromley and Asgaard (1993a) on a coastal karst surface on the island of Rhodes in Greece demonstrated a complex tiering structure with multiple ichnoguilds, namely the *Oichnus* ichnoguild (vagile, predator, very shallow-tier), the *Radulichnus*-*Gnathichnus* ichnoguild (vagile, algal grazer, surficial), the *Centrichnus*-*Renichnus* ichnoguild (permanent, predator, very shallow-tier), the *Entobia* ichnoguild (permanent, suspension-feeding, mid- to deep-tier), the *Trypanites*-*Caulostrepsis*-*Maeandropolydora* ichnoguild (vagile, predator, deposit feeder, and suspension feeder, deep-tier), and the *Gastrochaenolites*-*Phrixichnus* ichnoguild (permanent, suspension-feeding, deep-tier). This level of complexity in tiering structure remains undocumented for older macrobioeroding communities, although it is unclear if this is real or due to a paucity of observations.

Whale falls provided a suitable substrate for bioerosion during the Neogene (Muñiz et al. 2010; Belaústegui et al. 2012; Higgs et al. 2012). Bioerosion structures ascribed to the annelid *Osedax* (*Trypanites*) and bivalves (*Gastrochaenolites*) have been recorded in whale skeletons (Muñiz et al. 2010; Belaústegui et al. 2012; Higgs et al. 2012). From a microbioerosion standpoint, no major evolutionary innovations seem to have arisen during the Neogene (Glaub and Vogel 2004). In fact, the more recent compilation by Wisshak et al. (2006) indicated a decrease in ichnodiversity at ichnospecies level.

Walker and Brett (2002) indicated a new phase of predator intensification during the Neogene. Buccinid gastropods also diversified by the Neogene, further increasing frequency and intensity of durophagy (Walker and Brett 2002). Sea otters, which appeared by the Miocene, may have contributed to shell damage as well (Walker and Brett 2002). Overall, both drilling predation on gastropods and bivalves and shell repair frequencies seem to have increased during the Neogene, although not all estimates in this regard are consistent (Allmon et al. 1990; Kelley and Hansen 1993; Alexander and Dietl 2003).

To summarize, from an ichnologic perspective, the information available suggests that the shallow-marine Neogene is indistinguishable from the modern regarding both bioturbation and bioerosion structures. Shallow-marine ichnofaunas display a continued ichnodiversity increase, as well as more complex tiering structures, albeit without any significant change in overall taxonomic composition. A further increase in predation pressure also is evident (Huntley and Kowalewski 2007), most likely as a result of activity of predators such as stomatopod crustaceans and marine mammals.

9.4 The Paleoenvironmental Breadth of the Mesozoic Marine Revolution

Although the MMR essentially took place in shallow-water, fully marine settings (but see Walker and Voight 1994), its expression in other ecosystems, such as the deep sea and marginal-marine, brackish-water settings, also can be evaluated by the analysis of the trace-fossil record. Colonization of the deep sea has been analyzed in detail by Uchman (2003, 2004). He noted that the end-Permian mass extinction did not appear to have played a major role in decreasing trace-fossil diversity in the deep sea. His studies indicated that ichnodiversity in deep-marine environments displayed nonlinear changes, with peaks in the Late Jurassic–Early Cretaceous and Eocene, reaching a maximum in the latter and decreasing afterward. Irregular echinoids and decapod crustaceans, key players of the MMR in shallow seas at least since the Early Jurassic, apparently arrived to the deep sea by the Late Jurassic, as indicated by the presence of *Ophiomorpha* (Fig. 9.31a–d) and *Scolicia* (Fig. 9.31f–g) in turbidite deposits (Tchoumatchenco and Uchman 2001). The ichnogenus *Thalassinoides* is also relatively common in deep-marine deposits (Fig. 9.31e). The pellet-filled burrow *Tubotomaculum* seems to be restricted to deep-marine settings, which is consistent with the cache strategy used by its crustacean tracemaker (García-Ramos et al. 2014). Holothurids, as represented by the ichnogenus *Artichnus* (and its potential senior synonym *Naviculichnium*; Fig. 9.31h), can be added to this list. These bioturbators may have intensely ploughed the sea floor, increasing irrigation of oxygenated waters, and thereby deepening the redox discontinuity surface, which in turn allowed for colonization of deep tiers (Uchman 2004). *Scolicia* and *Ophiomorpha* show an increase in frequency of occurrence from the Late Cretaceous to the Eocene (Uchman 2004). Ichnologic information seems to suggest that the effects of the MMR were slightly delayed in the deep sea. Body-fossil information from deep-sea deposits is patchy, but Walker and Voight (1994) showed the existence of complex ecological interactions in Cenozoic deep-water gastropods, including high rates of shell repair in large specimens, pointing toward intense predation pressures in the deep sea.

The temporal changes in brackish-water ichnofaunas have been addressed by Buatois et al. (2005), who noted that, as in the case of the deep sea, the end-Permian mass extinction apparently did not play a major role. These authors suggested that the colonization of marginal-marine habitats did not occur at a constant rate, but rather in a number of discrete phases. Two phases relevant to understanding the expression of the MMR in brackish-water ecosystems were identified: Jurassic–Paleogene and Neogene–Recent. The Jurassic–Paleogene phase was marked by an

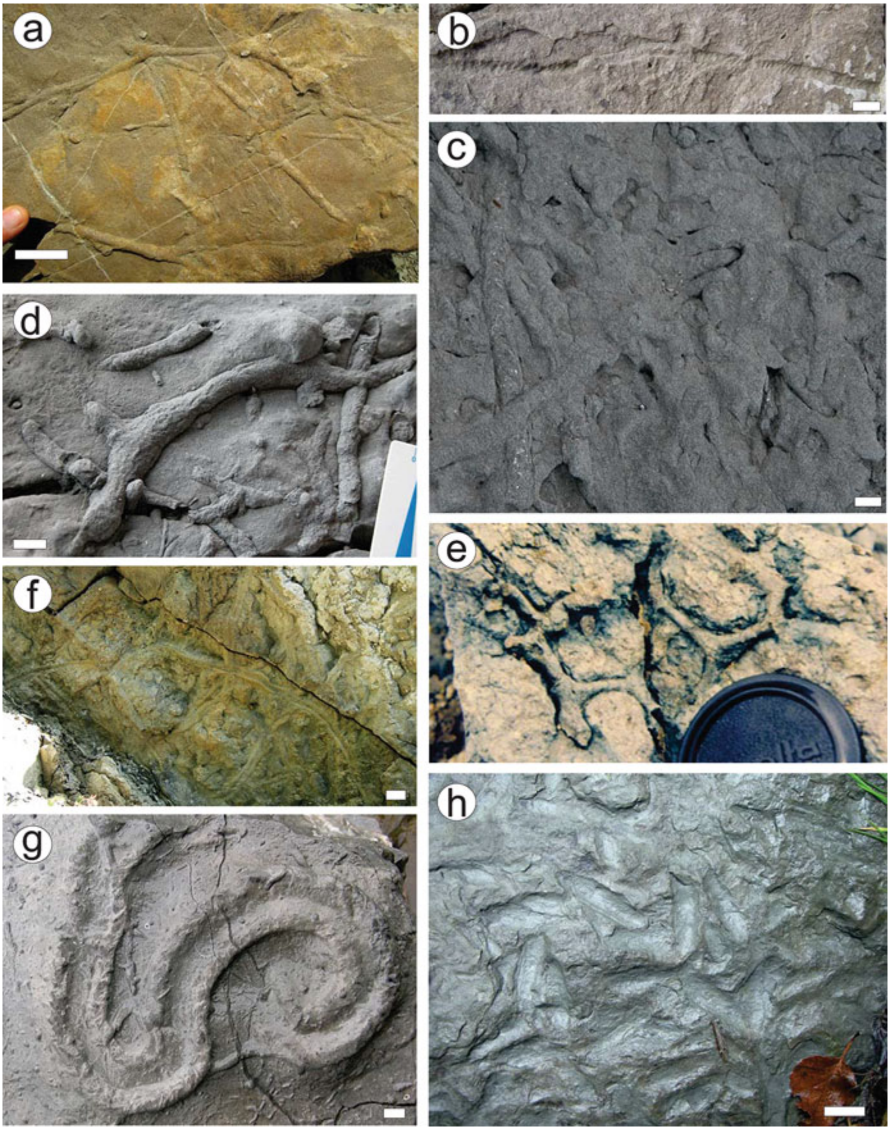

Fig. 9.31 Ichnologic representatives of the MMR in deep-marine environments. (**a**) *Ophiomorpha annulata*, Upper Eocene-Lower Oligocene, Ceylan Formation, Gelibolu Peninsula, western Turkey; (**b**) Close-up of *Ophiomorpha annulata* showing the diagnostic pelletoidal walls, Upper Eocene-Lower Oligocene, Ceylan Formation, Gelibolu Peninsula, western Turkey; (**c**) General view of surface with *Ophiomorpha rudis*, Middle to Upper Eocene, Cerro Colorado Formation, Cerro Colorado, Tierra del Fuego, Argentina; (**d**) Close-up of *Ophiomorpha rudis*, Middle to Upper Eocene, Cerro Colorado Formation, Cerro Colorado, Tierra del Fuego, Argentina; (**e**) *Thalassinoides suevicus*, Lower Cretaceous, Whisky Bay Formation, James Ross Island, Antarctica; (**f**) *Scolicia strozzi* at base of a thick-bedded sandstone turbidite, Eocene, Piwniczna Sandstone Member, Magura Formation, Tylmanowa-Baszta, Polish Carpathians; (**g**) *Scolicia* isp. at base of a thin-bedded sandstone turbidite, Upper Cretaceous–Paleocene, Ropianka Formation, Słopnice, Polish Carpathians; (**h**) High density of *Artichnus pholeoides*, a possible junior synonym of *Naviculichnium marginatum*, a burrow produced by holothurians, Eocene, Magura Formation, Tymbark-Miasto, Polish Carpathians. Lens cap diameter is 5.5 cm and *scale bars* are 1 cm

increase in ichnodiversity and degree of bioturbation in estuarine facies. In addition, colonization was not restricted to softgrounds and firmgrounds, but took place in hardground and xylic substrates as well. As in the case of fully marine ichnofaunas, the Neogene–Recent phase recorded the rise of the modern brackish-water benthos, accompanied by a further increase in ichnodiversity and intensity of bioturbation. Furthermore, cemented surfaces, shells, and clasts began to be colonized by sponges, polychaetes, gastropods, and bivalves, reflecting radiation of several groups of borers into brackish water. Most of the main players of the MMR in fully marine settings, such as decapod crustaceans, bivalves, and worms, were also dominant in brackish-water settings (Fig. 9.32a–f). Irregular echinoids, because of their lack of tolerance to dilution of normal marine salinity, were the exception, and continued for the most part to be restricted to fully marine settings.

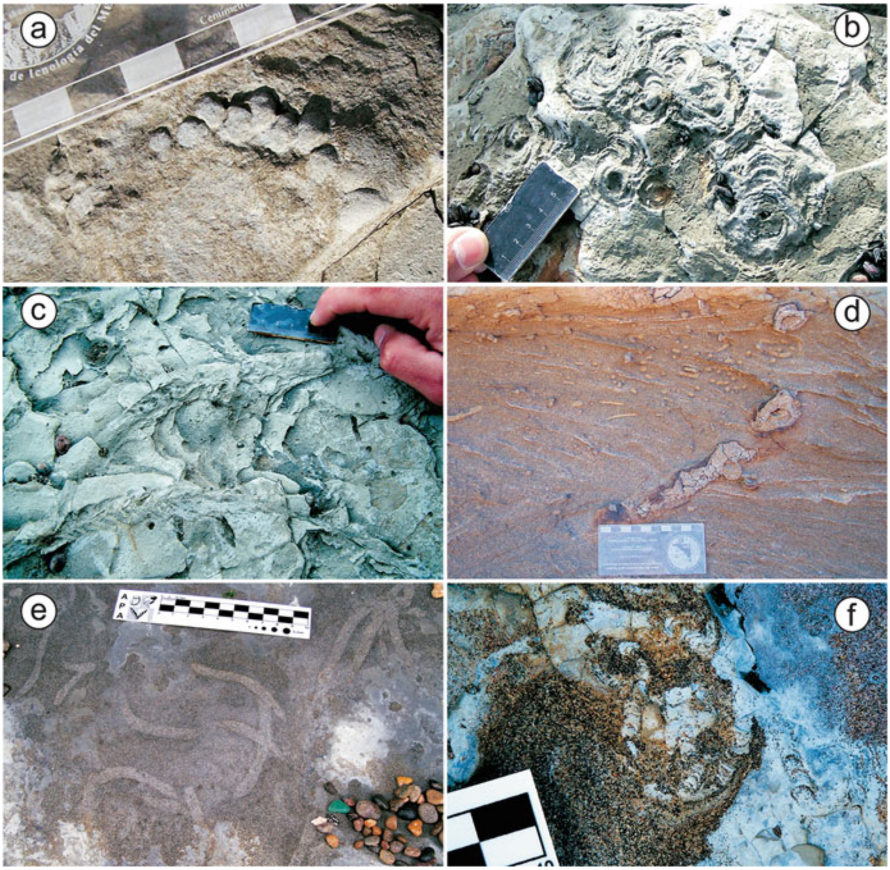

Fig. 9.32 Ichnologic representatives of the MMR in marginal-marine environments. (**a**) *Nereites* isp., bedding plane view; (**b**) *Asterosoma* isp., bedding plane view; (**c**) *Protovirgularia* isp., bedding-plane view; (**a–c**) prodelta deposits, Monte León Formation, Lower Miocene, Argentina; (**d**) *Rosselia socialis* and *Macaronichnus* isp. in cross-section view; (**e**) *Macaronichnus*, bedding-plane view; (**f**) *Nereites* isp., bedding-plane view; (**d–f**) delta-front deposits, Chenque Formation, Lower Miocene, Argentina

9.5 Behavioral Evolution and Environmental Shifts

In addition to the arrival to the deep sea of crustaceans and echinoids capable of creating extensive burrow systems during the MMR, other ichnotaxa experienced environmental shifts coupled with behavioral changes. This is particularly well illustrated by the trace fossil *Zoophycos*, which records a change in morphology and in penetration depth and inferred behavior of the producer during the MMR (e.g., Seilacher 1986; Chamberlain 2000; Kotake 2014; our Fig. 9.33a–e). The morphology of Paleozoic and early Mesozoic *Zoophycos* is relatively simple, consisting of irregularly lobate, "rooster tail"-like spreiten (Fig. 9.34a) with the tendency to turn into a spiral (Seilacher 1986; our Fig. 9.34b–c). In addition, forms were described with lobate spreiten deviating at several levels from a central shaft (e.g., Knaust 2004; Chamberlain 2000; Fig. 9.34d). Normally these *Zoophycos* were emplaced in a shallow-tier position, and the producers followed a sediment-feeding behavior (e.g., Knaust 2004). The host sediment is commonly muddy sand to sandy mud that accumulated in shallow-marine waters from above wave base to outer shelf settings (e.g., Bottjer et al. 1988). Some specimens, however, have been reported from deeper-water deposits, but these occurrences are rare (e.g., Wetzel et al. 2007). Morphologically similar *Zoophycos* specimens occur in fairly high abundance until the Middle Jurassic (Seilacher 1986).

However, since the Late Triassic, *Zoophycos* producers tended to move to deeper-water settings, and *Zoophycos* became sparse in deposits that accumulated above storm-wave base. Late Jurassic shelf settings immediately below storm-wave base were mostly abandoned by *Zoophycos* producers, and since the Oligocene outer-shelf settings also were almost no longer utilized by these tracemakers (Bottjer et al. 1988), with just a few exceptions (e.g., Carmona et al. 2008, 2012). Instead, the *Zoophycos* producers migrated to deeper-water environments (e.g., Seilacher 1986), and today they inhabit continental slope and abyssal plain sediments virtually exclusively (e.g., Wetzel 1991).

This shift in the habitat was accompanied by an evolution of behavior recorded by the formation of multi-lobate and coiled, increasingly complex spreite of *Zoophycos* (Seilacher 1986; Chamberlain 2000; Kotake 2014; our Fig. 9.34e–f), along with an increase in size (area occupied by an individual specimen) and penetration depth. The latter is documented by cross-cutting relationships with other burrows. Cretaceous *Zoophycos* was commonly cut by *Chondrites* (e.g., Frey and Bromley 1985), and *Chondrites* and *Zoophycos* may occupy the same tier in Upper Cretaceous chalks (Bromley and Ekdale 1984b), whereas today *Zoophycos* represents the deepest tier and cross-cuts all other burrows including *Chondrites* (e.g., Wetzel and Werner 1981). Furthermore, a change in nutritional behavior can be inferred, with a strip-mining, sediment-feeding strategy suggested for the Triassic (Knaust 2004) and even Middle Jurassic (Olivero and Gaillard 1996). For modern *Zoophycos,* a temporary-cache producer behavior can be deduced from material within the spreite that is significantly younger than the host sediment (e.g., Löwemark and Grootes 2004). Some *Zoophycos* producers may have employed a cache strategy as early as the Cretaceous, as some spreite exhibit obvious color

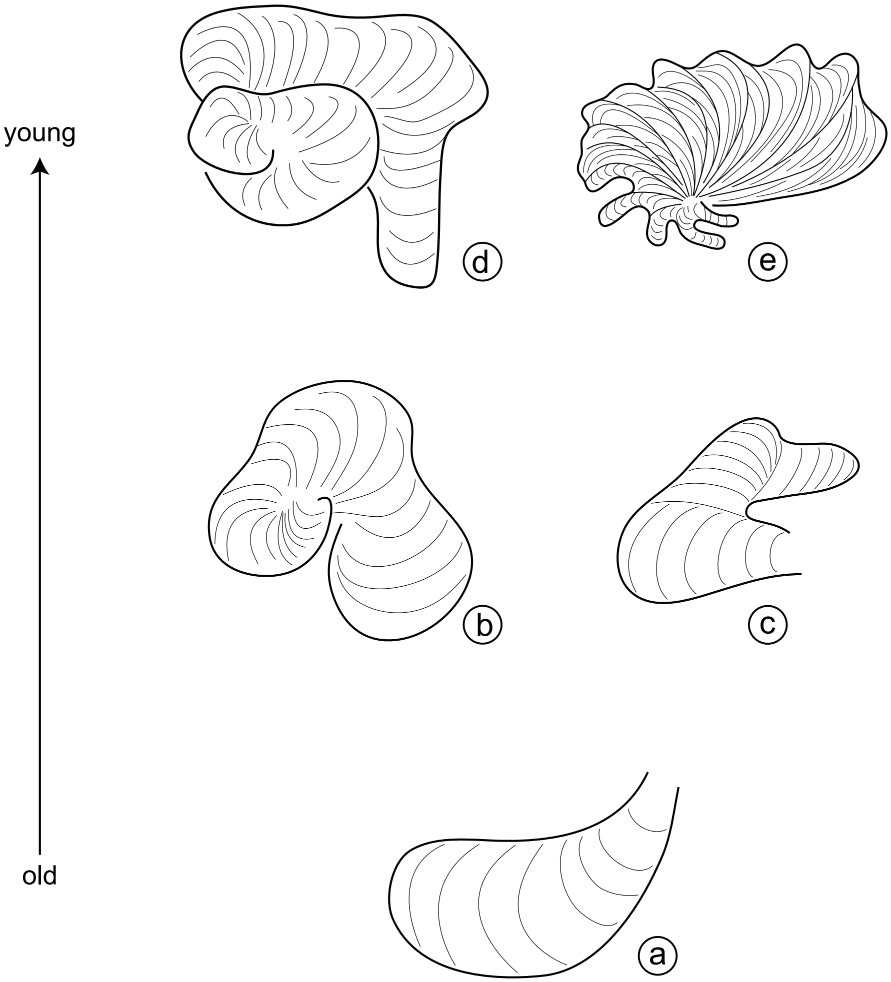

Fig. 9.33 Evolution of *Zoophycos* (based on Seilacher 1977 and Chamberlain 2000). (**a**) Basic, protrusive "rooster tail"-shaped spreite, which occurred in the Palaeozoic and is still produced today; (**b**) Continuous coiled spreite form, which occurred for the first time in the late Paleozoic to early Mesozoic; (**c**) Discontinuously formed spreite consisting of several "rooster-tail"-like spreite one attached to the side/tip of another, a morphology recorded for the first time in the late Paleozoic to early Mesozoic; (**d**) Multiply coiled, helicoidal spreite typical of the Mesozoic onward; (**e**) Helicoidal spreite system consisting of laterally assembled "rooster tail"-like spreite, also typical of the Mesozoic onward (redrawn from Seilacher 2007)

changes between lamellae of the spreite and with the host sediment as well. This can hardly be explained solely by in situ sediment sorting (for instance, see Fig. 3F in Locklair and Savrda 1998). However, this observation has not yet been investigated in detail. Furthermore, with time, it appears that the *Zoophycos* producers increasingly preferred muddy substrates.

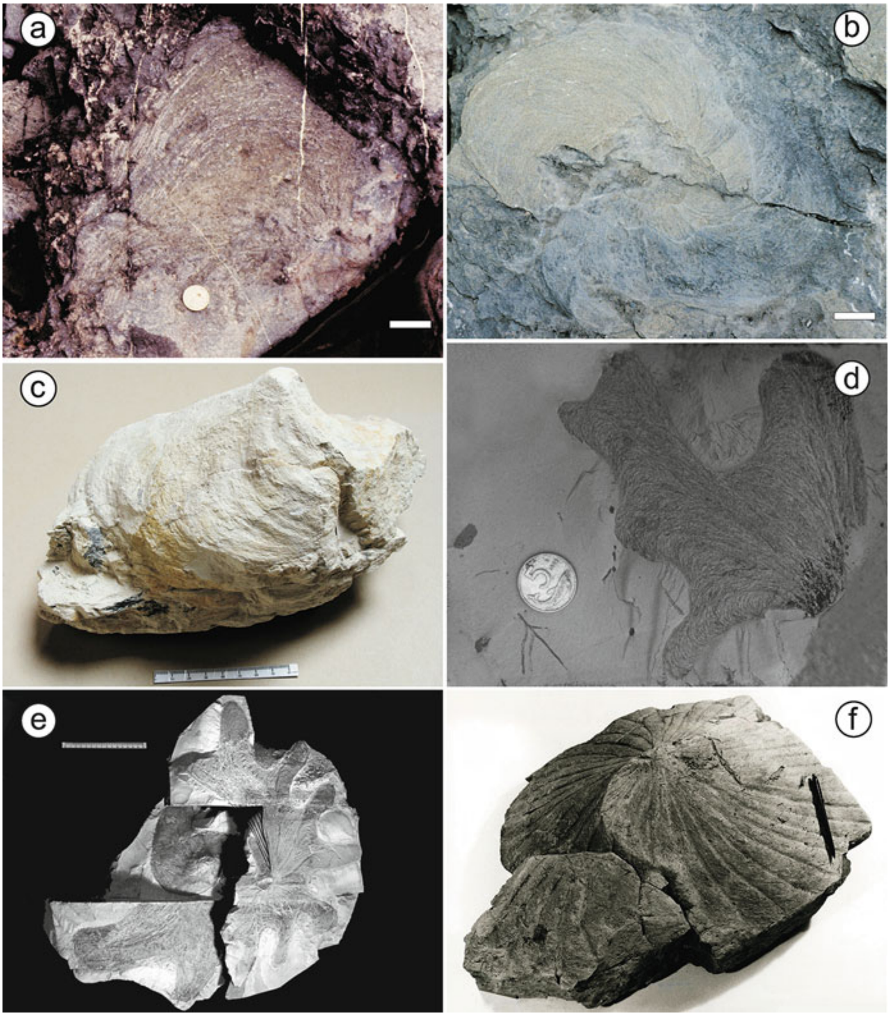

Fig. 9.34 Evolution of *Zoophycos*. (**a**) Simple, "rooster-tail"-like *Zoophycos* from Lower Carboniferous limestone deposited near storm wave-base, near Ogmore-by-Sea, Great Britain (for further details see Wu 1982); (**b**) Simply coiled *Zoophycos* from Bajocian siliciclastic fine-grained deposits near Hauenstein (northern Switzerland); (**c**) Excavated coiled *Zoophycos* specimen from Upper Cretaceous pelagic limestone ("Scaglia") north of Sciacca (Sicily, Italy); (**d**) Lobate *Zoophycos* from Upper Cretaceous Flysch showing major and minor lamellae (near Gropello, northern Italy); (**e**) *Zoophycos* from the Paleogene Flysch in the Apennine near Florence, on display in the Institut und Museum für Geologie und Paläontologie, University of Tübingen in 1995. The specimen was discovered by A. Seilacher, prepared by H. Luginsland and photographed by W. Wetzel (all Tübingen at that time); courtesy of A. Seilacher (for details see Seilacher 2007, plate 38 h); (**f**) *Zoophycos* with major and minor lamellae from Seravallian-Tortonian pelagic Marne ad Orbulina near Monte Aquilone (Latium, Italy); courtesy of P. Belotti (Roma, Italy), original figure (fig. 8) and further details in Bellotti and Valeri (1978)

The stratigraphic distribution of the U-shaped ichnogenus *Rhizocorallium* also seems to show some connection with the MMR. Knaust (2013) reviewed the taxonomy of *Rhizocorallium*, concluding that only two ichnospecies are valid, *R. commune* and *R. jenense*, although ichnosubspecies and varieties are recognized. *Rhizocorallium commune* is known since the Cambrian and has not displayed significant morphologic change, although size has shown some variation through the Phanerozoic, essentially an increase through the Paleozoic, with a decrease after the end-Permian mass extinction, followed by a time of new size increase (Knaust 2013). This ichnospecies has been attributed to worms (Knaust 2013). On the contrary, *Rhizocorallium jenense* originated in the Triassic, reflecting an adaptation to firm substrates that was unknown prior to the MMR, and having been produced most likely by crustaceans. Also, as is the case for *Zoophycos*, *Rhizocorallium* seems to show environmental shifts through time. In particular, *Rhizocorallium commune* is common in shallow-marine environments during the Paleozoic and Mesozoic, becoming relatively abundant in the deep sea during the Cenozoic (Knaust 2013).

9.6 Evolution of the Mixed Layer

The evolution of the uppermost interval of the seafloor, the mixed layer, cannot be described step-by-step over long time spans. This layer is homogeneous in appearance and lacks other diagnostic characteristics (Fig. 9.35a–d). Thus, its crucial parameter is only its thickness, the so-called mixed layer depth (e.g., Boudreau 1998). However, the mixed layer depth cannot be measured in continuously accumulating deposits, because deeper penetrating inhabitants of the transitional layer normally overprint the homogeneous ichnofabric (Wetzel 1981; Werner and Wetzel 1982). Therefore, the preservation potential of the mixed layer is low. Only in the case of frozen tiering resulting from abrupt de-oxygenation or non-erosive deposition of event beds will the mixed layer be preserved in the rock record (e.g., Savrda and Bottjer 1986; Savrda and Ozalas 1992). Evidence of the mixed layer can be detected, albeit indirectly, by the presence of burrow mottlings that are cross-cut by discrete trace fossils emplaced in the transition layer.

Today the mixed layer of the seafloor is normally up to 10 cm thick as defined by excess concentration of radiotracers (e.g., Boudreau 1998). In the rock record, however, the mixed layer thickness can be determined less exactly because its boundary to the transitional layer is gradational (Fig. 9.35b). The homogeneous appearance of the mixed layer is due to the production of biodeformational structures by meiofauna and crypto-bioturbators, shallowly burrowing macrofauna, or even bulldozing megafauna. These organisms utilize the organic matter close to or on the sediment surface and process the deposits in a way such that no discrete traces are left. Furthermore, a homogeneous appearance is favored by the very soft to soupy sediment consistency. Mixed layer depth also depends on environmental conditions, in particular (1) penetration depth of burrows; and (2) burrow diameter, with both decreasing with

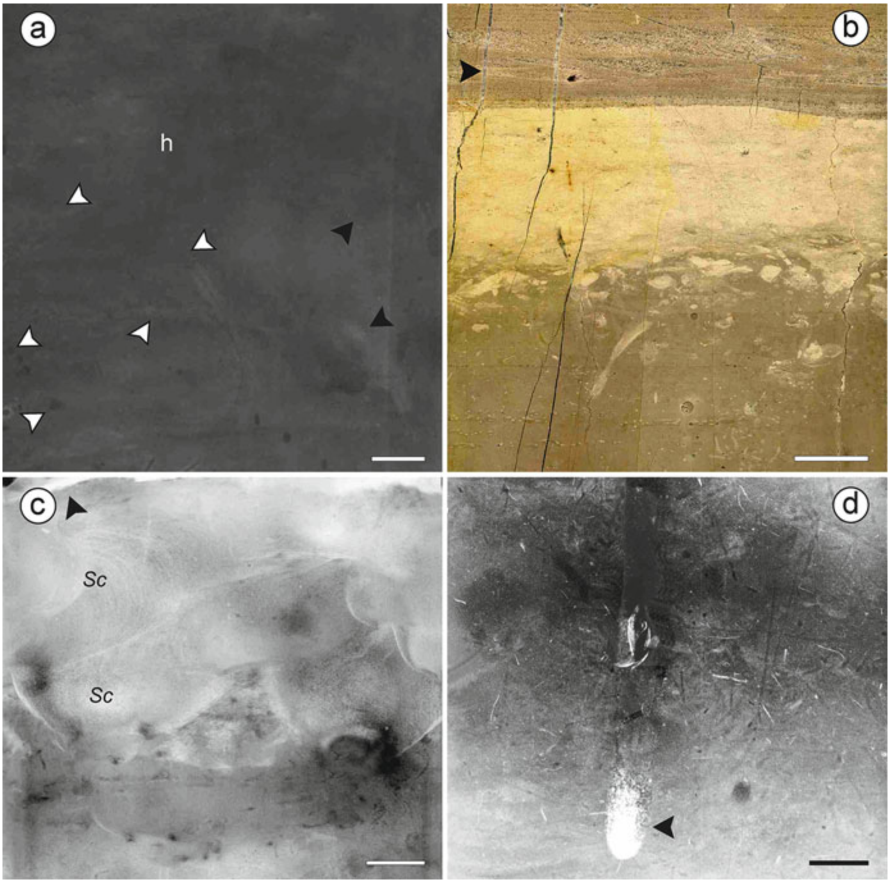

Fig. 9.35 Mixed layer traces. (**a**) Mixed layer (h) in modern muddy sediment; upper boundary of the transitional layer is marked by the occurrence of lined tubes (*black arrows*) or fairly sharp bounded sand-filled *Planolites*-like burrows (*white arrows*). Core Sonne 220 34–1 (19° 14.06′ N/108° 9.23′ E), South China Sea, 50 m water depth; for details see Wiesner et al. 2012); (**b**) Frozen-tiering structure underneath a low- to non-erosive turbidite having hydraulically light foraminifera shells at the base. The transition between mixed layer and transitional layer is gradational and occupies about ¼ of the maximum thickness of the transitional layer (~4 cm). Upper Cretaceous flysch from the area of Gropello, northern Italy; (**c**) *Scolicia* isp. (*Sc*) producers burrowing into the mixed layer from below and extinguishing it to a high degree; lower boundary of a recently deposited event layer is marked by an arrow. Core Sonne 132 35–1 (13° 37.12′ N/119° 58.43′ E), South China Sea, 3202 m water depth; for details see Wiesner et al. 1998), 0–13 cm core depth; (**d**) Basal part of a *Thalassinoides* filled with foraminifera shells (*arrow*) that have been collected by the burrow producer from the seafloor, probably as additional food source. In this way benthic food content of the mixed layer was lowered by a transitional-layer inhabitant. Core 12345–5 (15° 28.8′ N/17° 21.6 W), off NW Africa, 966 m water depth; for details see Wetzel 1981), 107–120 cm core depth

decreasing oxygenation and benthic food content (e.g., Wetzel and Uchman 2012). In turn, the burial of organic matter is affected by the sedimentation rate (e.g., Müller and Suess 1979).

Over geologic time, mixed-layer producers became capable of burrowing to increasingly greater depths. A behavioral evolution is also evident for burrows produced by inhabitants of the transitional layer. Besides a trend to explore increasingly deeper intervals within the seafloor, the burrow producers expanded their behavioral programs to supplement limited food resources. With respect to the mixed layer, three strategies of transitional-layer inhabitants are of importance, (1) temporary feeding directly on the sediment surface; (2) burrowing upward into the mixed layer from below; and (3) taking benthic food from the sediment surface to store in a cache. Again, with time, the number and abundance of ichnogenera exhibiting such behavioral programs increased. For example, the producers of some *Nereites* or *Scolicia* feed temporarily on or close to the sediment surface, respectively (Fig. 9.35c; Wetzel 2008), and the producers of *Zoophycos* and *Thalassinoides* can construct and utilize caches (Fig. 9.35d; e.g., Dworschak 1987; Löwemark and Werner 2001).

Mixed layer thickness is affected by two long-term strategies of burrowing organisms. The inhabitants of the mixed layer tend to expand their habitat vertically, whereas deep-burrowing organisms living in the transitional layer utilize food resources from the mixed layer. The mixed-layer inhabitants, however, often respond more rapidly to environmental changes. Therefore, thickness of the mixed layer, as evidenced by its homogeneous appearance, may fluctuate even during the course of a year, depending on oxygenation and benthic food supply and overprinting (competition) by transitional-layer inhabitants. Consequently, for an analysis of the development of the mixed layer, it is necessary to compare mixed layers that formed within similar environmental settings over geologic time. Given the low fossilization potential of the mixed layer, the data available at present are too sparse for drawing detailed conclusions. In any case, available ichnologic information suggests that the origin of the modern mixed layer can be traced back at least to the Mesozoic.

9.7 Role of Paleogeography and Climate

There is growing evidence that trace fossils may reveal paleogeographic patterns (e.g., Jensen et al. 2013), and that infaunalization trajectories may have been disparate in the different oceans surrounding various paleocontinents (e.g., Mángano and Buatois 2011) during the Cambrian explosion (see Chap. 3) and the Great Ordovician Biodiversification Event (see Chap. 4). Here we will explore potential similar ichnologic trends in connection with the MMR.

Understanding the role of paleogeography and climate on the MMR and its potential ichnologic expression is still in its infancy. However, information from modern environments provides an actualistic base that may help to detect potential patterns in the post-Paleozoic world. Thayer (1983) indicated that deposit-feeding taxa in warm-water settings tend to disturb sediment at a greater rate than is the case in cold-water regimes. Cadée (2001) noted an increase in degree of bioturbation and diversity from high-latitude Arctic coasts to low-latitude warm coasts. In addition, he pointed to latitudinal faunal changes, with a diverse callianassid and crab fauna in low latitudes, which is absent or has low diversity in Arctic regions. In the same vein, irregular echinoids tend to display a preference for low- and mid-latitudes (Goldring et al. 2004, 2007). Goldring and coworkers expanded these ideas, by integrating observations from modern environments with information from the Mesozoic and Cenozoic trace-fossil record. According to their model, the distribution of the benthos and associated biogenic structures can be summarized for the three major climatic zones: (1) tropics and subtropics with *Ophiomorpha* and echinoid trace fossils; (2) temperate zone with echinoid trace fossils and *Thalassinoides;* and (3) high latitude zone with only mollusk and worm trace fossils. Gingras et al. (2006) extended the dominance of mollusk and worm burrows to the temperate zone. In addition, Quiroz et al. (2010) summarized available information on the polychaete trace fossil *Macaronichnus*, demonstrating its preference for high to mid latitudes (see also Gingras et al. 2006).

Interestingly, Quiroz et al. (2010) noted the general absence of *Macaronichnus* in Paleocene to lower Eocene deposits, and interpreted this pattern as a result of overall high temperatures and expansion of subtropical belts during these times (Zachos et al. 2001; Hollis et al. 2009). Quiroz et al. (2010) also noted that the few middle to upper Eocene occurrences are from high latitudes (e.g., Olivero et al. 2008; Pearson et al. 2013), most likely reflecting the transition to overall colder climates by these times.

These trends are, however, not without exceptions. Both *Ophiomorpha* and *Scolicia* are abundant in Miocene mid-latitude shallow-marine deposits of Patagonia under temperate to cold climates, representing a departure to the proposed pattern (Buatois et al. 2003; Carmona et al. 2008). Also, *Macaronichnus* has been documented in the Neogene low-latitude nearshore deposits of Venezuela, representing an apparent anomaly to the overall pattern (Quiroz et al. 2010). However, as noted by these authors, this occurrence most likely reflects coastal upwelling of nutrient-rich cold waters, which was extensive in the Caribbean prior to the final closure of the Panama Isthmus in the Pliocene (O'Dea et al. 2007). Despite potential shortcomings, it seems that the present geographic distribution of infaunal organisms can be traced back to the onset of the MMR.

Ongoing research by Olivero and López-Cabrera (2014) indicates that complex spreite burrows, such as *Paradictyodora* and *Euflabella*, appear to be restricted to southern high paleolatitudes during the Late Cretaceous. Strong seasonal variations in primary production and cooling may have promoted the establishment of specialized strategies and behaviors. These authors also noted that this pattern in trace-fossil distribution parallels the increased provincialism in bivalves and ammonites during the Late Cretaceous in southern Gondwana, reflecting concurrent paleogeographical restrictions in the benthos and nekton.

Predation pressures in modern oceans also display a geographic component (Vermeij 1978, 1987). He noted that predation is apparently more intense in the

Western Pacific and Indian Oceans than in the Atlantic Ocean, with the Eastern Pacific occupying an intermediate position. From an ichnologic standpoint, this is revealed by contrasting frequencies of shell repair in neritid and terebrid gastropods in the different oceans. However, tracking these trends back in time to assess a paleogeographic component of escalation is still premature. Also, information from modern environments indicates that predation levels are higher in the tropics (Freestone et al. 2011).

9.8 Discussion: Secular Changes in Bioturbation and Ichnofaunas and the Mesozoic Marine Revolution

The pattern in trace-fossil distribution during the Mesozoic and Cenozoic as previously outlined provides a basis to discuss further how the MMR is expressed in the ichnologic record. First, evaluation of the trace-fossil record may help to detect the timing of this major evolutionary event. In this regard, the Triassic can be viewed as setting the stage for the revolution, albeit with burrows by decapod crustaceans already becoming dominant in carbonate settings (e.g., Knaust 2007). Interestingly, the MMR appears to be at full speed by the Early Jurassic. This is evidenced not only by the increased role of decapod crustaceans, but also by other key players of the Modern Evolutionary Fauna, such as irregular echinoids and bivalves. Infaunal tiering structure also displays a remarkable increase in complexity at this time (Fig. 9.36). The dominant tracemakers remained essentially the same during the rest of the Mesozoic and through the Cenozoic. Complexity of infaunal tiering structures also did not exhibit any further increase until the Neogene (Fig. 9.36). If this chronology is correct, then infaunalization resulting from the MMR can be viewed as a relatively rapid process followed by a long period of stasis. This pattern, essentially based on the analysis of the ichnologic record, is partially consistent with that derived from the analysis of the body-fossil record. In a series of classic studies (Ausich and Bottjer 1982, 1985; Bottjer and Ausich 1986), the tiering history of both infaunal and epifaunal communities of suspension feeders was assessed. These studies demonstrated that epifaunal suspension feeders were strongly affected by the end-Permian mass extinction, showing a relatively rapid recovery in the Triassic, reaching a plateau of maximum diversity during the Jurassic, a subsequent decrease through the Cretaceous, and then reaching another plateau in the Cenozoic. Infaunal suspension feeders displayed a remarkable increase in penetration depth by the late Paleozoic, being apparently unaffected by the end-Permian mass extinction and reaching a plateau all through the Mesozoic and Cenozoic. Ichnogeneric compilations show that the MMR was associated with an increase of global ichnodiversity of 35 % in marine environments (see Chap. 16).

Secondly, comparing the timing of infaunalization with respect to the timing of increase in predation pressures may yield some insights into the complexities of escalation. Although there are still doubts regarding secular changes in predation pressures, drilling apparently was not significant during the Jurassic (Harper 2003),

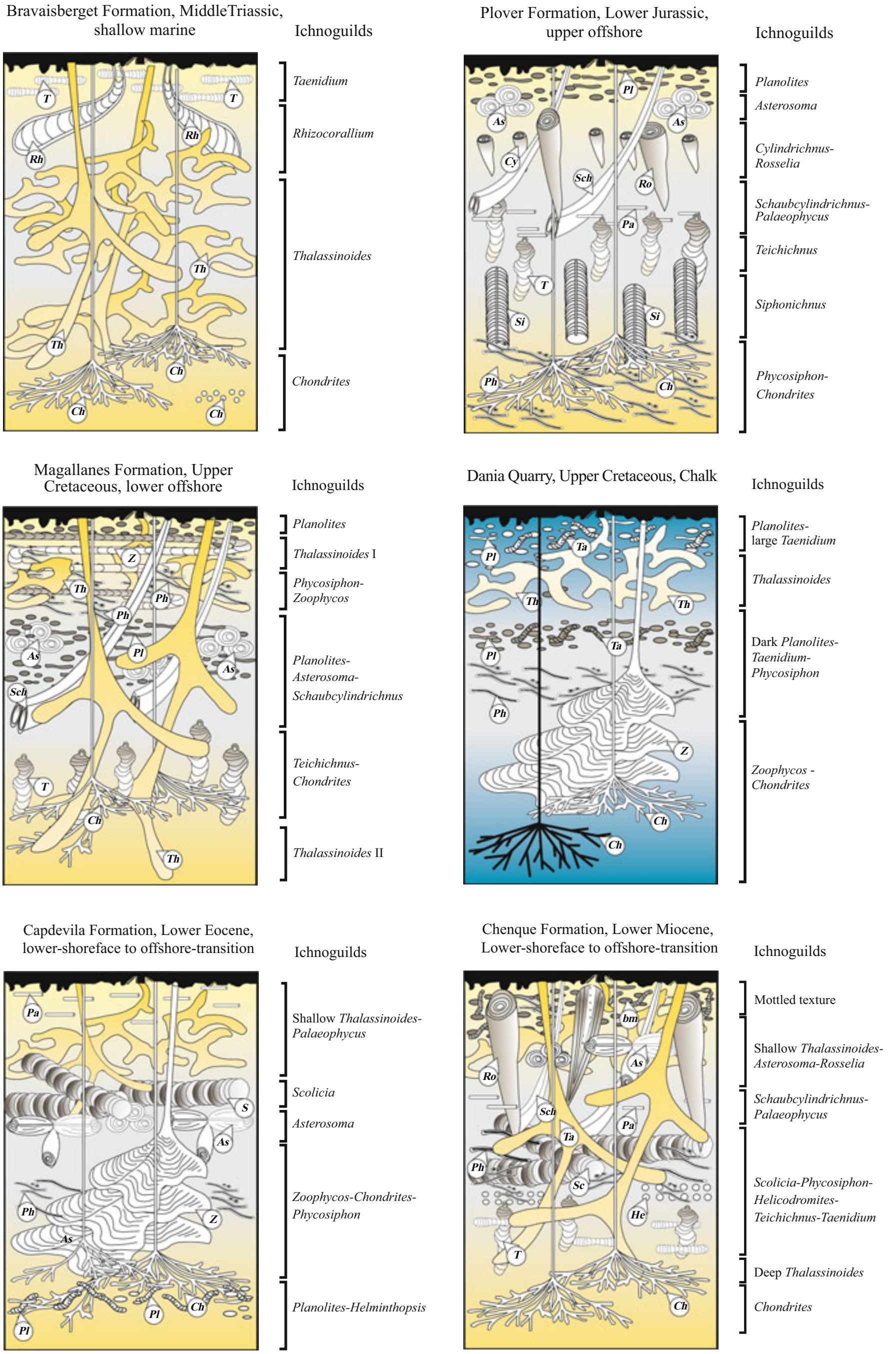

Fig. 9.36 Representative tiering structures and ichnoguilds from selected case studies illustrating infaunal colonization during and in the aftermath of the MMR. Note that by the Early Jurassic, complex tiering patterns have been established. However, an increase in complexity, particularly reflected by the increased number of ichnotaxa per ichnoguild, is apparent by the Miocene. Reconstructions based on Mørk and Bromley (2008); Burns et al. (2013); Buatois et al. (2013); Buatois et al. (2011); Ekdale and Bromley (1991); Villegas-Martín et al. (2014) and Carmona et al. (2012)

although durophagous predation may have displayed an increase in importance, albeit locally, by the Middle Jurassic (Zatoń and Salamon 2008). In any case, by the Cretaceous, predation pressures experienced a significant increase (Vermeij et al. 1981; Kelley and Hansen 2003). Therefore, ichnologic evidence suggests that infaunalization predates an overall increase of predation pressures by approximately 50 Myr. The infaunal environment is typically regarded as a haven from predation (Vermeij 1987) and, therefore, infaunalization could be perceived as an adaptive response to increased predation (Bottjer and Ausich 1986). However, the chronology presented above does not support this cause-effect scenario; rather a more complex set of feedback mechanisms between infaunalization and predation is thought to be the case. A similar conclusion was reached by McRoberts (2001) based on the analysis of Triassic bivalves. Interestingly, infaunalization occurring before an increase in predation has been noted during the Cambrian explosion as well (MacNaughton and Narbonne 1999). In the same vein, complex geobiologic feedbacks involving bioturbation have been invoked recently for the Cambrian diversification event (Mángano and Buatois 2014).

Thirdly, evaluation of the Mesozoic–Cenozoic ichnologic record provides impetus to revisit the bulldozing hypothesis of Thayer (1979, 1983), who proposed that biological disturbance increased through the Phanerozoic. Sediment disturbance tends to be greater when large, mobile bioturbators occur in dense populations (Thayer 1983). In particular, sediment bulldozers rank as the most efficient bioturbators, with their ability to displace sediment, manipulate sediment in burrowing and crawling, and manipulate sediment externally in feeding. Based on the integration of observations from modern environments with those from the fossil record, he noted that post-Paleozoic bioturbators rework sediment faster, tend to burrow deeper, and can generate shorter sediment-turnover times than Paleozoic taxa. The present review of the post-Paleozoic ichnologic record supports this view. In fact, it can be argued that a dramatic increase in sediment bulldozing is one of the diagnostic features of the MMR. Most, if not all, of the bioturbators ranked by Thayer (1983) as most efficient can be regarded as main players in the MMR. Examples include decapod crustaceans [e.g., *Callichirus major* (formerly *Callianassa major*) and many other callianassids, and the many species of *Uca*], clypeasteroid echinoderms (e.g., *Dendraster excentricus*), irregular echinoids (e.g., *Echinocardium cordatum*, *Meoma ventricosa*), tellinacean bivalves (e.g., *Macoma balthica*), protobranch bivalves (e.g., *Portlandia arctica*), and arenicolid polychaetes (e.g., *Abarenicola pacifica*). In addition to this list of invertebrates, it should be noted that marine mammals are important sediment bulldozers throughout Cenozoic (Thayer 1983). The turnover in ichnofaunal composition that took place in the early Mesozoic fully supports an impressive increase in sediment disturbance in connection with the MMR.

Fourth, it has long been argued that the fossil record indicates a pattern of onshore origination of evolutionary innovations and subsequent expansion of new forms to deeper water (Jablonski et al. 1983; Sepkoski and Miller 1985; Jablonski and Bottjer 1990; Sepkoski 1991; Jablonski 2005). Onshore-offshore trends are certainly displayed by individual ichnotaxa, such as *Zoophycos* (Bottjer et al. 1988) and *Rhizocorallium commune* (Knaust 2013). In the case of the innovations associated with the MMR, the pattern of trace-fossil distribution supports a delayed arrival to deep-marine settings. Whereas the changes of this significant evolutionary event were in place in shallow-water settings by the Early Jurassic, they may only have reached the deep sea by the Late Jurassic (Tchoumatchenco and Uchman 2001). Intense bioturbation in deep-marine sediments has been recorded at least since the Cretaceous (Ekdale 1977). In any case, biogenic mixing is even today much slower in the deep sea than in shelf areas (Thayer 1983).

9.9 Conclusions

The ichnologic record of the MMR provides information on various aspects of this major evolutionary event, such as the types of burrowers involved, the timing of this breakthrough, the complexity of infaunal tiering structures, the paleoenvironmental breadth of the event, and the interplay between predation and infaunalization, among other points. Crustaceans, bivalves, echinoids, and worms were arguably the most important burrowers. The MMR appears to be at full speed by the Early Jurassic, as indicated not only by the overall dominance of these key burrower groups, but also by the remarkable increase in complexity of tiering structures in shallow-marine deposits. The complexity of infaunal tiering structures did not experience further increase until the Neogene, suggesting that the MMR was a relatively rapid event followed by a long period of stasis. The MMR took place in shallow-water settings, both fully marine and brackish, by the Early Jurassic, but this evolutionary event may only have reached the deep sea by the Late Jurassic. Infaunalization predated an increase of predation pressures by approximately 50 Myr, suggesting a complex set of feedback mechanisms between predation and infaunalization rather than a cause-effect between the two. Ichnologic information suggests that post-Paleozoic bioturbators reworked sediment faster, tended to burrow deeper, and had shorter turnover times than Paleozoic taxa. Our review strongly supports the bulldozing hypothesis, indicating a dramatic rise in biogenic sediment disturbance during the MMR.

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Chapter 10
The Mesozoic Vertebrate Radiation in Terrestrial Settings

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10.1 Introduction

Given their worldwide abundance, it is not surprising that the study of Mesozoic vertebrate tracks is the most ancient branch of vertebrate ichnology. Dinosaur tracks were first observed and figured by Native Americans by, if not before, the seventeenth century (Lockley et al. 2006a), and the first document dates back to the earliest nineteenth century when Pliny Moody reported the discovery of large tracks in the eastern U.S. With Edward Hitchcock (who would eventually coin the world "ichnology"), tracks began to be approached scientifically (e.g., Hitchcock 1858) and subsequent papers by Wolfgang Soergel (Soergel 1925), Othenio Abel (Abel 1935)

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and Roland Bird (Bird 1939, 1944) brought consciousness and the first scientific methods into the discipline. Haubold (1971a, b) published two seminal papers which constituted the base of the first reliable track-trackmakers associations.

In the late twentieth century, the discovery of numerous and vast dinosaur tracksites contributed to the so-called "renaissance" in vertebrate ichnology (Lockley and Gillette 1987) and brought the first solid attempts to standardize study procedures (Leonardi 1987). With this new impetus the first ideas were put forward for using track data for palebiologic (mainly behavioral and physiologic) studies (Lockley and Gillette 1987). This continued in the last two decades with the publication of several seminal volumes, especially on dinosaur tracks (Leonardi 1987, 1994; Gillette and Lockley 1989; Thulborn 1990; Lockley 1991; Lockley and Hunt 1995a; Lockley and Meyer 2000). In order to fully contribute to the paleobiology of dinosaurs, however, the long-standing debate of the relation between tracks and trackmakers needed to be addressed. No paleobiologic inference can in fact be drawn except by interpreting tracks as the result of the activity of a trackmaker, identified as belonging to a particular taxon. It is commonly assumed that tracks can rarely be accurately associated with their producers at the species or genus level (Farlow and Pianka 2000; Carrano and Wilson 2001). During its two centuries of history, however, vertebrate ichnology built a broad consensus on the assignment of some footprint morphogroups to broad taxonomic categories, based on clear analysis of the morphologies of digits, hands, and feet, and comparisons of tracks with hand and foot skeletons (e.g., Haubold 1971a, b; Demathieu and Demathieu 2004; Padian et al. 2010; Heckert et al. 2010) or, rarely, on the direct association of track and fossil material (e.g., Voigt et al. 2012). Most authors agree that a trackmaker attribution at a high taxonomic level is often possible (e.g., Baird 1980; Sarjeant 1990; Olsen et al. 2002; Carrano and Wilson 2001; Thulborn 2006), and in fact morphofamilies or ichnofamilies have been referred to in the literature since the early twentieth century (Lull 1904). In the 1980s, Demathieu and colleagues began to elaborate on the possibility of implementing tracks in phylogenetic studies (Demathieu 1981; Demathieu and Haubold 1978). Demathieu also pioneered the use of vertebrate tracks in many other areas of paleobiologic studies (Demathieu 1986); since then, a synapomorphy-based approach has been employed in a number of studies (Olsen 1995; Olsen and Baird 1986; Olsen et al. 1998; Wilson and Carrano 1999; Haubold and Klein 2000, 2002; Padian 2003; Wilson 2005; Wright 2005; Brusatte et al. 2010b; Kubo and Kubo 2012; Bernardi et al. 2015). This perspective has considerably constrained potential trackmakers finally allowing full hypothesis testing and a better integration of vertebrate ichnology in paleobiologic analysis.

10.2 Trends and Events During the Mesozoic

10.2.1 Tetrapods Across the PT Boundary

A track is the result of the activity of a producer, or trackmaker, namely a track is the imprint of an autopodium (a limb) registered during locomotion. The vertebrate track record can be thought as an archive of the evolution of foot morphology and posture of extinct and extant vertebrates. Here we must also remember that tracks also record many details of soft tissue morphology, not revealed by body fossils, which in many cases may lack foot skeletons, even when other key diagnostic elements are present. When consecutive steps are impressed as an animal moves, in fact, a trackway is formed and its parameters (i.e., width, distance between single tracks, angle between tracks, distance of the tracks from midline, etc.) can be used to accurately define the walking posture of its producer. Assessing posture from a skeleton involves observing limb articular surfaces and manipulating (physically or virtually) bones at the hip, knee, and ankle in the hindlimb, and shoulder, elbow, and wrist in the forelimb. This procedure is time-consuming and necessitates good preservation of the joints, which is not often the case. On the contrary, basic trackway parameters, such as those listed here, can be easily measured in all kinds of trackways and are less dependent on substrate consistency and taphonomic deformation with respect to single-track descriptive measurements (i.e., interdigital angles). Furthermore, the track record is often much more abundant than the skeletal one, thus giving opportunities to statistically analyze the data.

Limb postures of tetrapods vary from sprawling to erect. An erect limb can be found within birds and cursorial mammals, where the limbs are held under the body and move in a parasagittal plane. On the other hand, a sprawling limb posture is seen in limbed squamates and all limbed amphibians, where the proximal limb segments are highly abducted and swing largely in a horizontal plane (Blob 2000). Posture can change during locomotion, a classic example being crocodiles which show a sprawling posture at low speeds and a semi-erect one when running (Zug 1974; Carpenter 2009). An erect limb posture is energetically advantageous over a sprawling limb posture, especially for large animals. Stresses over the knee and elbow joints are reduced and respiration is facilitated when the limbs are held vertical (Carrier 1987).

From skeletal studies, it is known that Late Permian tetrapods such as temnospondyl amphibians, pelycosaurs, and pareiasaurs were largely sprawlers (Carroll 1988; Benton 2005). Late Triassic faunas were instead dominated by erect forms such as dinosaurs and crurotarsan archosaurs (Nesbitt 2011). The postural transition from sprawling to erect between those times can be described by looking at skeletal remains, but these are scanty in the Early and Middle Triassic. Vertebrate ichnology has allowed a better understanding of this event, especially regarding the exact pattern, timing, and possible correlation with other events by studying fossil trackways.

A key study in this respect was developed by Kubo and Benton (2009). The authors used a classic, simple measure to distinguish sprawlers from erect walkers: the ratio of stride length to trackway width, indicated by the pace angulation (Peabody 1959). This is defined as the angle formed by three continuous front or hind footprints (Peabody 1959) (Fig. 10.1). Pace angulation is dependent on body size and speed, but limb posture is the key factor in determining pace angulation. As exemplified by neoichnologic studies, values lower than 107°, in fact, indicate the producer performed a sprawled locomotion while values greater than 138° indicate erect locomotion (Kubo and Benton 2009).

By analyzing a large dataset of Late Paleozoic to Early Mesozoic tetrapod trackways, the authors found a clear distinction between Permian and Triassic samples

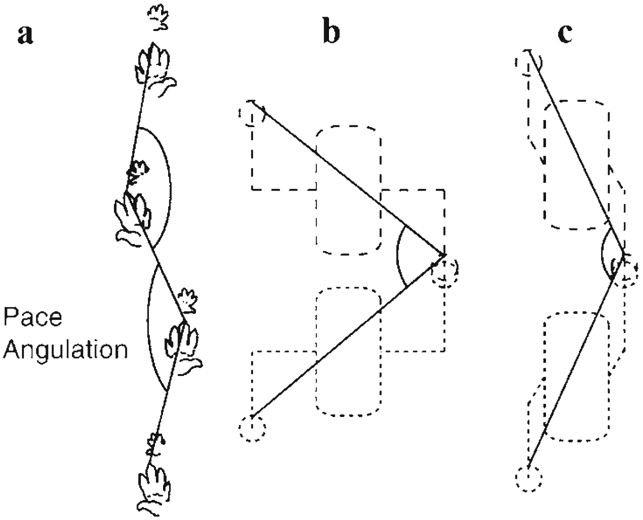

Fig. 10.1 Pace angulation, the angle formed by three consecutive footprints, can be used as a proxy for trackmaker's posture. Using the measuring method shown in (**a**), Kubo and Benton (2009) discovered that the shift from a sprowler posture (**b**) to a more erect one (**c**) occurred across the Permian-Triassic boundary, and may thus be related with the profound impact of the devastating mass extinction event. Modified from Kubo and Benton (2009)

when median values rise from 87.5° (Late Permian) to 139.5° (Early Triassic), whereas within those epochs no significative change in the distributions of pace angulation could be found. All tetrapods, whether synapsids or archosaurs, show the same postural shift across the Permo-Triassic boundary and once the posture had changed, there was no significant change in mean pace angulation through the Triassic. This shift was mostly caused by the increase in the number of chirotheriid trackways from the Early Triassic. The ichnofamily Chirotheriidae (Abel 1935) is a form family comprising the ichnogenera *Chirotherium* Kaup, 1835; *Brachychirotherium* Beurlen, 1950; *Isochirotherium* Haubold, 1971b; *Synaptichnium* Nopcsa, 1923; *Parasynaptichnium* Mietto, 1987, and *Protochirotherium* Fichter and Kunz, 2004. These have been consistently attributed to archosaurs, usually to crurotarsans (pseudosuchians) and basal archosauriforms (Krebs 1965; Haubold 1967, 1971a, 1971b, 1984, 1986, 1999; 2006; Lockley and Meyer 2000; Demathieu and Demathieu 2004; Gand et al. 2010; Bowden et al. 2010; Heckert et al. 2010; Lucas and Heckert 2011; Desojo et al. 2013; Bernardi et al. 2015) and show *manus* (fore foot) and *pes* (hind foot) imprints with a compact anterior digit group I–IV and a postero-laterally positioned, strongly reduced digit V, which are apomorphies of Archosauromorpha (Nesbitt 2011). Thus it is clear that archosaurs (and to a lesser extent, therapsids) were responsible for the high pace angulation of Triassic trackways. Footprints made by amphibians, procolophonids, and small basal diapsids indicate retained sprawling limb posture (Haubold 1971a, b). The abundance of trackways from the Permian up to the Triassic provides resolution that the rare skeletal fossil tetrapods of this age do not. In addition to providing a description of the pattern of this event, dating indicates that the shift was accomplished already 6 myr after the profound Permo-Triassic mass extinction; this is considerably earlier than the 15–20 myr suggested by the study of locomotory evolution based on skeletal fossils (Charig 1972; Kemp 1982; Bonaparte 1984; Parrish 1987; Kubo and Benton 2009). The ichnologic record also supports a late Permian-Early Triassic radiation of archosauriforms not well documented by skeletal material. By analizing several chirotheriid footprints from the upper Permian of the Southern Alps (Italy), Bernardi et al. (2015) showed that archosauriforms had already undergone substantial taxonomic diversification by the late Permian, widening the geographical distribution of this clade before and after the P-T boundary (Bernardi et al. 2015). Furthermore, analysis of body size, as deduced from track length, allowed formulating a new hypothesis on the response of archosauriforms to the end-Permian events, proposing that their body size did not change significantly from the late Permian to the Early Triassic (Bernardi et al. 2015).

10.2.2 The Origin of Dinosauromorphs

In vertebrate ichnology synapomorphy-based studies are still rare. However, it now appears possible to integrate this discipline into paleobiologic studies if rigorous descriptions are coupled by thoughtful character-based evaluation of potential trackmakers. When synapomorphic characters are found, potential trackmakers can be constrained considerably, allowing full hypothesis testing. More simply, each find that reveals new morphotypes of trackways or skeletal remains of limbs/feet showing apomorphic characters, helps constrain possible track-trackmaker correlations more accurately. Using this approach, tracks and trackways become “biologically informative” and can thus be of interest for paleobiologic analysis. The synapomorphy-based technique focuses on the identification of osteologic-derived character states in the tracks that result from the impression of corresponding (synapomorphic) characters in the autopodia of the trackmaker. These characters allow the recognition of a particular clade independent from the defined body-fossil distributions (see Olsen et al. 1998; Carrano and Wilson 2001; Wilson 2005). This approach has been applied only recently (e.g., Olsen 1995; Olsen and Baird 1986; Olsen et al. 1998; Wilson and Carrano 1999; Carrano and Wilson 2001; Haubold and Klein 2000, 2002; Padian 2003; Wilson 2005; Wright 2005; Brusatte et al. 2010b; Kubo and Kubo 2013; Bernardi et al. 2015).

The most recent advances in the understanding of the origin of dinosaur lineages are a good example of the potential for integrating ichnologic studies with cladistic approaches. The resulting contribution is that, conceived in this way, vertebrate ichnology can give to a deeper understanding of patterns and processes in the evolution of life. Dinosauromorpha is a clade including all taxa closer to dinosaurs than to the other main archosaur clades (i.e., pterosaurs and crocodylomorphs). Dinosauromorphs originated, and radiated in the Triassic, and several taxa are now known that vary in size, feeding, and locomotory features, and that were spread over most of western Pangea (Langer et al. 2013). However, both the timing and pattern of the early radiation of this lineage are poorly understood (see Marsicano et al. 2015 for a recent update). The oldest known body fossils of dinosauromorphs are silesaurids, which are Anisian in age (Nesbitt et al. 2010; Peecook et al. 2011; Barrett et al. 2015). Silesaurids occupy a derived position within Dinosauromorpha (Ezcurra 2006; Nesbitt et al. 2010; Nesbitt 2011), and therefore imply the presence of other dinosauromorph groups such as lagerpetids, and non-silesaurid dinosauriformes before that time. No such Early Triassic groups are documented in the body fossil record. However, the Early Triassic archosaur track record is rich (see Klein and Haubold 2007 and references therein), raising the intriguing possibility that dinosauromorph tracks can be recognized among the diverse ichnoassociations. *Rotodactylus*, a common ichnogenus in the latest Olenekian–Ladinian worldwide (Peabody 1948; Gand and Demathieu 2005; Gand et al. 2005; Klein and Haubold 2007), has been long attributed to basal dinosauromorphs (Haubold 1999; Haubold and Klein 2002); however, a strict synapomorphy-based assessment was lacking. Recently, Brusatte et al. (2010a) presented a formal analysis corroborating this identification. *Rotodactylus*, in fact, possesses unequivocal features of dinosauromorphs, such as reduction of digits I and V and digitigrade posture. Moreover Brusatte et al. (2010a, see also; Niedźwiedzki et al. 2013), described a new ichnogenus named *Prorotodactylus*, discovered in the Early Triassic of Koszary and Stryczowice, Poland. *Prorotodactylus* can be assigned to Dinosauromorpha thanks to the presence of unequivocal synapomorphies such as the bunched metatarsus, reduction of digits I and V, the posterior deflection of digit V, and the manifest digitigrady. Brusatte et al. (2010a) suggested *Lagerpeton* as possible trackmaker, and although this is (Niedźwiedzki et al. 2013) or might be (Langer et al. 2013) the case, an attribution of *Prorotodactylus* to dinosauromorphs appears quite solid (Niedźwiedzki et al. 2013; but see Klein and Niedźwiedzki 2012). The nearly complete absence of autopodia in the skeletal record (with the notable exception of *Lagerpeton*, Sereno and Arcucci 1994) prevents an evaluation of digit ratios across other dinosauromorph taxa (see Langer et al. 2013 for a discussion) and enhance the importance of the above cited ichnotaxa in exploring the early history of this group. The synapomorphy-based identifications of *Rotodactylus* and *Prorotodactylus* shed new light on the debate over the posture of the earliest dinosauromorphs; both show that these early forms were much more digitigrade than any other closely related archosaurs and that they walked on all fours (Fig. 10.2b). The ichnogenus *Sphingopus*, which is found in numerous Olenekian to Middle Triassic sites all over the world (Klein and Haubold 2007), shares the apomorphic characters described in *Prorotodactylus*; however, the lack of associated manus imprints and high pace angulation indicates that the trackmaker was walking bipedally. Furthermore, *Sphingopus* is much larger than the other dinosauromorph tracks. The tendency toward a full tridactyl morphology, with digit III being the longest, suggest that *Sphingopus* isp. was produced by a dinosauromorph more derived than the *Proroto dactylus*/*Rotodactylus* trackmaker, and therefore suggests that bipedality was acquired and the trackmaker was closer to the origin of dinosaurs (Fig. 10.2c).

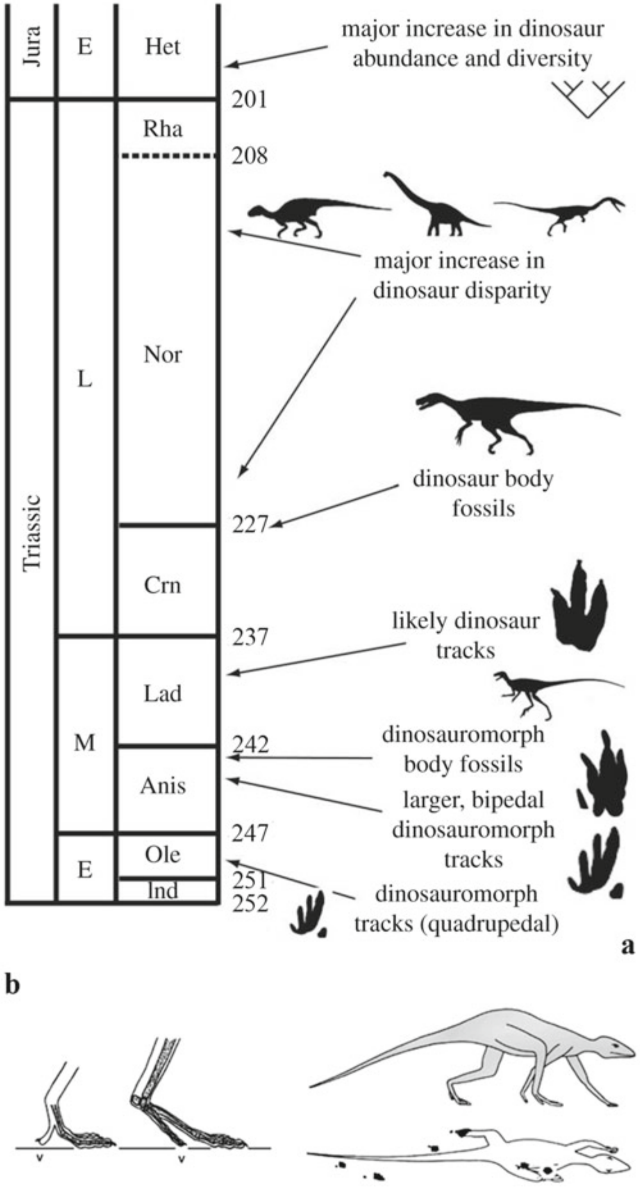

Fig. 10.2 Footprints attributed to dinosauromorphs and early dinosaurs can be integrated with skeletal data to build a general timeline of early dinosaur history. Footprints, as those described by Brusatte et al. (2010b), document the earliest phase of this radiation and predate timing of emergence of the various groups (**a**). (**b**) Shows a likely reconstruction of an early dinosauromoph as reconstructed on the base of *Rotodactylus* trackways. (**a**) Modified from Brusatte et al. (2010b), (**b**) modified from Haubold (1999) and Niedźwiedzki et al. (2013)

The stratigraphically successive records of *Prorotodactylus* and *Rotodactylus* documented by Brusatte et al. (2010a) show that changes in foot anatomy were occurring in dinosauromorphs during the Olenekian; the appearance of *Sphingopus* documents the evolutionary shift from quadrupedality to bipedality, and from small to large size, in the dinosaur lineage. Tracks, identified using synapomorphies, can thus provide new data on the timing and pattern of character acquisition during early dinosauromorph radiation (Fig. 10.2a). Such data are currently not visible in the body fossil record. Furthermore, being older than indicated by the skeletal record, tracks might indicate that the appearance of the dinosauromorph lineage can be linked with the Permian—Triassic mass extinction event (Brusatte et al. 2010a; Niedźwiedzki et al. 2013).

10.2.3 The Origin and Early History of Dinosaurs

The vertebrate track record can be used to make inferences about the spatial and temporal distribution of tetrapod taxa and can give reliable clues, although at a coarse taxonomic level, into tetrapod diversity. If parsimoniously interpreted, it can complement the skeletal record offering a "total evidence" approach to the study of evolutionary patterns and timing of events.

The study of early Mesozoic vertebrate terrestrial ecosystems is a lively field in both vertebrate paleontology and paleoichnology, mostly powered by the debates on dinosaur origins and their early history. The appearance of dinosaurs during the Triassic marked the onset of a faunal diversification that has dominated terrestrial ecosystems for almost 230 Myr (Brusatte et al. 2008a). As discussed, the possible contribution of track data to this and other taxon-based debates, depends on reliable identification of dinosaur trackmakers.

Triassic tridactyl prints are traditionally assigned to Dinosauria (see Lucas et al. 2006 and reference therein). Supposed dinosaur tracks are recognized on the base of few synapomorphies: (1) the prevalence of the digit II–IV group, (2) mesaxonic pattern of foot structure, (3) digit I reduced and shifted backwards (and thus often not preserved in tracks), and (4) tendency towards digitigrady (see also Thulborn 1990; Haubold 1999; Brusatte et al. 2010b). However, this morphotype cannot be unambiguously assigned to Dinosauria using apomorphy-based identifications; a functionally tridactyl pes is found also in some non-dinosaurian dinosauriforms (Gauthier 1986; Brinkman and Sues 1987; King and Benton 1996; Novas 1992; Carrano and Wilson 2001; Fraser et al. 2002; Dzik 2003; Marsicano et al. 2007; Nesbitt et al. 2007; Brusatte et al. 2010b). Furthermore, no synapomorphies of three-toed footprints can discriminate among theropods, basal saurischian, and basal ornithischian groups (Olsen et al. 1998). "Theropod-like" tracks can, however, be identified on the basis of the following characters: (1) asymmetry of the track with angle between digit III and II lower than III-IV, (2) digit III longer than IV > II, (3) sharp claw traces on all digits, and (4) tip of digit II turned inwards (Bernardi et al. 2013). Lockley (2001, 2007a, 2009) has also argued that narrowness and strong mesaxony distinguishes theropod tracks from those of tridactyl ornithischians. Nevertheless, no clear synapomorphy can be described in tridactyl tracks to clearly distinguish between dinosaurian- and non-dinosaurian-dinosauriforms. All Triassic functionally tridactyl tracks with digitigrade pes produced by bipedal parasagittal posture should be loosely attributed to an archosaur on the dinosaur line. Some derived characters, such as those listed by Bernardi et al. (2013), can be used in support of an attribution to Dinosauria, but a "gray zone" will always exist.

Debates on dinosaur origin thus focus around three main topics: (1) timing of appearance, (2) pattern and pace of early diversification (body size and biogeography), and (3) dynamics of replacement of crurotarsan archosaurs by dinosaurs. If the first relies on new discoveries of older specimens and reliable dating of the dinosaur-bearing formations, the second refers to dinosaurs having experienced a rapid diversification or having a deeper origin ("slow fuse") not documented (with the possible notable exception of Nesbitt et al. 2013) by current knowledge of the fossil record. The last needs data from mixed assemblages to test for habitat preferences and niche competition, and the in situ nature of footprints can be of great value in this respect.

10.2.3.1 Timing of Appearance

The exact timing of dinosaur origins remains unclear (Benton 1983; Brusatte et al. 2008a). The oldest record of dinosaurs based on skeletal remains is from the Carnian of Argentina (Benton 1983; Sereno and Arcucci 1994; Sereno 1999; Irmis et al. 2007; Brusatte et al. 2010b; Langer et al. 2010; Ezcurra 2010; Martinez et al. 2011), although Nesbitt et al. (2013) reported a possible earlier dinosaur from the Anisian of Tanzania. By the Carnian-Norian transition, all three major dinosaur lineages (Ornithischia, Sauropodomorpha, Theropoda) are documented (Brusatte et al. 2010b; Irmis et al. 2007; Langer et al. 2010). This forces researchers to focus mostly on the still poorly known Middle Triassic record. Furthermore, ghost lineages inferred from phylogenetic analyses predict that Dinosauria and its immediate stem lineage should be as old the early Middle Triassic (Sereno and Arcucci 1994; Nesbitt et al. 2010).

Early Triassic tracks previously attributed to dinosaurs have been reconsidered as partially or badly preserved "chirotheroids" (King and Benton 1996; see also Cavin et al. 2012). Although track-bearing formations cannot be always confidently dated, functionally tridactyl footprints are documented in the Middle Triassic of France (Demathieu 1989; Lockley and Meyer 2000), Germany (Haubold and Klein 2000, 2002), Italy (Avanzini 2002), and Argentina (Marsicano et al. 2007 and references therein), and have been generally attributed to dinosauromorphs. Dinosaur tracks have been reported from the Middle Triassic Los Rastros Formation (Argentina) by Marsicano et al. (2004, 2007; see also Marsicano and Barredo 2004; Melchor and Valais 2006) but have been considered ambiguously identified by others (Langer et al. 2010; Irmis 2011). Therefore the ichnologic record, although failing to definitively prove a Middle Triassic origin for dinosaurs, clearly indicates the presence of a diverse fauna of dinosauromorphs with functionally tridactyl digitigrade pedes, and possibly true dinosaurs during the Middle Triassic (Fig. 10.3), a condition that the body-fossil record is only recently beginning to document (Nesbitt et al. 2013).

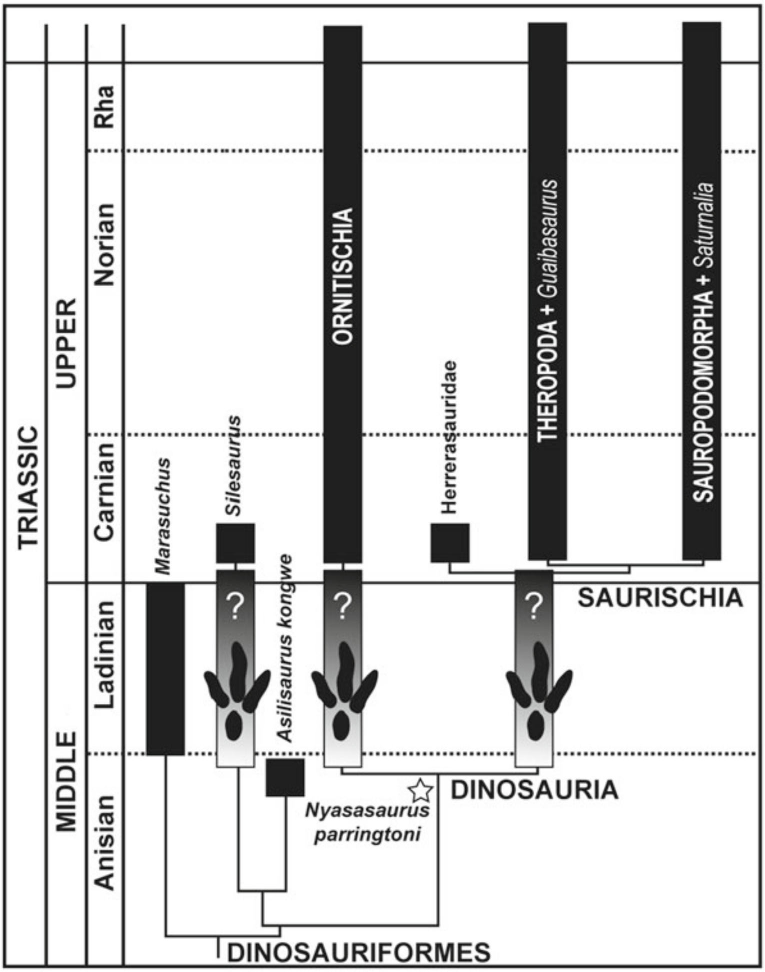

Fig. 10.3 A calibrated phylogeny of early dinosaurs and sister taxa based on both skeletal and ichnological data. The possible presence of dinosaurs in the Middle Triassic as testified by controversial footprints have recently received support from the description of *Nyasasaurus* which is considered either within, or sister-taxon of, Dinosauria. Modified from Marsicano et al. (2007) and Nesbitt et al. (2013)

10.2.3.2 Early Diversification

Although the first unequivocal dinosaur body fossils are known from the Carnian (Brusatte et al. 2010b; Langer et al. 2010; Nesbitt et al. 2013), Brusatte et al. (2008a, 2010b) demonstrated that dinosaurs increased their diversification and their morphologic disparity only from the Norian; dinosaurs experienced a burst of diversification only after the Triassic–Jurassic transition.

At the end of the Triassic the dinosaurs experienced an increase in maximum body size, later expressed as an increase in average body size (Sookias et al. 2012; Turner and Nesbitt 2013). Late Triassic tridactyl footprints are well known from USA, Europe, South America, Australia, and Africa (e.g., Tucker and Burchette 1977; Biron and Dutuit 1981; Mietto 1988; Olsen and Baird 1986; Thulborn 2000; Gatesy 2001; Knoll 2004; Milàn and Gierliński 2004; Weishampel et al. 2004; Lockley and Eisenberg 2006; Silva et al. 2007; Meyer et al. 2013). The Triassic record of large tridactyl tracks (e.g., Thulborn 2003; Bernardi et al. 2013; Meyer et al. 2013) has invalidated the hypothesis of Olsen et al. (2002) of a dramatic increase in size at the Triassic-Jurassic boundary. However, the increasing abundance toward the end of the Triassic of medium- and large-sized theropod tracks (*Eubrontes* and *Grallator* above all) marked a crucial phase in dinosaur history, when the main radiation or diversification of theropods and the evolution of large species got underway during the Late Triassic (Lockley and Hunt 1995a). Furthermore, if the attribution of the largest Late Triassic tracks is correct, the estimated body length, calculated according to Thulborn's (1990) equations ($h = 3.06 \times \mathrm{FL}1.14$ and $L = 4$ h), would be more than 5 m. Their estimated body mass value, following Weems (2006), would have been about 200 kg (Bernardi et al. 2013). This size is not known from dinosaur skeletal remains of Carnian age (Benton 2006; Brusatte et al. 2010b) and is approximated only by the Norian theropod dinosaur *Liliensternus* (Cuny and Galton 1993; Lucas et al. 2006).

Tracks are also a valuable tool that gives us insight into the geographic distribution of the first dinosaurs. The earliest skeletal remains of dinosaurs are from southern Pangaea and the oldest possible dinosaur tracks are from Argentina. The earliest dinosaur from northern Pangaea has recently been dated as "middle" Norian of western North America (Nesbitt et al. 2009). This has led to the view that the major dinosaurian clades (Ornithischia, Sauropodomorpha, Theropoda) may have originated in southern Pangaea (Brusatte et al. 2010b; Langer et al. 2010). The paleogeographic importance of this distribution, however, is compromised by the absence of well-preserved skeletal remains of Carnian age from northern localities (northern Africa, Europe, North America) (Langer 2005; Nesbitt et al. 2007; Martinez et al. 2011). Tracks, however, indicate that dinosaurs were already present by the Late Carnian in northern Pangea (Bernardi et al. 2013, Fig. 10.4). With the exclusion of the possible earliest dinosaur *Nyasasaurus* (Nesbitt et al. 2013), this would imply a nearly contemporaneous appearance of dinosaurs on all of Pangea (Bernardi et al. 2013).

10.2.3.3 Dynamics of Replacement

In the past, the Late Triassic was described as the period when the faunas dominated by crurotarsan archosaurs were competitively replaced by those dominated by dinosaurs (Bakker 1972; Charig 1984). A growing consensus now suggests that dinosaurs were initially rare components of Triassic terrestrial ecosystems and that their ascent was gradual (Brusatte et al. 2008b). It was only after the Triassic–Jurassic transition that dinosaurs became dominant in terrestrial vertebrate ecosystems

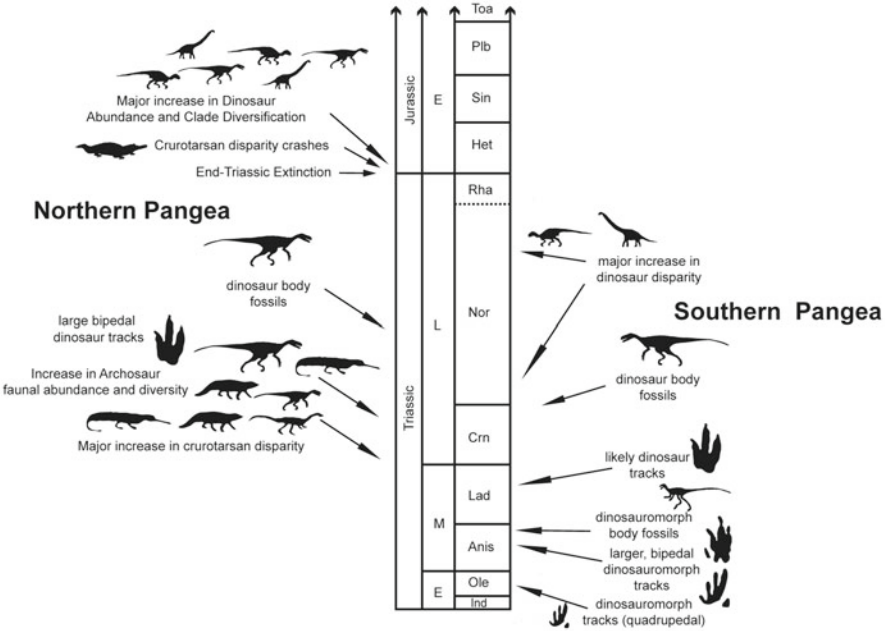

Fig. 10.4 The ichnological record provides valuable data on both temporal and spatial distribution of basal dinosaurs. Tracks, for example, indicate the presence of archosaur faunas, which include dinosaurs, during the early Late Triassic both in Laurasia and Gondwana. This pattern is not (yet) documented by body-fossil data. Modified from Brusatte et al. (2010a, 2011)

worldwide (Benton 1983; Sereno 1999 see also Brusatte et al. 2010b). The body fossil record has shown that in the Late Triassic, during the first 25–30 million years of dinosaur history, crurotarsans had double the variety of body plans, lifestyles, and diets in comparison with contemporary dinosaurs (Brusatte et al. 2008a, 2010b, 2011; see also, Benton 1983; Sereno 1999). In addition to crurotarsans, Triassic dinosaurs lived together with dicynodont synapsids (Dzik et al. 2008) and coexisted with dinosauromorphs for at least 20 million years (Irmis et al. 2007). The scarcity of Early to Middle Triassic terrestrial body fossils, however, leaves open questions on taxonomic abundance, composition, diversity, and regional specificity of such dinosaur communities (Irmis et al. 2007; Dzik et al. 2008; Nesbitt et al. 2009; Ezcurra 2010; Irmis 2011). The track record can be integrated into this picture.

As a general depiction, while the upper Triassic ichnologic record is characterized by dinosaur, dinosauromorph, crurotarsan archosaurs, and nonmammalian therapsid tracks (Marsicano and Barredo 2004; Bernardi et al. 2013; Lockley and Meyer 2000; Klein and Haubold 2007; Lucas and Tanner 2007), the Lower Jurassic record is dominated by saurischian dinosaurs (Lockley and Hunt 1995a; Lockley and Meyer 2000; Olsen et al. 2002; Avanzini et al. 2006; Avanzini and Petti 2008). Well-diversified tetrapod ichnoassemblages are known from the Middle to Late Triassic of both southern and northern Pangaea (see Bernardi et al. 2013). Olsen and Huber (1998) reported the co-occurence of *Apatopus*, cf. *Brachychirotherium*, and small bipedal and tridactyl forms, possibly produced by "dinosaurian" trackmakers in the Carnian of North Carolina, while Cameron and Wood (2003, 2004) described a rich association composed of *Atreipus*, *Brachychirotherium*, *Grallator,* and *Rhynchosauroides* from the Carnian of Canada. Similar assemblages are ubiquitous in the western USA (Lockley and Hunt 1995a). Marsicano and Barredo (2004) reported the presence of crurotarsal archosaurs, dinosaurs (sauropodomorphs and theropods) and nonmammalian therapsids (small cynodonts and large dicynodonts). Nicosia and Loi (2003) described a rich Carnian ichnoassociation from Italy with crurotarsan and dinosaurian tracks. D'Orazi Porchetti et al. (2008) and Bernardi et al. (2013) document the co-occurrence of large- and middle-sized dinosaurs, dinosauriforms, and crurotarsans in the late Carnian (Tuvalian) of the southern Alps. Therefore, the record of ichnofaunal assemblages composed of large and small dinosaurs, dinosauriforms and non-dinosaurian archosaurs and their co-occurrence with dinosauriforms and crurotarsal archosaurs provides support to the non-abrupt replacement of the more archaic faunas by dinosaur-dominated ones. Furthermore, the co-occurrence of dinosaurs, dinosauriforms, and crurotarsal archosaurs in the Middle to Late Triassic (Ladinian to Late Carnian) documents a prolonged coexistence of different groups of archosaurs, even in the same environment. This provides support to the view of crurotarsan-dominated faunas being neither rapidly outcompeted nor quickly opportunistically replaced by dinosaurs, but rather substituted by a more gradual process of ecologic replacement (Irmis et al. 2007; Nesbitt et al. 2010; Brusatte et al. 2010b; Martinez et al. 2011).

10.2.4 A Look into Sauropod Paleobiology

One key feature of tracks that neatly distinguishes them from body fossils is that they cannot be transported post-mortem, in this case, "post-emplacement". Tracks thus provide a direct indication of environmental and/or habitat preferences of the producer (Thulborn 1982; Lockley 1991; Wilson and Carrano 1999; Carrano and Wilson 2001). To better understand habits, locomotory attitudes or geographic distribution of particular groups, it is therefore useful to integrate body fossil findings with track data. A good example in this respect is provided by the sauropod dinosaur record.

Numerous studies of locomotory dynamics in this group attribute different footprint morphotypes to distinct trackmakers. Many authors (Farlow et al. 1989; Farlow 1992; Lockley et al. 1995a; Moratalla et al. 1995; Wilson and Carrano 1999; Lockley et al. 2002, 2005; Day et al. 2002a; Henderson 2002) have observed that sauropod trackways could be essentially subdivided into two broad categories: "narrow gauge" and "wide gauge" (Fig. 10.5). Sauropod trackways can also show (or lack) claw and phalangeal impressions in the manus (Farlow et al. 1989; Lockley et al. 1995a; Wilson and Carrano 1999; Day et al. 2004). "Wide-gauge" trackways are those in which manus and pes prints are well separated from the midline, and which frequently lack pollex claw impressions (e.g., *Brontopodus* Farlow et al. 1989); "Narrow gauge" trackways have manus and pes prints that approach or intersect the trackway midline, and have pollex claw impressions (e.g., *Parabrontopodus*

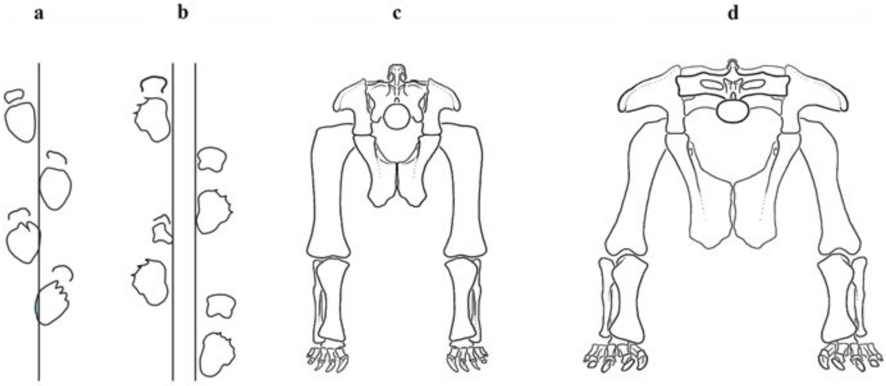

Fig. 10.5 Many authors (see text for discussion) have observed that sauropod trackways could be essentially subdivided into two broad categories: "narrow gauge" (**a**) and "wide gauge" (**b**). These reflect the postural difference between non-titanosaur (**c**, here represented by *Camarasaurs*—pelvic girdles and hindlimbs in anterior view) and titanosaur sauropods (**d**, here *Opisthocoelicaudia*). This inference allowed full integration of ichnogical and skeletal data, which contributed to a better understanding of sauropod paleobiology. Modified from Lockley et al. (1995b), and Wilson and Carrano (1999)

Lockley et al. 1995a). Lockley (1999, 2001, 2007a) also argued that there is a positive correlation between narrow gauge and small manus forms, and between wide-gauge and large manus forms. Furthermore, large and small manus forms have been independently identified among the various chirotherian ichnotaxa (Lockley 2007a). Such differences in turn speak to changes in the position of the center of gravity in various archosaur clades.

Ichnologic investigations suggest that the transition from narrow- to wide-gauge occurred during the Kimmeridgian-Tithonian (Wilson and Carrano 1999). "Wide-gauge" trackways show a trend towards an increase of manus print dimensions through time. This feature and the age of "wide-gauge" trackways closely match the evolutionary trend seen in the sauropod body fossil record. Skeletal remains record a gradual shift of the center of gravity toward the front, with the consequent growth of the forelimbs in response to the greater weight they had to support. This evolutionary change coincides with the appearance of Titanosauriformes Salgado, Coria and Calvo 1997 (including Brachiosauridae Riggs 1904 and Titanosauria Bonaparte and Coria 1993) (Wilson 1995; Upchurch et al. 2004), animals that would have produced tracks with larger manus impressions. The lack of digital impressions in the manus ichnites of the "wide-gauge" trackways could also be referred to the appearance of Titanosauriformes; indeed both Brachiosauridae and Titanosauria are characterized by the progressive reduction and loss of phalanges and claws in the manus (Wilson and Sereno 1998; Upchurch et al. 2004; Apesteguía 2005). In particular, Titanosauria probably walked only on the distal parts of their metacarpal bones (Salgado et al. 1997; Wilson and Sereno 1998). It is thus difficult to envisage digital or claw marks produced by individuals belonging to Titanosauriformes. Wilson and Carrano (1999) argued that hindlimb modifications, such as outwardly angled femora, offset knee condyles, and a more eccentric femoral midshaft cross-section, could be responsible for wide-gauge tracks. All these features are synapomorphies of titanosaurs, and thus support the hypothesis that they were the producers of wide-gauge trackways. Temporal and geographic distribution of titanosaurs is coherent with this hypothesis; "wide-gauge" trackways predominate during the Cretaceous and are found worldwide. After Wilson and Carrano's (1999) proposals, other studies have cast some doubt on this correlation. D'Emic (2012) suggested that some Late Jurassic non-titanosaurs might have femoral cross-sections similar to those of titanosaurs. Henderson (2006) proposed that all large sauropods (over 12.6 tonnes) would have been constrained to adopt a wide-gauge stance in order to maintain stability during locomotion; trackway gauge could also be influenced by the degree of lateral motion of the trackmaker (Carpenter 2009). Recent discovery of sauropod trackways from Switzerland, Morocco (both of Jurassic age), and Spain (Cretaceous age) show that single sauropod trackmakers were able to adopt both narrow and wide gauge as testified by the occurrence of differently spaced tracks along single trackways (Marty et al. 2010; Castanera et al. 2012a, b). Furthermore, wide-gauge trackways could have appeared more than once in sauropod evolution. Wide-gauge trackways are not exclusive to titanosauriform sauropods and caution must be applied ascribing a trackway to an ichnotaxon on the basis of this character (Castanera et al. 2012a, b).

Sauropod tracks have provided important clues for the understanding of the environmental preferences of this clade. Based on the analysis of a dataset of sauropod trackways, Lockley et al. (1995b) found a good correlation between sauropod tracksites and coastal environments, and noted that they are primarily associated with tropical and subtropical paleolatitudes (mean average Northern Hemisphere = 25°), and semi-arid or seasonal climatic carbonate depositional environments (lacustrine or marine carbonate platform). Butler and Barrett (2008) partially confirmed these results: the percentage of Cretaceous sauropod tracks in coastal environments is remarkable (32 %) if compared with the contemporaneous sauropod body fossil record (7 %). Nevertheless, statistic analysis of the ichnologic data does not indicate that sauropod trackways are overrepresented if compared to those of other herbivorous dinosaurs. In contrast, the body fossil record supports previous hypotheses of a preference for inland settings (e.g., Lehman 1987; Hunt et al. 1995a). However, it should be noted that these results might be hindered by preservational biases that are not yet fully understood (Mannion and Upchurch 2010). Using a new large data set of sauropod skeletal remains, Mannion and Upchurch (2010) found a significant positive association between non-titanosaurs and coastal environments, and between titanosaurs and inland environments. Their analysis of track records also highlighted a positive correlation between narrow-gauge trackways and coastal environments, and wide-gauge trackways and inland environments; this reinforced the hypothesis of Wilson and Carrano (1999) that wide-gauge trackways were produced by titanosaurs. The hypothesis of Mannion and Upchurch (2010) has been partially put into question by isolated findings of wide-gauge trackways preserved in coastal environments (e.g., Castanera et al. 2011).

10.2.5 Clues About Theropod Paleobiology

Most famously among track features, trackways allow estimation of speed (Alexander 1976, 1989; Thulborn 1981, 1990). In fact, debates about speeds attained by dinosaurs led to a revival of tetrapod ichnology (Alexander 1976; Lockley 1998). Early estimates of rapid progression of large dinosaurs were proposed in support of the idea that dinosaurs were highly active and possibly warm-blooded (Russell and Belland 1976; Czerkas and Olson 1987); however, later studies based on larger samples and updated formulae concluded that most medium- to large-sized theropods walked fairly slowly (Farlow 1981; Thulborn 1990). Estimates of the speeds of theropod dinosaurs are based on the formula of Alexander (as corrected by Thulborn 1990); speed (v, velocity) is calculated on the basis of stride length (SL) where $v \approx 0.25\ \mathrm{g}^{0.5}\ \mathrm{SL}^{1.67}\, h^{-1.17}$, where hip height ($h$) of a trackmaker can be estimated from footprint length (FL): $h \approx 8.60\ \mathrm{FL}^{0.85}$ (Thulborn 1984; Thulborn and Wade 1984). This formula was successively slightly modified by Weems (2006) to estimate basal theropod dinosaur speeds ($v = 0.16\ \mathrm{SL}^2\ \mathrm{h}^{-1.5}\, g^{0.5}$). The same formula can be used for any bipedal dinosaurs (see Currie 1983, 1995), while no similar, reliable formulae are available for quadrupedal dinosaur taxa. Using musculoskeletal modeling and Computer Aided Engineering, Mallison (2011) questioned the validity of the Alexander formula to assess speed in dinosaurs without knowing the frequency of the stride. He suggested that speeds calculated from tracks should be better considered as the slowest speeds at which the animals moved.

Tracks and trackways have also been long used to establish dynamics of foot movement (Avanzini 1998; Gatesy et al. 1999; Gatesy 2001, 2003; Manning 2004; Milàn et al. 2004, 2006; Avanzini et al. 2012; Ellis and Gatesy 2013), locomotion (Alexander 1976, 1985, 1989; Thulborn 1981, 1990) and contributed in the debate about theropod posture (Lockley 1998). The high pace angulation exhibited by theropod trackways, for example, shows that theropods placed their hind feet close to, or on, the midline (Alexander 1976, 1985). This optimizes the efficiency by reducing the energy lost through lateral displacement of the center of gravity (Thulborn 1981, 1990), and is characteristic of a highly specialized locomotory control system. Lockley (2007a) regarded such narrow trackway configurations as a manifestation of an intrinsic morphodynamic organization in theropods. Furthermore, saurischians in general had narrow bodies, narrow feet, and other laterally compressed skeletal elements, although this contrasts with the wide-gauge trackway configurations and wide bodies and feet seen in derived saurischians such as the titanosaurs. Furthermore, Day et al. (2002b) showed that large theropods were able to change their speed instantaneously, highlighting their high maneuverability and balance control.

Theropod trackways do not typically include hand imprints, which is again an expression of a posterior center of gravity (Lockley 2007a). Only when the trunk was lowered toward a substrate, as in a crouched posture, could the hands potentially produce impressions. Crouching has been demonstrated by a few extraordinary discoveries of impressions of autopodia associated with metatarsals and pelvic girdle imprints. Milner et al. (2009) reported unambiguous theropod manus impressions associated with a crouching trace that indicate the avian orientation of the manus (with a medially facing palm) evolved early within the history of Theropoda (see Gierliński et al. 2009 and references therein for further examples). The crouching trace was registered when the animal rested on the substrate in a posture similar to that of modern birds; the traces include well-defined impressions made by both hands, the ischial callosity, pedes, and the tail. This trace constitutes evidence that an Early Jurassic theropod expressed two bird-like features: anatomic restriction to a palms-medial manual posture, and symmetric leg positions while resting (Fig. 10.6). Inferences that theropods displayed behavior analogous to modern birds are intriguing but often too speculative. Recently discovered Cretaceous theropod tracks in Colorado provided extensive physical evidence of substrate scraping behavior by large theropods; they were considered as compelling evidence of "display arenas" or leks, and consistent with "nest scrape display" behavior among many extant ground-nesting birds (Lockley et al. 2016).

Another iconic example of the impact that ichnology has had on postural biomechanic reconstructions is the case of the orientations of dinosaur trunks and tails. Analysis of trackways have clearly shown that most dinosaurs walked with their tails carried well off the ground, so tail-drag traces are rare (Irby and Albright 2012; García-Ramos et al. 2004, 2006; Platt and Hasiotis 2008; Kim and Lockley 2013). The presence of tail traces, therefore, implies either a pathologic condition of the

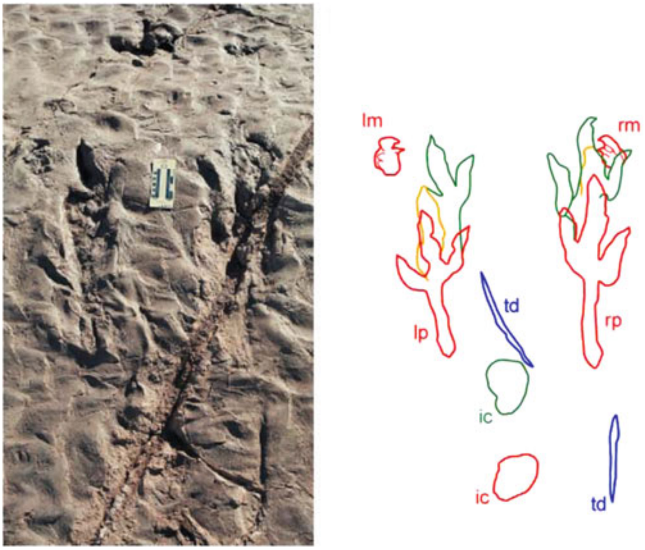

Fig. 10.6 Footprints provide clues to the individual behavior of trackmakers. These crouching traces described by Milner et al. (2009), for example, demonstrate that avian orientation of the manus, with medially facing palms, evolved by the Early Jurassic within Theropoda. Such conclusion would have never been reached on the base of skeletal record alone. Modified from Milner et al. (2009)

trackmaker or an atypical mode of locomotion because dinosaurs used their tails for balance on land (Galton 1970; Farlow et al. 2000; Fujita et al. 2012).

Tracks can also be used to assess the effects of traumas and illness in dinosaur bones and therefore the evolution of phatologic behavior. Tracks and trackways indicative of pathologies (e.g., fractures in pedal phalanxes) are relatively frequent, especially in middle to large-sized theropods (Tanke and Rothschild 1997, 2002; Rothschild et al. 2001; Rothschild and Tanke 2005). Many of the trackways described refer to large carnivorous dinosaurs that show missing or curled digits (Lockley 1991; Tanke and Rothschild 1997). Footprint and trackway evidence of limping theropods (Ishigaki 1986; Dantas et al. 1994; Lockley et al. 1994b) suggests injury or arthritis. Foot pathologies in large bipedal dinosaurs however have also been used to infer more active life-styles or natural fragility of the narrow, protruding digits (Laws 1997; Tanke and Rothschild 1997). For other good examples of pathologic tracks, see Abel (1935), Thulborn (1990) and Avanzini et al. (2005).

Tracks have also helped unveil another aspect of dinosaur behavior: their ability to swim. No skeletal remains can help addressing this question, and tracks attributable to swimming theropods have been reported, among others, by Coombs (1980), Milner et al. (2006), Ezquerra et al. (2007) and Xing et al. (2013a) (similar reports are available also for other dinosaur taxa; e.g., Currie 1983; Fujita et al. 2012). Theropods could float, as demonstrated by clawing traces left in the sediment as they swam (Ezquerra et al. 2007); the trackway shows that this theropod used a pelvic paddle motion, i.e. they were powered by alternating movements of the two hind limbs, like in living aquatic birds, and swam with amplified asymmetric walking movements to maintain its direction while swimming perpendicular to a water current (Ezquerra et al. 2007). The track record, therefore, has shown that dinosaurs (mostly theropods) colonized areas that included aquatic environments and were therefore probably able to swim.

10.2.6 Evidence for Gregariousness

Gregariousness is a form of social interaction between individuals that probably evolved to increase the fitness of single individuals within a group (Alexander 1974). Gregariousness allows greater defense of individuals from predators, increases effective access to food, efficiency of breeding, effective migration, and enhances the probability of safely raising the young (Currie and Eberth 2010). In order to maintain group cohesion, individuals within a group must synchronize their behavior in terms of time spent resting, foraging, and moving (Conradt 1998).

Tracksites, together with nesting sites, provide some of the most reliable proof about the gregariousness in extinct animals, in particular among dinosaurs (Ostrom 1972; Currie 1983; Lockley et al. 1986; Farlow et al. 1989; Horner and Gorman 1990; Carpenter 1999). Fossil trackways made by multiple individual animals can provide important qualitative and quantitative information about their social behavior.

Evidence for gregariousness in dinosaurs is difficult to gain from the body fossil record, and only bone bed assemblages may reflect such group behavior. Bone beds are concentration of bones in a localized area or stratigraphically limited sedimentary unit, in which the bones belong to more than one individual (see Rogers et al. 2007 for more details). Significant work on bone beds assemblages has provided compelling evidence on the gregarious habits of some ornithischian dinosaurs and the coexistence of multispecific individuals in the same habitat (Rogers 1990; Varricchio and Horner 1993; Mathews et al. 2009; Zhao et al. 2007).

In the study of dinosaur tracks, gregariousness may be deduced by the recognition of some peculiar features, primarily by the occurrence of multiple parallel trackways, exhibiting a preferring directionality (Ostrom 1972; Currie 1983; Lockley 1991). However, there is no arbitrary minimum number of adjacent parallel trackways for indicating gregarious behavior (Lockley and Matsukawa 1999). The presence of many parallel trackways does not necessarily constitute proof of a herding behavior, and data should be critically examined: trackways could have been made by animals that have walked alone at different times, and selected the same direction for the presence of a physical constraint, such as narrow river valley, shoreline, or the banks of a river (e.g., Ostrom 1972). Depths of the tracks in each trackway must be taken into consideration; similar-sized dinosaurs, walking contemporaneously on a substrate characterized by similar physical properties, probably produced parallel trackways with comparable depths. By contrast, parallel trackways with different track depths suggest that the animals walked on that substrate at different times, perhaps months, days, or even years later one from the other. A useful parameter to recognize gregariousness from track data is the intertrackway spacing (i.e., an index of regularity of spacing between parallel trackways; Lockley 1989; Lockley et al. 1998). In recent years, several trackways characterized by regular intertrackway spacing have been reported (Lockley et al. 1986, 2006b; Farlow et al. 1989; Lim et al. 1989; Li et al. 2008), suggesting animals that walked shoulder to shoulder, and thereby substantiating the hypothesis of their social behavior. Parallel trackways curving or swerving in unison could also provide evidence of herd habits among the trackmakers (Lockley and Hunt 1995a, b; Lockley and Matsukawa 1999).

Such ichnologic evidence for gregarious behavior in dinosaurs has been reported from Jurassic and Cretaceous sites in North America (Currie 1983, 1995; Lockley et al. 1983, 1986, 1992a, 1998; Farlow 1987; Farlow et al. 1989; Pittman and Gillette 1989; Hawthorne 1990; Carpenter 1992; Barnes and Lockley 1995; Lockley and Hunt 1995a, b; Cotton et al. 1998; Kvale et al. 2001; Schumacher 2003; Myers and Fiorillo 2009), South America (Leonardi 1989; Lockley et al. 2002; Fig. 10.7), East Asia (Lim et al. 1989; Matsukawa et al. 1997, 2001, 2005; Lockley et al. 2002, 2006b, 2012a, b; Hwang et al. 2004; Li et al. 2008; Xing et al. 2013a), Europe (Kaever and Lapparent 1974; Delair 1981; Agirrezabala et al. 1985; Viera and Torres 1992; Lockley et al. 1995c; Moratalla et al. 1997; Day et al. 2002a, 2004; Piñuela et al. 2002; Pérez-Lorente 2003; García-Ramos et al. 2004; Clark et al. 2005; Vila et al. 2008; Castanera et al. 2011, 2013, 2014; García-Ortiz and Pérez-Lorente 2014), Africa (Lingham-Soliar et al. 2003) and Australia (Thulborn and Wade 1979, 1984).

Fig. 10.7 Footprints provide clues on the social behavior of dinosaurs. Here spectacular parallel trackways at the Humaca dinosaur tracksite (Chuquisaca, Bolivia) interpreted as evidence of gregarious behavior by Lockley et al. (2002). Direction of progression is towards the *right* of picture. From Lockley et al. (2002)

Evidence suggests that large herbivorous dinosaurs, especially sauropods and ornithopods often traveled in herds, and that both groups acquired gregarious tendencies early in their histories (see Lockley and Matsukawa 1999 and Myers and Fiorillo 2009 and references therein). Sauropod trackways indicate groups of 40 or more individuals (Day et al. 2002a, 2004) and show either mixed-age or are age-segregated ichnologic assemblages (Lockley et al. 1986, 1995c, 2002; Castanera et al. 2011). The co-occurrence of adult and juvenile trackways may suggest protracted parental care far beyond the hatchling stage of development; groups of small-sized trackways may be interpreted as herds of juveniles or (as in the case of archipelago paleoenvironments) as the presence of dwarfed populations (Benton et al. 2010). Few tracksites exhibit parallel trackways of different species or groups (e.g., Day et al. 2002a, 2004).

Much evidence of possible social behavior in other groups of herbivorous dinosaurs, such as ankylosaurs (McCrea and Currie 1998; McCrea 2000) and ceratopsians (Lockley and Hunt 1995b) has now also accumulated. Evidence of gregariousness in carnivorous dinosaur trackways, particularly non-avian theropods, is less common than in other groups of dinosaurs, and the interpretations of such evidence remain more controversial. Some researchers support this hypothesis (Lockley and Matsukawa 1999; Carvalho and Pedrão 2000; Smith et al. 2002; Lingham-Soliar et al. 2003; Clark et al. 2005; Barco et al. 2006; Li et al. 2008; Currie and Eberth 2010; McCrea et al. 2014) while others prefer to consider trackway data as coincidental instances of normally solitary individuals converging on a common point (e.g., food source, Roach and Brinkman 2007).

10.2.7 On the Tracks of Birds

Birds are among the most diversified and thoroughly analyzed vertebrate groups, but both their origin and evolution remain controversial. The skeletal record of birds is strongly biased by the nature of bones that, in this group, are mostly small and delicate so that limbs are commonly lost in taphonomic decay processes (Davis and Briggs 1998; Brand et al. 2003). This makes the bird fossil record highly incomplete, and only a multidisciplinary approach, including paleornithology, paleoichnology, and molecular studies, can help in the understanding avian origins and radiation.

The skeletal record indicates an initial avian radiation around the Jurassic-Cretaceous boundary (about 145 million years ago) and an early Paleogene diversification for modern birds (Neornithes) (e.g., Clarke et al. 2005; Dyke and Kaiser 2011; Brocklehurst et al. 2012; Ksepka and Boyd 2012). Molecular studies and recent combined molecular and morphologic analyses, instead, indicate that modern birds began radiating in the Early Cretaceous (Cooper and Penny 1997; Haddrath and Baker 2012; Jetz et al. 2012; Lee et al. 2014).

Tracks similar to those of modern birds (i.e., shorebirds, small ducks, small herons, roadrunners) are only 15-20 million younger than the oldest avian skeletal remains, which is in agreement with molecular data (Brown et al. 2008). In contrast, the oldest body-fossil records of anseriforms and possibly charadriiforms date to the latest Cretaceous (ca. 70 million years ago), and are even younger for ciconiiforms and cuculiforms (Lockley and Harris 2010; Fig. 10.8). This could be explained through the following two hypotheses: (1) pre-latest Cretaceous occurrence of neornithians, implying that the body fossil record is strongly biased toward the preservation of non-neornithian birds, or (2) neornithians converged in foot morphology with their non-neornithian, Cretaceous ancestors. The latter appears more parsimonious suggesting that convergent evolutionary programs, in similar niches and at different periods, produced not only similar pedal morphologies but also similar size (Lockley and Harris 2010).

Feeding behavior has been also inferred from different fossil bird tracks by comparing them with traces characteristic of modern birds. For example several *Ignotornis* trackways exhibit reduced pace length, interpreted as a type of “foot stirring” behavior characteristic of modern herons “stirring” up the substrate for feeding (Lockley et al. 2008, 2009). The most noticeable example of feeding behavior was reported from the Cretaceous of Korea (Lockley and Harris 2010; Lockley et al. 2012a; Kim et al. 2012). Traces consist of sets of fine, zigzag, arcuate to semicircular grooves that “sweep” back and forth across the trackway, indistinguishable from those of modern spoonbills (Swennen and Yu 2005). But spoonbills are not recorded in the Cretaceous fossil record, and no spoonbill morphology is known in any Cretaceous bird. The ichnologic record thus adds new data to the Cretaceous avian diversity.

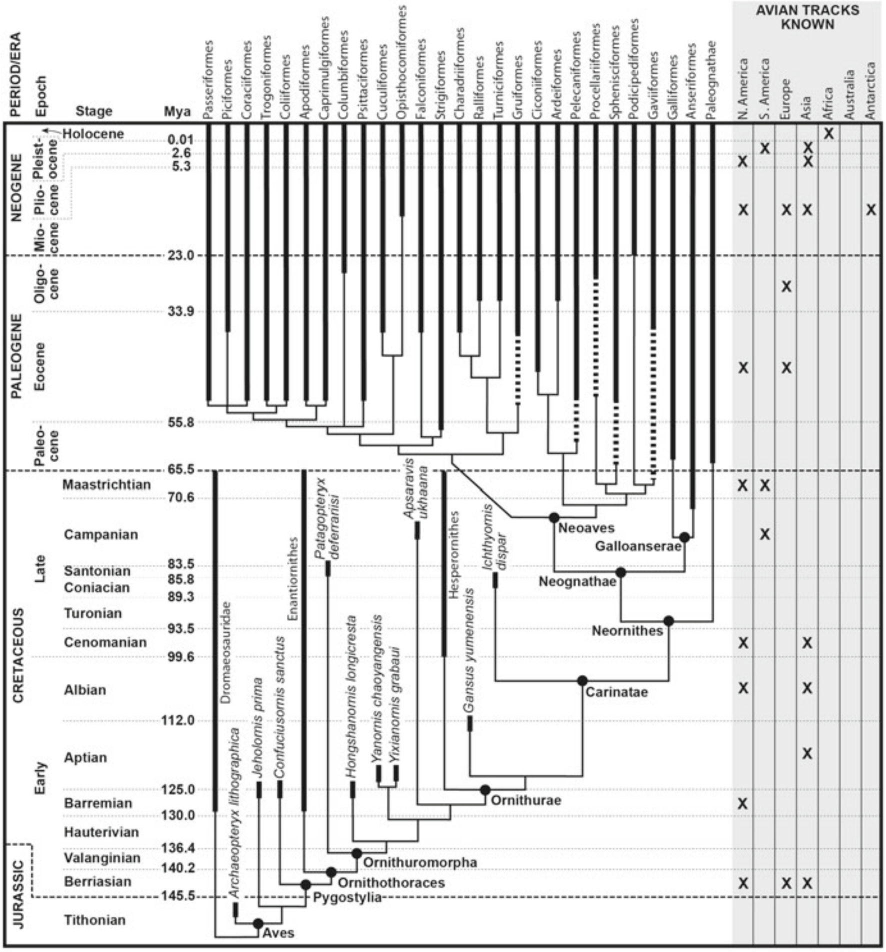

Fig. 10.8 Paleornithology and avian paleoichnology provide complementary data on the evolution of birds. This cladogram superimposed on geologic time scale shows both taxon ranges based on skeletal data and associated footprint occurrences. See text for discussion. Modified from Lockley and Harris (2010)

The primary Mesozoic bird tracksites were recently reviewed by Lockley and Harris (2010) but there are new findings reported every year (Falk et al. 2010, 2014; Falk 2011; Fiorillo et al. 2011; Xing et al. 2011, 2013b; Contessi and Fanti 2012; Huh et al. 2012; Kim et al. 2012; Lockley et al. 2012c, d; Azuma et al. 2013; Martin et al. 2014). Most fossil bird tracks exhibit sizes and morphologies similar to those of extant shorebirds and water-birds (Greben and Lockley 1992), and are generally associated with lake basin, fluvial floodplain, coastal plain, and marine shoreline deposits (Lockley and Harris 2010). This bias is strictly related to the physical properties of these environments that apparently facilitate the registration and preservation of tracks, and the creation of what has been called the shorebird ichnofacies (Lockley et al. 1994a; Lockley 2007b). Tracks of birds with feet adapted for perching, such as songbirds or raptors, have much less chance to be produced and preserved; the same happens with birds that live in environments where the burial and preservation of tracks is less frequent or improbable (mountain, forest, open marine, etc.). Even though there are many avian skeletal and track fossils, the two records do not match each other and few footprints were probably produced by the feet represented by the skeletal remains (Lockley and Harris 2010). This mismatch and all the previously mentioned data strongly indicate that morphologies and behaviors of many modern birds actually evolved convergently with many of their extinct, Mesozoic relatives. A striking example is provided by the discovery of an Early Cretaceous (Aptian-Albian 120–110 Ma) trackway: *Shandongornipes muxiai* (Li et al. 2005). This discovery shows the evolution of a terrestrial, zygodactylous bird that is unknown in the body fossil record; it probably occupied a roadrunner-like niche indicating evolutionary convergence of an early Cretaceous bird with the locomotory habits and possible ecology of modern birds (see Lockley et al. 2007).

The majority of the fossil bird tracksites discovered to date are in East Asia, primarily in China and South Korea (Azuma et al. 2002, 2013; Li et al. 2002; Kim et al. 2006, 2012; Lockley et al. 2006b, 2007, 2009, 2012c, d; Xing et al. 2011, 2013b; Contessi and Fanti 2012; Huh et al. 2012; He et al. 2013; Falk et al. 2014). The high frequency could be related to the abundance of lake deposits in these regions, but the contemporaneous Chinese and North Korean skeletal records are also very rich in birds. The complementary evidence thus indicates that the distribution pattern may reflect a true center of avian radiation (Lockley and Harris 2010).

10.2.8 Pterosaur Locomotion

Pterosaurs are the earliest known vertebrates to have evolved powered flight. These winged reptiles first appeared in the Late Triassic and went extinct at the end of the Cretaceous period (Buffetaut and Mazin 2003). Since their first discovery, there has been considerable debate over their terrestrial locomotor capabilities, in particular whether they walked bipedally (Cuvier 1809) or quadrupedally with their hindlimbs splayed (Soemmerring 1812, 1817). Some eminent paleontologists considered that pterosaurs were unable to walk (Abel 1925) or were bad walkers with their hindlimbs unsuitable for a quadrupedal gait (Wellnhofer 1978). The hypothesis that pterosaurs were digitigrade bipeds with an erect stance was supported and argued with phylogenetic and osteologic analysis by Padian (1983, 1984, 1985, 1987, 1988, 1991), Padian and Rayner (1993), Paul (1987) and Bennett (1990). In contrast, several researchers, on the basis of osteologic arguments, claim that pterosaurs were quadrupedal plantigrades, with semi-erect or possibly even sprawling stances (Pennycuick 1986; Unwin 1987, 1989; Wellnhofer and Vahldiek 1986; Wellnhofer 1988, 1991a, b).

As was the case for other extinct track-making animals, ichnology provided unequivocal evidence in resolving this long-standing dispute. Already in 1957 Stokes described a short trackway composed of tridactyl manus and tetradactyl pes prints

(Stokes 1957). He instituted the new ichnotaxon *Pteraichnus saltwashensis* that he identified as produced by a quadrupedal pterodactyloid pterosaur. This attribution was endorsed by subsequent findings (Stokes 1978; Wellnhofer 1978; Stokes and Madsen 1979), but was strongly opposed by Padian and Olsen (1984) who proposed they were made by a crocodilian trackmaker. *Pteraichnus* was no longer considered a pterosaur ichnotaxon (Unwin 1986, 1989; Prince and Lockley 1989; Lockley 1991; Wellnhofer 1991a; Bennett 1992). New discoveries provided new information (Logue 1994; Hunt et al. 1995b; Lockley and Hunt 1995a) and Mazin et al. (1995) and Lockley et al. (1995d) independently demonstrated that *Pteraichnus* could be attributed to pterosaurs (Fig. 10.9). To date, this interpretation is accepted by most pterosaur researchers (Lockley et al. 1996, 1997; Bennett 1997; Mazin et al. 1997, 2001; Unwin 1997a, b, 2006; Wright et al. 1997; Kubo 2008; Witton 2013). Ichnology therefore provided definitive evidence that pterosaurs walked on all fours.

These studies also demonstrated that at low-velocity walking, the body was held upright, with the forelimbs held more vertically and the *mani* brought close to the axis of the trackway, so they could not be starched much foreword. Conversely, at

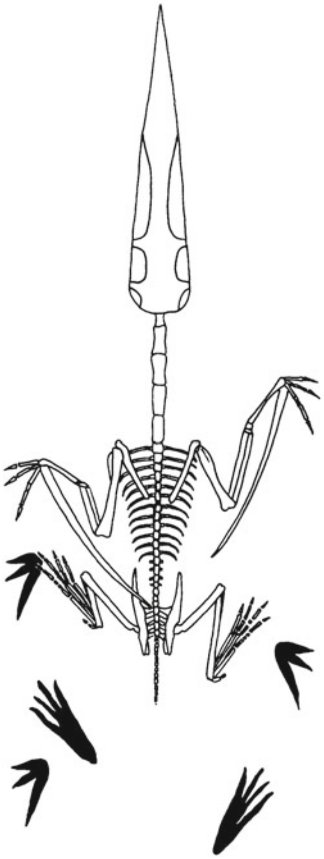

Fig. 10.9 Fossil trackways attributed to pterosaurs provided exceptional insight into the functional morphology and behavior of these flying reptiles. Furthermore, they solved the long-standing debate over pterosaur terrestrial locomotion. The tracks called *Pteraichnus* show that pterosaurs employed a plantigrade, quadrupedal stance and gait with the hind limb partially—to fully—abducted. From Unwin (1996)

higher velocities, the body was held less erect (possibly subhorizontally) allowing the long forelimbs to reach a more distant anterior point (Mazin et al. 2001). Trackways were also useful to infer the landing behavior of pterosaurs, which like modern birds used their wings to stall before landing (Mazin et al. 2009).

Pterosaur tracks are abundant in the Upper Jurassic rocks of Arizona, Colorado, Oklahoma, Utah and Wyoming (Stokes 1957; Lockley et al. 1995d, 1996; Lockley and Wright 2003; Lockley et al. 2008), France (Mazin et al. 1997, 2003, 2009; Billon-Bruyat and Mazin 2003), Poland (Pienkowski and Niedzwiedzki 2005), and Spain (García-Ramos et al. 2000, 2002, 2006; Meijide Calvo and Fuentes Vidarte 2001; Fuentes Vidarte et al. 2004a, b; Sánchez-Hernández et al. 2009). Tracks of Cretaceous age are much larger than those of the Late Jurassic, which agrees with body size trends of skeletal remains (Buffetaut and Mazin 2003). Large body size in this group can have evolved as early as Late Jurassic as testified by abundant footprints from Spain (García-Ramos et al. 2000, 2002, 2006) and few skeletal remains from Switzerland (Meyer and Hunt 1999). Pterosaur tracks have been reported from the Lower Cretaceous of China (Li et al. 2002; Zhang et al. 2006; Xing et al. 2013b, c), England (Delair 1963, re-interpreted by Wright et al. 1997), Germany (Hornung and Reich 2013), Japan (Lee et al. 2010), South Korea (Kim et al. 2006; Lee et al. 2008), Spain (Pascual Arribas and Sanz Pérez 2000; Meijide Calvo 2001; Fuentes Vidarte 2001; Hernández Medrano et al. 2006; Moratalla and Hernán 2009; Sánchez-Hernández et al. 2009), and USA (Maryland; Lockley and Rainforth 2002). In the Upper Cretaceous, they are known from Argentina (Calvo and Lockley 2001), Mexico (Rodríguez de la Rosa 2003), South Korea (Lockley et al. 1997; Hwang et al. 2002) and USA (Colorado, Lockley and Rainforth 2002; Utah, Lockley et al. 1995d). Upper Cretaceous Korean tracks, known as *Haenamichnus*, are the largest pterodactyloid tracks (up to 33 cm) and were made by a trackmaker not yet known from the body fossil record.

Pterosaur tracks have been also used as an indicator of body mass. Kubo (2011) tried to correlate the foot area with weight. He used seven ichnospecies of pterosaur tracks and estimated body weights of pterosaurs as ranging from 110 to 145 kg. This result indicates that large pterosaurs were ten times heavier than the heaviest modern birds.

The pterosaur track record provides evidence about the preferred environments and behaviors of these flying reptiles. Most Upper Jurassic pterosaur tracks are found in marginal marine, carbonate, and clastic-evaporitic lagoonal deposits whereas Cretaceous tracksites are associated with fluvial and freshwater deposits (Lockley and Rainforth 2002). The Late Jurassic record is consistent with the hypothesis, inferred also through the body fossil record, that pterosaurs inhabited marine shoreline habitats. This view is further corroborated by the discoveries of “swimming” and “feeding traces” (García-Ramos et al. 2000, 2002, 2006; Lockley and Wright 2003; Witton 2013; Lockley et al. 2014). They consist of scrape marks that are interpreted as traces produced by paddling limbs, a random distribution of tracks without evidence of trackways, and small circular paired depressions left in the substrate by beak prods of pterosaurs in search of food. This evidence reveals that pterosaurs could probably swim, or at least float on the surface of the water, like modern seabirds (Witton 2013; Hone and Henderson 2014; Li et al. 2015).

10.3 Conclusions

By applying rigorous analytic methods, which allow full hypothesis testing, vertebrate ichnology can provide reliable information about paleobiology (documenting evolutionary patterns, tempo of evolution, locomotion, posture, size, speed, social and individual behavior), paleobiodiversity (indicating the presence of taxa undocumented by the skeletal record), paleoecology (giving hints on environmental/habitat preferences and faunal composition) and paleobiogeography (providing presence/absence data on geographic distribution) of trackmakers, vertebrate ichnology is finally sitting at the "high table" of paleobiology.

In this review of Mesozoic reptile tracks some milestones of paleoichnologic research have been evaluated with the aim of highlighting the potential of these studies in contributing to the knowledge of evolutionary history and coevolution on the changing Earth. We have shown that vertebrate track record can be used to study the evolution of posture. Studies of the Permian to Triassic tetrapod-track record documents the appearance of upright stance in reptiles and shows a previously hidden correlation between this event and the Permo-Triassic mass extinction. Using synapomorphic characters in tracks has been essential in developing the present understanding of the origin of the dinosauromorph clade. Tracks show that the most basal dinosauromorphs were quadrupedal and that bipedalism was acquired phylogenetically closer to the origin of dinosaurs. An earlier origin of dinosauromorphs might imply a possible link with the Permo-Triassic mass extinction. The ichnologic record can be used to make hypotheses about the spatial and temporal distribution of basal dinosaurs. Tracks indicate the presence of a diverse and widespread fauna of dinosaurs during the early Late Triassic both in Laurasia and Gondwana, a distribution not yet documented by the body-fossil record. Track records provide evidence that habitats were shared by dinosaurian and non-dinosaurian archosaurs in the Late Triassic, and support the hypothesis that crurotarsan-dominated faunas were replaced by dinosaurs through a gradual process of ecologic replacement. Combined analyses of body and track fossils provide insights in the understanding of both environmental preferences and evolution of locomotory mechanisms in sauropod dinosaurs. Ichnologic data reveals the inland preference of wide-gauge titanosaurs highlighting the importance of considering track data in ecologic analysis. Trackways are used to estimate the speeds of trackmakers and provide clues to individual behaviors of theropod dinosaurs. Empiric formulae derived from extant animals constitute the basis of these interpretations, and show that theropods primarily used walking gaits, although some were runners, and there are a few records of individuals using trotting gaits. Crouching traces demonstrate that the avian orientation of the manus, with a medially facing palm, had evolved by the Early Jurassic within Theropoda. Footprints provide clues on social behavior in dinosaurs. Many sites have shown that herbivorous dinosaurs were at times gregarious. Carnivorous non-avian theropods were sometimes gregarious although interpretations are more controversial. A strong link between paleornithology and avian paleoichnology illuminates aspects of avian evolution, particularly with regard to paleoenvironmental preferences. Ichnology is particularly relevant when studying shorebirds evolution, given the completeness of the track record for this group. Footprints are crucial to understand pterosaur terrestrial locomotion and stance, to estimate body mass, and to learn about their physiology and behavior (swimming, feeding, landing).

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Chapter 11
The Mesozoic Lacustrine Revolution

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11.1 Introduction

The Mesozoic lacustrine revolution (MLR) represents a major evolutionary event in the continental realm (Cohen 2003). The decline in taxic diversity at the family level in lacustrine environments that took place during the late Paleozoic–Middle Triassic was reversed later in the Mesozoic, with diversification seeming to have continued to the Quaternary, although potential biases may have affected this trend (Cohen 2003). Major novelties and innovations that took place in lacustrine

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settings during the mid-Mesozoic include the diversification and increase in morphological disparity of aquatic macrophytes, aquatic insects, and teleosts. By the mid Cretaceous (125–90 Ma), the basic ecologic structure of the MLR was well established, defined by an ecologically significant increase of herbivory within ecosystems which previously had been overwhelmingly composed of detritivores and predators. This trophic readjustment was minimally altered by the end-Cretaceous global crisis and the subsequent ecologic rearrangement of the Paleogene world (Dunne et al. 2014).

It is a basic premise of this chapter that a review of this formative interval from a comparison of the body- and trace-fossil records will illuminate our understanding of the MLR. Although direct links between individual ichnotaxa and producers commonly are not possible, a comparison of the trace-fossil and body-fossil records through time is valuable in detecting the timing of large-scale ecologic changes in lacustrine ecosystems. Consequently, in this chapter we review the trace- and body-fossil record of lake and related continental aquatic deposits to establish and assess the importance of the MLR. As part of our examination, we discuss how ichnologic evidence may provide insights into major evolutionary innovations within lacustrine ecosystems. To do so, we provide an extensive summary of the available ichnologic information for Mesozoic–Cenozoic lacustrine successions. In addition, a review of the paleoecologic structure of Eurasian paleolakes in particular provide important evidence for understanding the impact this event had on trophic relationships throughout the water column (Zherikhin et al. 1999; Sinitshenkova 2002) as well as the lacustrine benthos and associated sediments during this formative interval (Buatois et al. 1998a; Mángano and Buatois 2007; Voigt and Hoppe 2010). Although this chapter is focused on the evolutionary novelties and innovations that took place during the Mesozoic, in order to place these changes within a broader context, we briefly outline the basic features of lacustrine ecosystems prior to the MLR (see Chap. 6 for a detailed discussion on the ichnology of Silurian-Permian lakes). A more complete context for understanding the MLR involves a search for the roots of Mesozoic MLR novelties and innovations in older deposits to establish relevant ichnological, biotic, and physical contrasts between the late Paleozoic and the Mesozoic worlds. Similarly, we provide a discussion of the post-Mesozoic record in order to evaluate the aftermath of the MLR.

11.2 Methods and Terminology

For this study, all ichnotaxonomic determinations have been checked and adjusted based on a reevaluation of the available literature. Because the literature essentially provides two contrasting trace fossil-assemblages, a distinction is made between lake-margin settings and fully subaqueous lacustrine conditions. Lake-margin settings are characterized by periodic fluctuations of the water table, leading to highly variable conditions in substrate consistency. Typically, a characteristic zonation from softgrounds near the edge of the water body to drier substrates outward from the lake develops (Scott et al. 2012a). Lake-margin ichnofaunas commonly display activity of a combined terrestrial to shallow subaqueous biota. The degree of consolidation of the substrate plays a major role for preservation of biogenic structures in lake-margin deposits (Buatois and Mángano 2004, 2009). Ichnofaunas from lake-margin settings typically comprise the *Scoyenia* Ichnofacies (Buatois and Mángano 1995, 2004, 2009) and less commonly the *Camborygma* Ichnofacies (see Chaps. 1 and 13).

Fully lacustrine settings (i.e. the permanent subaqueous zone), particularly in hydrologically open systems, may host a relatively diverse benthic fauna. In this zone a where a lake experiences a high degree of environmental stability and appropriate ecologic conditions, particularly high levels of oxygenation, low energy, constant food supply, the presence of freshwater, and cohesive substrates (Buatois and Mángano 1995, 2004, 2009; Miller and White 2007; Scott et al. 2012a). Oxygenation is a first-order limiting factor, because in lakes with year-round thermal stratification the hypolimnion becomes anoxic or dysoxic and bioturbation is precluded in the lake bottom below the mixolimnion. Low-energy turbidity and underflow currents may provide oxygen and food to lake bottoms. Colonization by macrobenthos and preservation of their trace fossils are both unfavorable in soupy substrates and, accordingly, some degree of substrate cohesion is required to allow the passage of discrete biogenic structures through the fossilization barrier. Ichnofaunas from fully lacustrine settings typically form the *Mermia* Ichnofacies (Buatois and Mángano 1995, 2004, 2009; see Chap. 1).

At the scale of the basin, we commonly refer to the scheme developed by Bohacs et al. (2000), who recognized three different types of lake basins, namely overfilled, balanced-fill, and underfilled. Overfilled-lake basins occur if the rate of sediment/water input exceeds the rate of formation of potential accommodation. These systems are typically hydrologically open, and form deposits of fluvio-lacustrine, siliciclastic sediments that display parasequences resulting from shoreline progradation and delta-channel avulsion. Balanced-fill lake basins are formed when rates of sediment/water supply are in balance with the formation of potential accommodation. These lakes tend to shift periodically from hydrologically open to closed and vice versa, producing both carbonate and siliciclastic deposits which display parasequences that record both progradational parasequences and aggradation of chemical sediments during periods of desiccation. Underfilled-lake basins are characterized by rates of accommodation formation that exceed the rate of supply of sediment/water. These are typically hydrologically closed lakes, dominated by evaporite deposits which display parasequences that record vertical aggradation. This scheme has been successfully used to frame both ichnologic (Buatois and Mángano, 2004, 2007, 2009) and paleobiologic (Gierlowski-Kordesch and Park, 2004) information.

In order to frame the major ecosystem changes discussed in this chapter, we have used the distinction between novelties and innovations outlined by Erwin and Krakauer (2004) and Erwin (2012). According to these authors, invention is the creation of something new, whereas innovation is a successful development of an invention. Evolutionary novelties only result in innovations when they drive ecologic transformation (Erwin 2012).

For better clarity in specifying the immatures of non-holometabolous versus holometabolous insects, we employ the standard entomological terminology used in North America (China et al. 1958). For those insects possessing egg to naiad/nymph to adult development, the term “naiad” is used for an aquatic immature instar that lacks holometabolous development (Snodgrass 1954). Immatures consisting of naiads occur in the Ephemeroptera (mayflies) and Odonata (dragonflies and damselflies), the extinct archaeorthopteroid Chresmodida, Plecoptera (stoneflies), and some groups of Heteroptera (true bugs) within the Hemiptera. A terrestrial immature of these non-holometabolous insects is termed a “nymph” (Snodgrass 1954; Davies 1958), and nymphs commonly occur within the same major groups as species with naiad immatures. Examples of taxa with nymphs include the terrestrial Orthoptera (grasshoppers, crickets), Blattodea (cockroaches), Isoptera (termites), and Mantodea (mantids). We restrict the term “larva” solely to insects with holometabolous development, consisting of egg to larva to pupa to adult development (Snodgrass 1954). Holometabolous taxa that have aquatic larvae include certain groups within the Coleoptera (beetles); the Megaloptera (alderflies and dobsonflies); a few groups of Neuroptera such as spongillaflies; certain, especially nematocerous, Diptera (true flies); and the Trichoptera (caddisflies). Restriction of the term, larva, to holometabolous insects offers more precision than application of the term broadly to multiple developmental modes that would encompass developmental stages such as aquatic naiads, terrestrial nymphs, and probably forms that lack developmental change. The distinction used herein generally has been accepted by a broad spectrum of evolutionary developmental biologists (Gilbert 2014).

The body-fossil record of ancient lacustrine basins is strongly biased as a result of the distribution of fossil *Lagerstätten*. Fortunately, these spectacular deposits are quite common in lacustrine successions (see Table 14.1 in Cohen 2003). However, integrating body-fossil evidence from fossil Lagerstätten with ichnologic information frequently is problematic because many of the former records accumulated as event beds under anoxic conditions, preventing bioturbation, and therefore having a sparse trace-fossil record. Notwithstanding this limitation, there are a number of Mesozoic examples where exceptional body-fossil accumulations have been recovered in association with trace fossils, most notably the Madygen (Voigt and Hoppe 2010), El Montsec (de Gibert et al. 2000) and Las Hoyas (Buatois et al. 2000a; de Gibert et al. 2016) biotas.

11.3 Lacustrine Ecosystems in Deep Time

Exploration of lacustrine ecosystems in deep time is a challenging enterprise because lakes are geologically ephemeral (Cohen 2003). However, the long-term evolution of organisms in freshwater settings provides continuity, allowing reconstruction, albeit tentative, of secular changes in lacustrine biotas (Anderson and Dean 1988; Buatois et al. 1998a; Labandeira 1999; Park and Gierlowski-Kordesch 2007). Because of the patchiness and lack of connection between individual lakes in space and time, as opposed to the more continuous record of oceans, the fossil record of lacustrine organisms is sporadic (Cohen 2003).

As with other depositional settings, lakes are affected by a number of taphonomic megabiases (Behrensmeyer and Kidwell 1985; Behrensmeyer et al. 2000).

Taphonomic megabiases are defined as "largescale patterns in the quality of the fossil record that affect paleobiologic analysis at provincial to global levels and at timescales usually exceeding ten million years" (Behrensmeyer et al. 2000). In particular, the fossil record of lacustrine basins is strongly affected by both intrinsic changes and extrinsic abiotic and biotic changes. The former results from the evolution of new body plans and the impact of behavior on fossilization potential (Behrensmeyer et al. 2000). As in the archetypal case of marine environments, development of mineralized hard parts is one of the intrinsic factors in lake settings, as is the establishment of fossorial behavior by vertebrates. The increased depth and extent of bioturbation through time exhibited by the lacustrine infauna is certainly one of the most important, extrinsic biotic factors contributing to taphonomic megabiases in these settings (see Sect. 11.8.2). Finally, tectonic and climatic controls on the establishment and evolution of lacustrine basins are prime examples of extrinsic, abiotic factors in the generation of taphonomic megabiases. These interpretive limitations notwithstanding, our understanding of this record are informed by several key observations.

(1) **Lacustrine habitats have experienced a history of regular and repeated formation, isolation, and destruction**. Because of the combined effects of climate variability and change as well as sediment infill, most individual lakes only persist over timescales of ~10^2–10^4 yrs, with only a small percentage of lakes, generally those originating from tectonic, volcanic, and meteoritic impact processes, persisting over longer intervals of time (Cohen 2003; Cohen et al., 2015). Most of the processes that create lakes, such as fluvial diversion from damming, glacial blockage of drainage systems and delta-plain subsidence, are also predilect for the eventual destruction of these same habitats. The creation and destruction of lakes often occur at quasi-predictable tempos scaled by the lake formation process, including determining potential sediment accommodation space, coupled with the typical range of sediment accumulation rates associated with lacustrine systems.

(2) **The need for dispersal of organism populations among lakes is a primary driver of both evolutionary innovations and constraints on the lacustrine biota**. The excellent dispersal adaptations of organisms are a hallmark characteristic of most lacustrine systems. Organisms have evolved adaptations for dispersal as well as for the constraints emplaced on them by the "typical" lacustrine environment mentioned above. These features include adaptations for flight, such as active flight by aquatic insects, and passive carriage by birds, fish, and wind (Boag 1985; Bilton et al. 2001; Green and Figuerola 2005; Van Bocxlaer et al. 2011); active parasitism on animal dispersal vectors (Graf and Cummings 2006); and desiccation resistance (Watanabe et al. 2002; Watanabe 2006). Conversely, the very adaptations for dispersal between ephemeral waterbodies also promote gene exchange between populations and reduce the likelihood of population isolation and speciation (Bilton et al. 2001). These adaptations inherently constrain and scale the rates of lacustrine evolution to the stability and persistence of their waterbodies, with the faunas of shorter-lived lakes (better migrants or desiccation survivors) associated with slower evolutionary rates and overall lower diversity. Morphological novelties arising from new functional and behavioral modifications take advantage of changing lacustrine

food resources, of which herbivory on aquatic plants or tiered detritivory exploiting deeper substrates are prime examples. These novelties become innovations when in the case of dispersal, the spread of disseminules is severely impeded by a periodic scarcity of quasipersistent lakes, and the energetic requirements of adaptations for exploiting lacustrine resources run up against the competing need to migrate to new habitats.

(3) **Lacustrine evolution in long-lived lakes is highly iterative and lacustrine habitats can act as refugia for evolutionary novelties and innovations.** Comparative studies of the living and fossil faunas of long-lived Neogene African Great Lakes and early Mesozoic Newark Supergroup paleolakes show that speciation and diversification trends often are highly iterative. The iteration of homologous morphological novelties in lacustrine clades evolve repeatedly in space and time whenever lakes persist sufficiently long for the results of diversification to be expressed (McCune 1996; Salzburger et al. 2014). Particular body plans and evolutionary novelties have been observed resulting from the convergence of lineages within isolated lakes. One such convergence is the iconic example of cichlid fish pharyngeal jaw mechanics and overall body structure converging among species populations in Lakes Tanganyika and Malawi (Kocher et al. 1993). Perhaps even more remarkable, trophic interactions have also been observed to converge among long-lived lakes, albeit occasionally with slightly different players. One example involves patterns of escalatory predator–prey coevolution (West and Cohen 1996; Van Damme and Pickford 2003). Occasionally, the resulting species of these radiations are themselves later dispersed into other lake systems, providing the beginnings for more widespread spatial diversification of the original clade (Van Damme and Pickford 1999; Anderson et al. 2010).

(4) **The tempo of evolutionary innovation related to trophic interactions in lakes is probably modulated by the history of geochronologically long-lived lakes**. If long-lived lakes can serve as incubators for diversification and evolution of key innovations and interactions in aquatic organisms, then it is likely that during times of such lake abundance, the most favorable opportunity exists for large scale trophic "revolutions" within lacustrine biotas. The mid-Mesozoic breakup of Pangaea probably represented the peak period of long-lived lake formation. These lakes were coupled with an ever increasing provinciality as they were progressively rafted on different continental land masses around the planet (Cohen 2003).

11.4 The Lacustrine World Prior to the Mesozoic Revolution

In this section we provide a brief review of the basic features of lacustrine communities that immediately preceded those of the Mesozoic world. Evidence of Proterozoic lacustrine biotas is scarce, to say the least, essentially being restricted to stromatolites most likely formed by cyanobacteria (e.g. Hoffmann et al. 1980) and leiosphaeridian acritarchs that may have been adapted to freshwater, although this is a contentious issue (Martín-Closas 2003). There is a paucity of evidence for body-fossils in Cambrian through mid-Silurian continental aquatic habitats (Labandeira 2005a). Tasmanitids (green algae) were abundant during the early Paleozoic, but most likely inhabited brackish rather than fresh water (Martín-Closas 2003). The Cambrian-Ordovician evidence for the incipient colonization of land originates from trace fossils of arthropods that were able to foray into intertidal areas, coastal dunes and ponds (see Chap. 5), and stromatolites that were similar in structure to, but commonly more diminutive than those of the Precambrian (Ponomarenko 2009). In addition, the occurrence of a diverse cryptospore assemblage in Lower to Middle Ordovician deposits represents the earliest evidence of land plants, suggesting an early origin of embryophytes (Rubinstein et al. 2010). Chlorophytes were represented mainly by the Chlorococcales, which became dominant in lacustrine plankton by the Ordovician (Martín-Closas 2003), and the closely related Charophytes that were present in freshwater bodies at by the Late Silurian, if not earlier (Feist et al. 2005). The presence of liverwort and embryophyte-grade spores toward the end of this interval, and continuing into the Early Devonian, signals the establishment of an incipient subaerial plant cover, probably adjacent to bodies of brackish and freshwater inland and along coastlines (Strother 2000). These developments, in conjunction with the presence of lacustrine (and fluvial) sediments, particularly during the Late Ordovician and Silurian, indicate the emergence of a depauperate lacustrine biota consisting of transient and permanent microorganisms, plants, fungi, and invertebrate animals. The fossil history of lacustrine zooplankton is notably poor. However, molecular clocks may help to provide some constraints. For example, cladoceran crustaceans are thought to have originated by the Devonian (Sacherová and Hebert 2003). The Silurian-Devonian lacustrine trace-fossil record is restricted to lake-margin settings, and is dominated by arthropod trackways (Buatois and Mángano 1993a; Buatois et al. 1998a; see Chap. 6). The restriction of biogenic structures to lake margins and the apparent absence of fully lacustrine ichnofaunas are consistent with extremely inefficient nutrient delivery in the absence of an extensive upland plant cover (Cohen 2003). These lakes may have been ultraoligotrophic and limited in phosphorous (Cohen 2003), precluding the establishment of a lacustrine benthos.

With few exceptions (Grenier 1974; Clarkson et al. 1993; Rolfe et al. 1993; Jeram and Selden 1993; Shear 1993), the Lower Carboniferous (Mississippian) lacks a significant record of well-documented lake deposits and associated biotas. During the Late Carboniferous (Pennsylvanian), two major types of ecosystems appeared that were displaced by differing environmental conditions. The Wet Biome emerged during the earlier Pennsylvanian and included a wide variety of wetlands, notably coal-swamp communities that consisted of water-tolerant lycopods, sphenopsids, medullosan seedferns, and arborescent marattialean ferns, occupying much of humid equatorial Euramerica (Gastaldo et al. 1996). By contrast, evidence for a Dry Biome appears toward the latter half of the Pennsylvanian, and included communities dominated by a desiccation-tolerant biota, such as cordaites, noeggeranthialeans, conifers, gigantopterids, peltasperms, and probably cycads that occupied more continental, extra-tropical environments (Opluštil et al. 2013). Regarding zooplankton, copepods were already present by the Mississippian in glacial lakes of

Gondwana (Selden et al 2010). During the Permian, the tropical to paratropical Wet Biome diminished significantly, at least in North America and Europe, although it survived largely intact in China (D'Rozario et al. 2011). By contrast, the Dry Biome, which first appeared during the latter half of the Pennsylvanian (Opluštil et al. 2013), temporally overlapped with the Wet Biome, and became prominent in more inland, drier basins of the Permian as it assumed a distinctive biotal character in many habitats. Aquatic herbivory was still absent, in contrast to a pulse of significant herbivory that had evolved on land by the Late Pennsylvanian (Labandeira 2006). In addition to ichnofaunas in lake-margin deposits, Mississippian and Pennsylvanian trace fossils also are present in fully subaqueous lacustrine deposits, indicating a significant environmental expansion of the benthic fauna (Buatois and Mángano 1993a; Buatois et al. 1998a) (see Chap. 6). These lacustrine deposits were colonized by a moderately diverse, mobile, detritus-feeding epifauna. This expansion was probably linked to the rapid diversification, and increase in abundance of land plants, attributable to vegetational changes that introduced abundant organic detritus into previously nutrient-poor, lacustrine habitats (Maples and Archer 1989). Also, ichnologic information suggests a major diversification event during the Mississippian and Pennsylvanian, which parallels the diversification of freshwater organisms, such as arthropods, annelids, fish, and mollusks (Maples and Archer 1989; Buatois et al. 1998a). The ichnologic evidence of the Dry Biome during the subsequent Permian consists of a high abundance and moderate diversity of arthropod trackways emplaced in subaerially exposed sediment of playa-lake systems (see Chap. 6). By the Permian, the presence of meniscate trace fossils (e.g. *Scoyenia*) records the establishment of a mobile, shallow- to mid-tier, infauna in firm, desiccated substrates. However, these structures still were relatively rare and for the most part have been recorded in overbank environments rather than in lake-margin settings that are overwhelmingly dominated by arthropod and tetrapod trackways.

11.5 The Mesozoic Lacustrine Revolution

The Mesozoic trace-fossil record of lacustrine successions is uneven in time and space. The Lower Triassic ichnologic record of lake-margin environments is remarkably poor, and we are not aware of well-documented, fully lacustrine, Early Triassic ichnofaunas. In contrast, Middle to Late Triassic lacustrine ichnofaunas have been documented in great detail. The Jurassic ichnologic record is uneven, with a number of detailed studies documenting both Early and Late Jurassic ichnofaunas, but less information is available for the Middle Jurassic. The Early Cretaceous record is relatively good, but the record of Late Cretaceous fully lacustrine ichnofaunas is particularly poor.

Unsurprisingly, body fossils of the MLR are unevenly distributed as well. Triassic paleontologic information is essentially based on Eurasian localities and, to a lesser extent, eastern North America and South Africa. The Jurassic body-fossil record, particularly for aquatic insects, is still significantly centered in Eurasia, but includes a few localities in western North America as well. In contrast, the Early Cretaceous tends to show a more widespread distribution of lacustrine fossiliferous localities, but still is heavily represented by Eurasian lake deposits, most likely resulting from extensional tectonics during the breakup of Gondwana. However, information from the Late Cretaceous is patchy.

11.5.1 Early Triassic Denouement

After the ecologic crisis at the Permian–Triassic boundary, the short-lived, five million-year-long Early Triassic represents a period that ranges from biotal stasis to subtle increases in the diversity of aquatic and terrestrial communities (Looy et al. 1999). The ichnology of Lower Triassic lake-margin deposits has been documented in a few places, namely Germany (Knaust and Hauschke 2004, 2005) and the western United States (Lovelace and Lovelace 2012). A moderate diversity of invertebrate trace fossils has been recorded in marginal facies of an underfilled playa-lake system in Germany (Knaust and Hauschke 2005). The playa-lake ichnofauna contains arthropod trackways and trails (*Diplichnites*, *Stiallia*, *Diplopodichnus*), arthropod bilobate structures (*Cruziana*, *Rusophycus*), vertical burrows (*Skolithos*), bivalve burrows (*Lockeia*), branching burrow systems (*Phycodes*), and the horizontal J-shaped ichnogenus *Fuersichnus*. Pseudofossils, such as *Aristophycus*, are present in the same deposits (Knaust and Hauschke 2004). Body fossils have been recovered from these deposits, including conchostracans, notostracans, and xiphosurids, as well as indeterminate fish remains (Knaust and Hauschke 2005). The arthropod trackway *Diplichnites* and the bivalve dwelling/resting structure *Lockeia* also occur in Lower Triassic shallow-lacustrine deposits of the western United States (Lovelace and Lovelace 2012).

In contrast to younger lake-margin ichnofaunas, meniscate, backfilled trace fossils are absent in these Lower Triassic examples, and arthropod trackways seem to be relatively common. In this respect, Lower Triassic lake-margin ichnofaunas apparently are more similar to those from the Permian (see Chap. 6) than to the archetypal Mesozoic suites, revealing the persistence of Paleozoic types of animal–substrate interactions. Also, as is commonly the case for Paleozoic lacustrine ichnofaunas, shallow tiers were dominant and penetrative structures, such as those responsible for ichnofabric formation, were absent (Knaust and Hauschke 2005).

The Early Triassic continental body-fossil record is sparse as well (Shcherbakov 2008a). Freshwater insects originate mostly from Eurasian localities and generally consist of mayfly wings (Sinitshenkova 2013), archaeorthopteran and related orthopteroid taxa (Shcherbakov 2008b), cockroaches (Żyla et al. 2013), a few basal hemipteran lineages (Shcherbakov 2008a), and isolated elytra of schizophorid and permosynid beetles and related lineages (Ponomarenko 2004, 2008). Many of these fossil taxa preferentially are represented by immatures, especially naiads, that when compared to conspecific adults, occur at frequencies greater than is typical of the Permian (Shcherbakov 2008b). As with Early Triassic plants (Looy et al. 2001), contemporaneous insect faunas are characterized by four major changes when compared to their Late Permian precursors (Shcherbakov 2008b). These shifts are: (1) the evolution of new, Early Triassic dominant groups at the expense of earlier Late Permian dominants; (2) movement into the high-latitude Triassic by groups that formerly occurred at Permian low latitudes; (3) preferential survival of small-sized, generalist feeding taxa; and (4) emergence of lineages that were aquatic or otherwise tied to water bodies such as lakes. Although these changes promoted diversity, it was not until the Anisian stage of the early Middle Triassic, 5–11 m.yr. after the end-Permian crisis, when insect taxa, including aquatic forms, and their interactions with plants approached the diversity that had existed during the Late Permian (Gall 1996; Labandeira 2005b).

Another important component of the Triassic benthos was charophytes, which are particularly well known in lacustrine carbonates and marls (Martín-Closas 2003). *Isoetes*-related, nonflowering vascular plants were present in the littoral zone (Cohen 2003; Moisan et al., 2012b). As in the Paleozoic, lacustrine phytoplankton was still dominated by Chlorococcales, but an increase in diversity is apparent (Brenner and Foster 1994; Martín-Closas 2003).

11.5.2 Rediversification During the Middle to Late Triassic

Ichnofaunas have been documented in detail in Middle to Upper Triassic lake-margin deposits (including those of playa lakes) from the eastern (Metz 1995, 1996, 2000; Szajna and Hartline 2003) and western (Gillette et al. 2003; Lucas et al. 2010) United States, Argentina (Melchor et al. 2003, 2006; Melchor 2004; Genise et al. 2009; Marsicano et al. 2010), Greenland (Bromley and Asgaard 1979), England (Porter and Gallois 2008), Germany (Schlirf et al. 2001), Morocco (Hminna et al. 2015), and China (Shi et al. 2007; Li et al. 2014). These lake-margin deposits commonly contain a relatively wide variety of vertebrate and invertebrate trace fossils.

Vertebrate ichnofaunas in Middle to Upper Triassic lake-margin deposits typically are dominated by tetrapod trackways (e.g. *Brachychirotherium*, *Brasilichnium*, *Dicynodontipus*, *Characichnos*, *Evazoum*, *Grallator*, *Gwyneddichnium*, *Rhynchosauroides*, *Tetrasauropus*) and, more rarely, lungfish burrows (*Redondarefugium*) (Melchor et al. 2006; Lucas et al. 2010). Typical invertebrate trace fossils in lake-margin deposits are shallow-tier, ornamented, meniscate, unbranched (*Scoyenia*), and branched (*Spongeliomorpha*) structures, as well as meniscate structures lacking bioglyphs (*Taenidium*), arthropod bilobate structures (*Cruziana*, *Rusophycus*), and simple horizontal (*Palaeophycus*, *Planolites*) and vertical (*Skolithos*) burrows (Bromley and Asgaard 1979; Metz 1995, 1996; Schlirf et al. 2001; Gillette et al. 2003; Melchor et al. 2003, 2006; Melchor 2004; Shi et al. 2007; Porter and Gallois 2008; Lucas et al. 2010; Li et al. 2014; Hminna et al. 2015). In some cases, great densities of the bivalve burrow *Lockeia* (Lucas et al. 2010) and the ichnogenus *Fuersichnus* (Bromley and Asgaard 1979) have been documented, typically forming monospecific trace-fossil suites. Arthropod trackways, although extremely common in Paleozoic lake-margin settings (Buatois and Mángano 1993a; Buatois et al. 1998a; see Chap. 6), and are quite rare in Middle to Upper Triassic deposits that were formed in similar environments, typically represented as isolated occurrences (Melchor 2004; Melchor et al. 2006). Horizontal, nonspecialized grazing trails, such as *Helminthopsis* and *Cochlichnus*, may be present (Melchor 2004; Shi et al. 2007; Li et al. 2014; Hminna et al. 2015), but they are never dominant and tend to reflect emplacement in substrates that did not experience periodic desiccation. Three-dimensional branching burrow systems (*Treptichnus*) may be present, but are uncommon (Porter and Gallois 2008). These structures were typically emplaced close to the sediment surface, the only exception being those produced by crayfish, referred to the ichnogenus *Camborygma*, which display variations in architecture as a response to the depth of the water table. Complex architectures with many branches and chambers were constructed by primary burrowers in areas of high water table, whereas deep and simple burrows are dominant in areas of low and/or highly fluctuating water table (Hobbs 1981; Hasiotis and Mitchell 1993).

Middle to Late Triassic, fully lacustrine ichnofaunas are known from the eastern United States (Metz 1995, 1996, 2000), Argentina (Melchor et al. 2003, Melchor 2004), Kyrgyzstan (Voigt and Hoppe 2010), England (Porter and Gallois 2008), and Greenland (Bromley and Asgaard 1979). Ichnofaunas in low-energy deposits are essentially represented by invertebrate trace fossils, with a dominance of very shallow-tier, simple, horizontal trails of deposit and detritus feeders (e.g. *Helminthopsis*, *Helminthoidichnites*, *Cochlichnus*, *Mermia*) and of shallow-tier, three-dimensional, branching burrow systems (*Treptichnus*) (e.g. Metz 1995, 1996, 2000; Melchor et al. 2003; Melchor 2004; Porter and Gallois 2008). Vertebrates are represented by the fish trail *Undichna* (Melchor 2004).

One of the first lacustrine ichnofaunas studied in detail is that of the Fleming Fjord Formation of Greenland (Bromley and Asgaard 1979) (Fig. 11.1a–f). Integration of ichnologic and sedimentologic information indicates that three main trace-fossil assemblages are present in these ephemeral lacustrine deposits (Bromley and Asgaard 1979, 1991; Dam and Stemmerik 1994; Bromley 1996). *Skolithos*, *Arenicolites,* and *Polykladichnus* occur in tempestites, whereas *Fuersichnus* (Fig. 11.1a–b) and *Lockeia* (Fig. 11.1c) are present in fair-weather deposits. *Scoyenia* (Fig. 11.1d–f) and *Skolithos* (Fig. 11.1d–f) occur in marginal-lacustrine deposits.

Upper Triassic ichnofaunas preserved in deposits of the Newark Supergroup, which record sedimentation in lakes within an extensive rift system in eastern North America, formed during the initial breakup of Pangaea (Olsen 1989; Schlische 2003). These ichnofauna have been analyzed in detail (e.g. Olsen and Flynn 1989; Metz 1995, 1996, 2000) (Fig. 11.2a–g). One of these units, the Lockatong Formation, records sedimentation in a balanced-fill lake characterized by recurrent base-level fluctuations. As a result, successions show well-defined, vertically stacked, transgressive–regressive cycles (Olsen 1980). The invertebrate ichnofauna consists of a combination of feeding (*Planolites montanus*, *Scoyenia gracilis, Treptichnus pollardi*), dwelling (*Spongeliomorpha milfordensis*), grazing (*Cochlichnus anguineus*), resting (*Lockeia siliquaria*), and locomotion (an undetermined arthropod trackway)

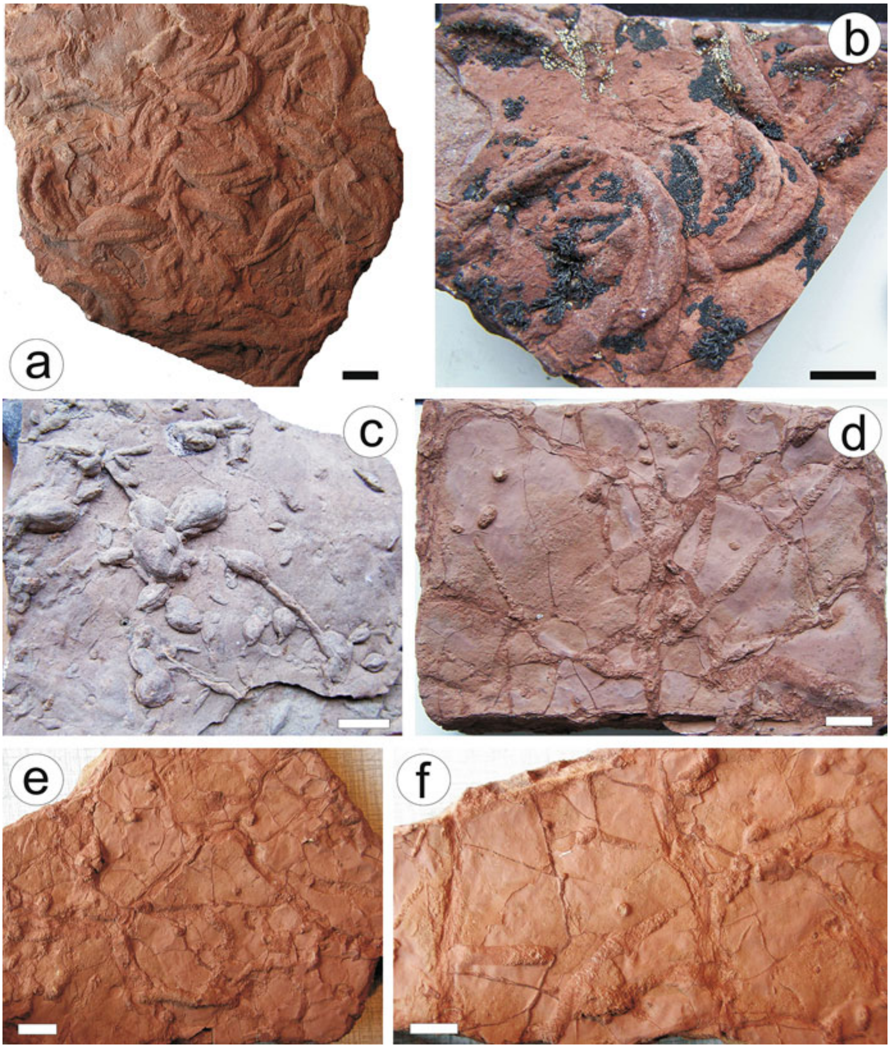

Fig. 11.1 Characteristic trace fossils from Upper Triassic ephemeral lacustrine deposits of the Flemming Fjord Formation of Greenland. (**a**) General view of a surface displaying a high density of *Fuersichnus communis*; (**b**) Close-up of *Fuersichnus communis* showing its characteristic banana shape; (**c**) The almond-shape trace fossil *Lockeia amygdaloides*. The associated horizontal burrows may be referred to the ichnogenus *Ptychoplasma*; (**d**) General view of a surface showing several specimens of the meniscate ichnotaxon *Scoyenia gracilis*. Note the presence of circular cross-section of vertical *Skolithos* isp.; (**e**) *Scoyenia gracilis* with less developed meniscate infill and bedding-plane expression of *Skolithos* isp.; (**f**) Close-up of *Scoyenia gracilis* and *Skolithos* isp. All scale bars are 1 cm long

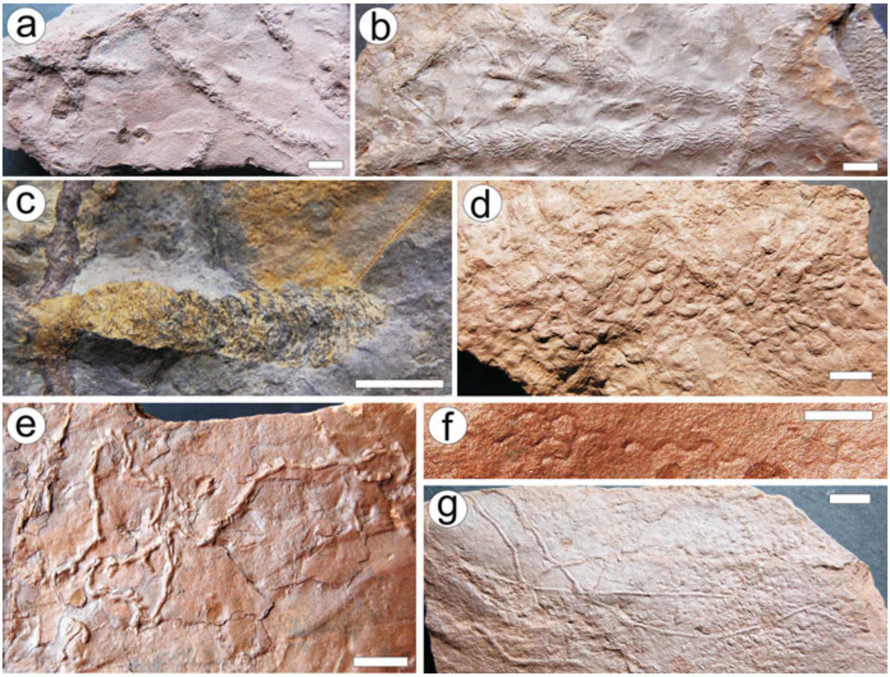

Fig. 11.2 Characteristic trace fossils from Upper Triassic lake-margin deposits of the Newark Supergroup of eastern United States. (**a**) General view of a surface with *Scoyenia gracilis*, Passaic Formation; (**b**) Close-up showing bioglyphs in *Scoyenia gracilis*, Passaic Formation; (**c**) Close-up showing meniscate infill in *Scoyenia gracilis*, Lockatong Formation; (**d**) General view of a surface with high density of *Lockeia amygdaloides*, Passaic Formation; (**e**) *Treptichnus bifurcus*, Passaic Formation; (**f**) *Cochlichnus anguineus*, Passaic Formation; (**g**) *Helminthoidichnites tenuis*, Passaic Formation. All scale bars are 1 cm long. Photographs courtesy of Robert Metz

structures (Metz 1995). The reptile trackway *Gwyneddichnium* is present as well (Olsen and Flynn 1989). Trace fossils are almost invariably restricted to lake-margin deposits. Whereas some of these structures most likely were emplaced in wet substrates (e.g. *Treptichnus pollardi*, *Lockeia siliquaria*), other ichnotaxa, such as *Scoyenia gracilis* and *Spongeliomorpha milfordensis*, support their formation in firm substrates resulting from desiccation (Metz 1995). Under extremely dry conditions, all other ichnotaxa disappear, and only *Spongeliomorpha* and *Scoyenia* are present. Collectively, the Lockatong ichnofauna represents the *Scoyenia* Ichnofacies (Metz 1995). A slightly more complicated picture is revealed by the Passaic Formation. Overall, this unit displays similar ichnologic characteristics to the Lockatong Formation, namely the widespread presence of the *Scoyenia* Ichnofacies in lake-margin deposits, and the presence of *Spongeliomorpha* and *Scoyenia* as the only ichnotaxa present in sediments deposited under extremely arid conditions (Metz 1996). However, some elements of the *Mermia* Ichnofacies are present in this unit as well, illustrating transitions from subaqueous portions during the initial phase of lake regression (Metz 1996).

Another extensively studied continental unit, containing well-exposed lacustrine intervals and represented by abundant trace fossils, is the Middle to Upper Triassic Agua de la Peña Group of the Ischigualasto–Villa Unión Basin of western Argentina (Melchor et al. 2003; Melchor 2001, 2004, 2007). As in the case of the Newark Supergroup, this rift basin developed during the breakup of Pangea (Uliana and Biddle 1988; Milana and Alcober 1994). In particular, the most abundant and diverse ichnofaunas occur in the Los Rastros Formation, which represents sedimentation in a shallow, overfilled lake characterized by successive prograding delta deposits (Melchor 2007). Deposits are typically arranged in coarsening-upward parasequences encompassing prodelta, delta-front, and delta-plain facies. The highest ichnodiversity occurs in the distal delta-front deposits, which are dominated by grazing trails (*Helminthoidichnites tenuis*, *Gordia marina*, *Archaeonassa fossulata*, *Cochlichnus anguineus*) and fish trails (*Undichna britannica*, *U. bina*, *U.* cf. *insolentia*). Also present are feeding (*Treptichnus pollardi*), dwelling (*Palaeophycus tubularis*), locomotion (*Bifurculapes* isp., *Cruziana problematica*, *Diplopodichnus biformis*, *Didymaulichnus lyelli*, *Diplichnites* isp., *Protichnites* isp.) and resting (*Rusophycus stromnessi*, *Avolatichnium* isp.) structures (Melchor 2001). Middle delta-front deposits display a similar ichnologic composition to distal delta-front deposits, being dominated by grazing trails (*Helminthoidichnites tenuis*, *Helminthopsis abeli*, *Gordia indianaensis*, *Archaeonassa fossulata*, *Cochlichnus anguineus*), with fish trails (*Undichna britannica*) and dwelling structures (*Palaeophycus tubularis*) also present (Melchor et al. 2003). Upper delta-front to lower delta-plain deposits reflect a decrease in ichnodiversity that parallels a shallowing of the lake, with only *Palaeophycus tubularis*, *Skolithos* isp., and *Cochlichnus anguineus* recorded. Upper delta-plain deposits contain dwelling trace fossils, some of which contain striations (e.g. *Palaeophycus striatus*) and vertebrate trackways (*Rhynchosauroides* isp.). Collectively, the Los Rastros ichnofauna reflects the vertical transition from the *Mermia* to the *Scoyenia* Ichnofacies as a result of shallowing caused by deltaic progradation.

The Middle to Upper Triassic Madygen Formation of Kyrgyzstan contains abundant trace fossils formed in an overfilled lake (Voigt and Hoppe 2010; Voigt et al. 2016). Lake-margin deposits are characterized by pervasive root trace fossils (Voigt et al. 2016) (Fig. 11.3a). The most abundant trace fossils in this unit occur in permanent subaqueous deposits, and consist of horizontal networks of multiple-branched burrows (Voigt and Hoppe 2010) (Fig. 11.3b–e). These structures have been compared with *Thalassinoides* by Voigt and Hoppe (2010), but were placed in the ichnogenus *Virgaichnus* by Knaust (2010). Further work is required to unravel the ichnotaxonomic affinity of these burrows. Regardless of these ichnotaxonomic complexities, these trace fossils represent feeding structures of worm-like deposit feeders. These burrows occur at their highest densities in deposits formed around the sublittoral–profundal boundary, probably coincident with the paleo-thermocline and chemocline (Voigt et al. 2016). It has been speculated that the producers of these burrows may have been able to tolerate dysoxic conditions, allowing them to colonize deeper parts of the lake which may have acted as a refugium from predators (Voigt et al. 2016). Other structures documented in these deposits are the grazing trail

Helminthoidichnites tenuis (Fig. 11.3f), unidentified sand-filled radiating burrow systems, and ribbon-like burrows with transverse segmentation, which have been interpreted as branchiopod locomotion traces (Voigt and Hoppe 2010; Voigt et al. 2016).

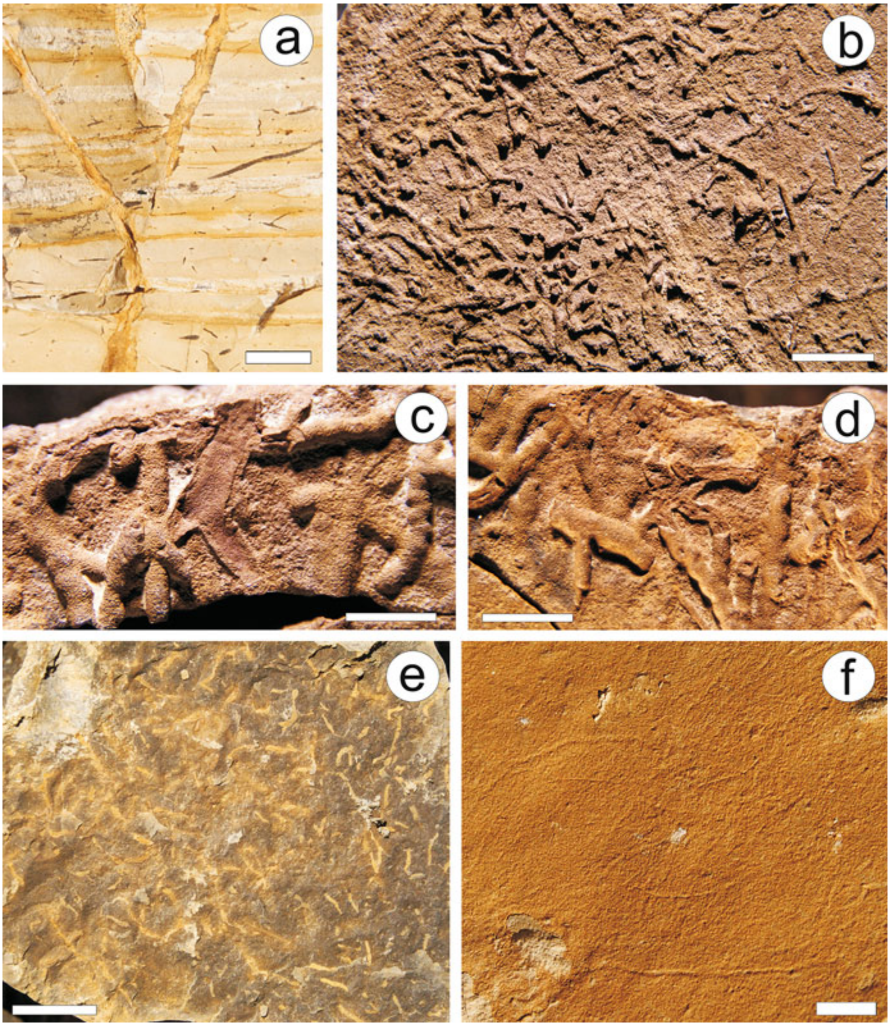

Fig. 11.3 Characteristic trace fossils from Middle to Upper Triassic lacustrine deposits of the Madygen Formation of Kyrgyzstan. (**a**) Root trace fossils in lake-margin deposits; (**b**) General view of a sandstone surface with horizontal networks of multiple-branched burrows in permanent subaqueous lacustrine deposits; (**c**) and (**d**) Close-up of networks showing branching patterns; (**e**) Preservational variation of horizontal networks as cleavage relief in mudstone; (**f**) *Helminthoidichnites tenuis* in lacustrine deltaic deposits. All scale bars are 1 cm long, with the exception of **c** and **d**, which are 0.5 cm long

Globally, Middle to Late Triassic ichnofaunas from lake-margin deposits are of modern aspect and record the widespread establishment of the *Scoyenia* Ichnofacies. In addition, the presence of trace-fossil suites dominated by the crayfish burrow *Camborygma* records the appearance of the homonymous ichnofacies (see Chap. 13). Middle to Late Triassic, fully lacustrine ichnofaunas resemble trace-fossil assemblages described from similar, late Paleozoic settings (Buatois and Mángano 1993a; Buatois et al. 1998a; see Chap. 6). However, more penetrative trace fossils occur, as revealed by the presence of networks of irregularly branched burrows in the Madygen deposits (Voigt and Hoppe 2010). In addition, higher-energy sandy, storm, and mouth-bar deposits tend to contain relatively deep vertical burrows, such as *Skolithos*, *Arenicolites,* and *Polykladichnus* (Bromley and Asgaard 1979; Mángano et al. 1994; Bromley 1996) (Fig. 11.4), representing freshwater equivalents of the *Skolithos* Ichnofacies (Buatois and Mángano 2004, 2009).

In short, ichnologic data seem to support Sinitshenkova's (2002) view that the Triassic is a time of significant evolutionary innovation in lacustrine communities. This is particularly evident in lake-margin settings which exhibit trace-fossil assemblages that would dominate these environments for the rest of the Phanerozoic. The picture in fully lacustrine settings is slightly different because central lake deposits display some ichnofaunas reminiscent of the late Paleozoic, with the addition of more penetrative burrows typical of the rest of the Mesozoic and Cenozoic.

During the late Middle to Late Triassic there was a major, qualitative increase in the abundance of lacustrine insect taxa. Fossil assemblages of this age contain a prevalence of immature over adult aquatic insects, such that in many deposits immature stages (naiads and larvae) outnumber adult specimens (Sinitshenkova 2002)—a situation that reverses that of the Permian. For this, and other reasons, Sinitshenkova (2002) mentions that "…the Triassic [is] a starting point of a new, Mesozoic evolutionary stage of lacustrine biocoenoses." This novelty may be

Fig. 11.4 *Arenicolites* isp. in deltaic mouth bar deposits of the Upper Triassic Tanzhuang Formation of central China. Scale bar is 1 cm long

attributable to greater stability of the hydrological and water-chemistry conditions in the physical environment of Eurasian, Late Triassic lakes (Kalugina 1980). Also, part of the diversification event may be attributed to increased provinciality from the breakup of Pangaea or to sizable increases in number and persistence of long-lived lakes associated with the breakup (Cohen 2003).

Late Triassic aquatic taxa included new lineages representing a diversity of functional feeding groups. For crustaceans, the major lineages were detritivorous ostracods, conchostracans, notostracans and the bizarre central Asian lineage, Kazakharthra. Dasyleptid bristletails were holdovers from the Permian, and persisted until the Late Triassic along bodies of water. Mayflies diversified, with benthic naiads assuming nektonic, epifaunal and infaunal filter-feeding strategies; some benthic forms constructed U-shaped burrows, representing potential producers of the biogenic structures typically found in lacustrine deposits of this age (e.g. Bromley and Asgaard 1979; Mángano et al. 1994) (Fig. 11.4). Odonatans are represented by fewer fossil occurrences of naiads than adults, and all of the mostly benthic naiads possessed a prominent, raptorial labial mask. The Plecoptera were represented by obligately aquatic, benthic naiads, as were their Permian counterparts, and included the extinct benthic–lentic taxa of the Euxenoperlidae, *Mesoleuctra* and *Siberioperla* (Sinitshenkova 2002). Grylloblattids (rock crawlers), a surviving lineage from the Permian, may have inhabited lakeshores or even shallow-aquatic habitats.

Most of the trophically dominant predators were streamlined, agile nectic heteropteran bugs and adephagan beetles. A few lineages of dominantly predatory, aquatic heteropteran bugs appeared during or just before the Late Triassic, consisting of the dominant naucoroid lineages of the extinct Triassocoridae, and the extant Notonectidae (backswimmers) and Belostomatidae (giant water bugs) (Popov 1980). Aquatic adephagan lineages, such as the extinct Schizophoridae, Ademosynidae, Colymbothetidae, and the extant Dytiscidae (predaceous diving beetles) had similar dietary habits. The extant algivorous Haliplidae (crawling water beetles) and its extinct Triassic relative, the Triaplidae, occurred on bottom substrates and in aquatic plant entanglements (Fraser et al. 1996). Both adults and larvae of the nectic Coptoclavidae were major predators, and had agile, active life habits based on legs equipped for rapid movement and raptorial mouthparts, likely feeding on small vertebrates and large insects. Megalopteran larvae are very similar to present-day alderflies (Marchal-Papier 1998). A few taxa of Mecoptera (scorpionflies) have been encountered, such as liassophilids that resemble modern aquatic Nannochoristidae. The earliest, definitive, aquatic Trichoptera (caddisflies) are from the Late Triassic, and include adults of the basal lineages Prorhyacophilidae and Necrotaulidae, but also immatures that likely were predatory (Sinitshenkova 2002).

These lacustrine biotas still lacked a significant herbivore component, which emerged later in the Mesozoic. Supporting this observation is the absence of submerged or emergent aquatic macrophytes, which did not occur in significant abundance until the Early Cretaceous. There is limited evidence, however, for a flora fringing lakes and pools during the earlier Mesozoic, as indicated by the presence of aquatic quillworts such as *Isoetes*, and *Azolla*-related ferns (Retallack 1997; Moisan et al. 2012a, 2012b; Sun et al. 2014). In any case, the contribution was overwhelmingly dead plant matter for detritivores rather than live plant tissues. For herbivores as in the Early Triassic, charophytes continued to be the dominant macrophytes and Chlorococcales the dominant phytoplankton (Martín-Closas 2003).

Six major community types have been recognized in Triassic Eurasian freshwater deposits (Sinitshenkova 2002). These community types are characterized by distinctive groupings of major taxa that occur in particular types of lakes and habitats. Although Sinitshenkova's (2002) general trophic analysis of lake ecosystems demonstrated significant partitioning of available lotic and lentic resources, evidently the herbivore guild was largely absent.

The most diverse Triassic insect assemblage is in an upper-Middle to lower-Upper Triassic lacustrine deposit near the village of Madygen, in Kyrgyzstan, central Asia, whose ichnofauna has been summarized above. In particular, one locality, Dzhailoucho, and nearby outcrops have provided some of the best insights into later Triassic aquatic and terrestrial life, including a diverse assemblage of 20 orders and ca. 106 family-ranked lineages of insects, such as the earliest definitive occurrences of Diptera (true flies) and Hymenoptera (sawflies, wasps, ants, and bees) (Shcherbakov 2008c). The Madygen Biota consists of typical, early Mesozoic plant groups, including cryptogams, sphenopsids, lycopsids, filicalean ferns, broadleaved conifers, diverse peltasperms, corystosperms, a variety of ginkgophytes and rare bennettitaleans (Dobruskina 1995). Aquatic invertebrates include several microconchids, bivalves, gastropods, bryozoans, and a spectrum of crustaceans consisting of phyllopods, ostracods, conchostracans, kazakharthrans, and malacostracan decapods (Voigt et al. 2006). The vertebrate fauna is rather diverse, and is comprised of a broad variety of fishes, such as lungfish, coelacanths, hybodontid, and xenacanthid sharks, and ray-finned fish, including palaeoniscids, evenkiids, perleidids, and a saurichthyid (Sytchevskaya 1999; Kogan et al. 2009; Fischer et al. 2011). The fauna also includes six genera of lake-margin tetrapods, notably an early urodelan, basal reptiliomorph, primitive cynodont, and three small diaspids including tree-climbing, gliding, and insectivorous reptiles (Voigt et al. 2006; Schoch et al. 2010; Alifanov and Kurochkin 2011). The lacustrine aquatic food web consisted of a variety of lakeside plants, numerous insects and other aquatic invertebrates, fish and occasional tetrapods (Shcherbakov 2008c). The aquatic portion of the biota included eight orders of insects and ca. 25 families of primarily aquatic or amphibiotic insects, of which a fifth of the lineages are extant. The Ephemeroptera included only the single, extant family, Siphlonuridae (small minnow mayflies); by contrast, ten families of Odonata were present, none of which are extant. Extinct Miomoptera constituted one family, and Plecoptera were represented by two extinct families. The Hemiptera included one family, the extant Ochteridae (velvet shore bugs). As for holometabolous insects, aquatic Coleoptera were represented by five, early to mid-Mesozoic, structurally streamlined families, but only one lineage, the Hydrophilidae (water scavenger beetles) are extant, likely appearing as large, black, and shining species. Similarly, the Trichoptera was represented by the basal and extant Philopotamidae (fingernet caddisflies). Likewise, the Diptera consisted of two new taxa, notably the diverse, extant Limoniidae (short-palped crane flies).

Neoichnologic data suggest that dipterans, in particular larval Limoniidae, produce zigzag burrows that in the fossil record may be referred to the ichnogenus *Treptichnus* (Muñiz-Guinea et al. 2014). This ichnogenus is quite common in Middle to Upper Triassic lacustrine deposits (Fig. 11.2e), which is consistent with paleoentomologic information on the earliest definitive occurrences of Diptera. However, *Treptichnus* is known in late Paleozoic lacustrine to fluvio-estuarine deposits as well (Buatois and Mángano 1993b, c; Buatois et al. 1998b). Interestingly, a molecular analysis placed the origin of crown group Diptera in the middle Permian (Bertone et al. 2008).

11.5.3 Continued Jurassic Diversification and Increased Infaunalization

Lower Jurassic, lake-margin ichnofaunas have been documented in both eastern (Gierlowski-Kordesch 1991; Metz 1992; Collette et al. 2011) and western (Lucas et al. 2006; Tanner and Lucas 2008) United States, whereas Upper Jurassic equivalents are widespread only in the latter (Hasiotis 2004; Foster and Lockley 2006; Hunt and Lucas 2006). Among invertebrate trace fossils, shallow-tier, meniscate, backfilled structures with striated walls (*Scoyenia*) or without bioglyphs (*Taenidium*) are typical, as are striated, branched burrows (*Spongeliomorpha*) (Gierlowski-Kordesch 1991; Hasiotis 2004). Simple horizontal (*Planolites*, *Palaeophycus*) and vertical (*Skolithos*) structures, together with crayfish burrows (*Camborygma*) and banana-shaped structures (*Fuersichnus*), also are common (Gierlowski-Kordesch 1991; Hasiotis 2004; Tanner and Lucas 2008). Grazing trails (*Helminthoidichnites*) and arthropod trackways (*Diplichnites*, *Kouphichnium*) are only abundant locally (Lucas et al. 2006). Borings in stromatolites have been mentioned, but it is uncertain if these were formed in lacustrine or marine coastal settings (Hasiotis 2004).

Although the earliest body-fossil record of dinosaurs is Late Triassic, dinosaur tracks are known at least since the Middle Triassic (Marsicano et al. 2007; see Chap. 10). However, it is by the Early Jurassic that dinosaur tracks (e.g. *Grallator*, *Eubrontes*) become the dominant vertebrate-generated structures in lake-margin deposits (Hunt and Lucas 2006). Dinosaur tracks also occur in Lower Jurassic deposits where the first megatracksites are recorded (Hamblin et al. 2006). These megatracksites include trampled surfaces, although these seem to occur in wet interdunes, rather than in lake margins (Seiler and Chan 2008). However, by the Late Jurassic spectacular megatracksites are known from lake-margin deposits of the Morrison Formation (Lockley et al. 1986; Jennings and Hasiotis 2006), among other sites. The Morrison tracksites are associated with intense bioturbation and the development of trampled surfaces (Lockley et al. 1986; Jennings and Hasiotis 2006). These Jurassic trampled surfaces are significant because, as demonstrated by studies in Quaternary and modern lake-margin deposits (e.g. Laporte and Behrensmeyer 1980; Ashley and Liutkus 2002), activities by large vertebrates play a major role in disturbing primary sedimentary fabric.

Fully lacustrine ichnofaunas have been documented in the Lower Jurassic of the eastern United States (Metz 1992) and China (Wu 1985; Buatois et al. 1995, 1996; Hu et al. 1998; Uchman et al. 2011), the Middle Jurassic of England (Whyte et al. 2007), and the Upper Jurassic of the western United States (Hasiotis 2004). These ichnofaunas show a combination of shallow-tier, simple trails and burrows (*Helminthopsis*, *Helminthoidichnites*, *Palaeophycus*, *Diplopodichnus*, *Paracanthorhaphe*) and deeper-tier, branching burrow systems (*Vagorichnus*) (Metz 1992; Buatois et al. 1996; Uchman et al. 2011). Vertical U-shaped burrows (*Arenicolites*) (Hasiotis 2004) and bivalve burrows (*Lockeia*) (e.g. Whyte et al. 2007) are present as well. As in the case of earlier assemblages, the fish trail *Undichna* is the typical vertebrate ichnotaxa in this setting (Whyte et al. 2007).

The Lower Jurassic Anyao Formation of central China is arguably the most studied deep-lacustrine succession of this age, providing valuable insight into the colonization of a fully lacustrine setting (Wu 1985; Buatois et al. 1995, 1996; Hu et al. 1998; Uchman et al. 2011). This formation represents deposition in a deep overfilled lake system developed in a pull-apart basin (Buatois et al. 2000b). The Anyao trace fossils are mostly present in thin-bedded turbidites which were formed in lobe-fringe areas of lacustrine turbidite systems. This ichnofauna is relatively diverse, encompassing both pre- (open burrows casted by the incoming turbidite sand) and post- (burrows penetrating from a colonization surface at the top of the turbidite sand) turbidite suites (Buatois et al. 1996) (Fig. 11.5a–i). The pre-event suite consists of *Helminthopsis abeli* (Fig. 11.5a), *Helminthoidichnites tenuis* (Fig. 11.5b), discrete specimens of *Tuberculichnus vagans* (Fig. 11.5c–d), *Monomorphichnus lineatus*, *Paracanthorhaphe togwunia* (Fig. 11.5e–f), and thin irregular trails. The post-event suite consists of *Vagorichnus anyao* (Fig. 11.5g–h), *Cochlichnus anguineus* (Fig. 11.5i) and *Helminthopsis hieroglyphica*. Specimens of *Gordia marina* and *Tuberculichnus vagans* intergrading with *V. anyao* also are part of this suite. The ichnofauna is dominated by feeding and grazing trace fossils produced by deposit feeders. From an evolutionary perspective, the Anyao ichnofauna is significant because it is dominated by infaunal burrows that reflect the activity of invertebrates that were able to penetrate into discrete sandy layers for subsequently expanding along sand–mud interfaces, a behavior unknown in older deposits in similar environmental settings. The producer of these burrows is uncertain, although it has been noted that in modern environments oligochaetes construct structures that radiate from a surface tube and branch horizontally within the sediment (Chamberlain 1975; Buatois et al. 1995). Amphipods and isopods may potentially construct similar structures, but the paucity of modern analogues precludes further evaluation (Buatois et al. 1995). In addition, this behavior shows the appearance of more organized branching patterns, such as *Paracanthorhaphe togwunia*, that reveal an increase in complexity with respect to Paleozoic lacustrine ichnofaunas.

Overall, the taxonomic composition of invertebrate ichnofaunas in lake-margin Jurassic deposits is quite similar to that of the Middle to Upper Triassic. No major evolutionary novelties or innovations are apparent in these settings from the perspective of invertebrate ichnnology. However, the appearance of megatracksites and trampled surfaces represents a major change with respect to older deposits, implying substantial sediment reworking and modification by dinosaurs. This was probably the first time in the history of the biosphere that lake-margin landscapes were significantly transformed at a large scale by biogenic activity.

In addition, trace-fossil information from fully lacustrine environments provides a different picture to that of older deposits. Ichnodiversity levels are similar

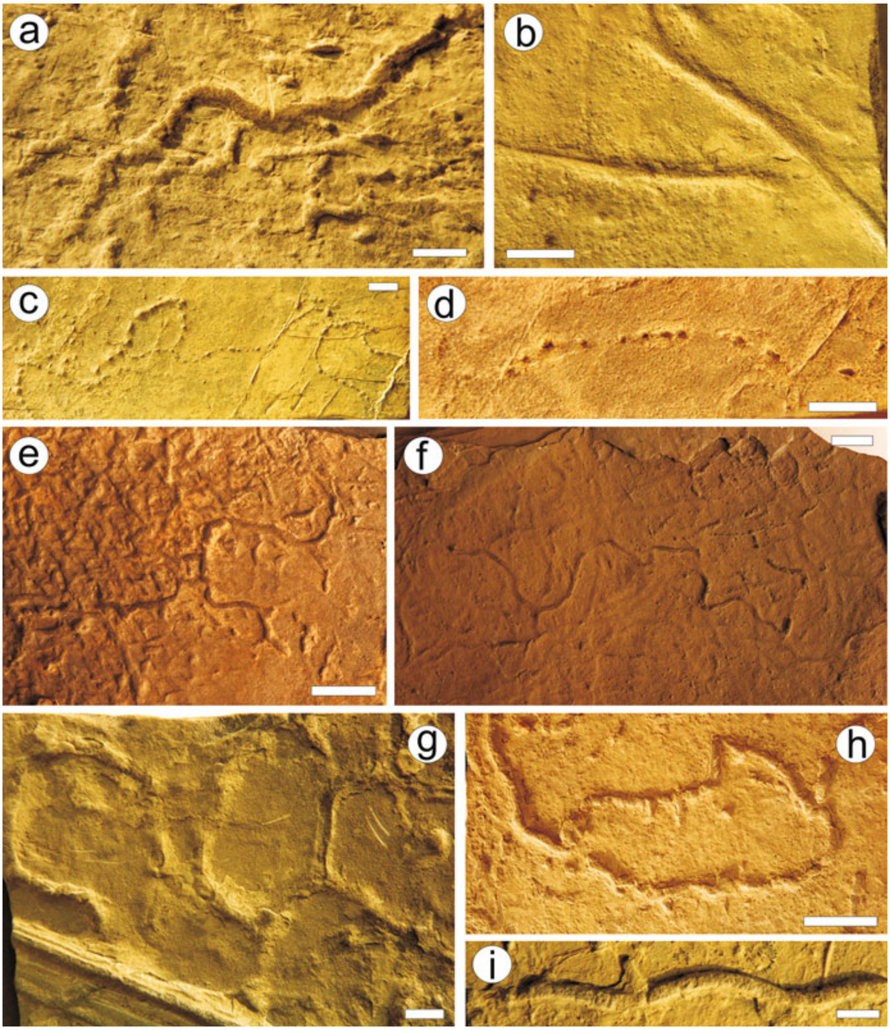

Fig. 11.5 Characteristic trace fossils preserved at the base of Lower Jurassic lacustrine turbidites of the Anyao Formation of central China. (**a**) *Helminthopsis abeli*; (**b**) *Helminthoidichnites tenuis*; (**c**) General view of *Tuberculichnus vagans* displaying a meandering pattern; (**d**) Close-up of *Tuberculichnus vagans*; (**e**) and (**f**) *Paracanthorhaphe togwunia*; (**g**) *Vagorichnus anyao* cross-cutting and inorganic sole mark; (**h**) Close-up of *Vagorichnus anyao*; (**i**) *Cochlichnus anguineus*. All scale bars are 1 cm long

to those of the Middle to Late Triassic, and even to those of the late Paleozoic, but the principal difference is the degree of infaunalization, as revealed by the widespread occupation of mid tiers in deep lacustrine sediments.

During the Early Jurassic there was further taxonomic, morphologic, and ecologic diversification of continental aquatic biotas. Much of the Jurassic zooplankton was represented by diverse cladoceran crustaceans, indicated by fossil occurrences (Zherikhin and Kalugina 1985), supported by molecular-clock data from phylogenetic analyses (Colbourne and Hebert 1996). One of the more distinctive differences from Triassic aquatic insect assemblages was the greater presence of immature stages (naiads, larvae) in Jurassic deposits, a consequence of a different preservational mode. The opposite situation of adult stages predominating over immature stages was much less common, and may have been attributable to poor preservation in habitats frequented by adults or the presence of adults in distant, more upland environments that have low preservation potential. Another distinction is the absence of virtually all Permian insect faunal elements and the first occurrences of many modern family-level lineages (Sinitshenkova 2002).

The dominant insect groups of Jurassic lotic and lentic ecosystems represent a spectrum of lineages that would occur in the same habitats today, although not necessarily with the same ecologic tolerances or proportional abundances as their present-day descendants. Ephemeropterans and odonatans were significantly more speciose than their Triassic equivalent taxa. Ephemeropterans experienced a major diversification, with the naiads of many groups, such as the Siphlonuridae and extinct Mesonetidae and Epeorominidae having laterally positioned abdominal gills and reaching considerably larger sizes than their Triassic confamilial antecedents. Currently, ephemeropterans occur in high numerical abundance at local scales, are present at significant diversities, and apparently were the major collector and filter-feeding functional feeding groups (Merritt and Cummins 1984) in many Jurassic localities. The Jurassic mayfly fauna is found in almost every aquatic environment, in streams ranging from cascade-like rhythral settings, to calm water sites on floodplains such as oxbow lakes and overbank ponds, to lowland playas, and highland graben-formed lakes. Like ephemeropterans, odonatans were diverse, best illustrated by several, large, dragonfly genera which co-occur in the Solnhofen Formation of southern Germany, including a relict lineage of late Paleozoic meganeurid forms. Jurassic odonatan naiads typically resemble modern damselfly naiads with a narrow body and three, flap-like, heavily sclerotized, and terminal abdominal structures, the cercus and paracerci. The formidable labial-masks of naiads indicate predation on other larger aquatic insects and small vertebrates, such as fish and tadpoles. In some lacustrine environments odonatan naiads likely were top predators in the absence of fish (Sinitshenkova 2002).

Plecopteran nymphs occur commonly in Lower Jurassic deposits and are represented by three life-habit groups that are different from their modern representatives taxa. The Mesoleuctridae possessed unusually long and slender legs, suggesting an unusual detritivorous feeding habit. By contrast, the Platyperlidae bore an opposite, flat habitus, with exceptionally squat, wide legs indicating a benthic insectivorous diet. The Siberioperlidae, judging from robust mouthparts unusual for the Plecoptera, were consumers of fibrous or otherwise indurated plant tissues (Sinitshenkova 2002). An unrelated group is the extinct Chresmodidae of the Archaeorthoptera. The family Chresmodidae includes large, water-strider-like insects presumably occurring on water surfaces. Chresmodids have had a checkered history of being taxonomically poorly resolved and having equally contentious dietary preferences. Some specimens display mouthparts designed for active predation but possess external, sawtooth ovipositors that functioned for insertion of eggs into substrates such as aquatic plant stems (Delclòs et al. 2008). Based on ovipositional lesions on preangiospermous Mesozoic plants associated with lake deposits, the most likely hosts for ovipositing chresmodids were lycopsids (Moisan et al. 2012b) and horsetails (Kräusel 1958), or less likely a seed plant such as a bennettitalean (Pott et al. 2008).

Jurassic lotic and lentic biotal assemblages commonly are dominated by aquatic heteropteran bugs or adephagan beetles, or both. Heteropteran aquatic bugs included the dominant nepomorph taxa of Corixidae (water boatman) and Nepidae (water scorpions), as well as giant water bugs, backswimmers, and the Mesoveliidae (mesoveliid water striders), distant relatives of modern Gerridae (water striders) that likely skimmed the water surface of lakes and streams. These taxa were predaceous, except for mostly algivorous corixids and shurabellids (Popov 1971). Based on mouthpart structure that employed a triturating device (Cobben 1978), these microvorous corixid and shurabellid microvores filter fed on unicellular or very small multicellular algae. Some heteropterans inhabited hypersaline playas and coastal brackish lagoons or estuaries (Santiago-Blay et al. 2001). Like heteropteran bugs, aquatic adephagan beetles were ecologically diverse and mostly predaceous, although some were scavengers and microvorous consumers of algae. There is no indication of macrovorous herbivorous forms.

During the Early Jurassic the dominant beetle clade is the Schizophoridae, but its diversity and abundance decreases towards the latest Jurassic (Ponomarenko 1995). During this time extinct aquatic lineages include large, predaceous Coptoclavidae with active, nektonic larvae, the Liadytidae, possessing benthic larvae, and the Parahygrobiidae, of unknown feeding habits. The extant, large Gyrinidae (whirligig beetles) appear in significant numbers in Jurassic lentic deposits, consisting of predaceous larvae and detritivorous adults. The Parahygrobiidae are known only from larvae of mid-Mesozoic lake deposits and are presumed predaceous. In contrast to the commonness of beetle taxa, alderfly and dobsonfly larvae of the Megaloptera are rare and confined to lotic habitats.

Other holometabolan taxa are the larvae of scorpionflies, caddisflies, and true flies which typically were rare at most sites. The extinct Liassophilidae belongs to a scorpionfly lineage that survived into the Early Jurassic, and whose modern close relatives are the primitive, aquatic Nannochoristidae (Novokshonov 1997). Caddisflies are represented primarily by the Necrotaulidae and the larger complex of families constituting the Phryganeina. The Phryganeina appeared during the Late Jurassic (Sukatcheva 1991) and their presence is indicated by some of the earliest caddisfly cases in the fossil record. Caddisflies were mostly microvores, and likely were algivorous, detritivorous, or omnivorous, commonly occurring in eutrophic environments (Zherikhin and Kalugina 1985). Unlike other abundant holometabolan groups, true flies represent a major radiation throughout the Jurassic, particularly involving several nematocerous lineages, principally the Limoniidae, Chironomidae (midges), Chaoboridae (phantom midges), Psychodidae (moth flies), Simuliidae (black flies), Dixidae (nonbiting midges), and the extinct Eoptychopteridae, a clade related to modern phantom crane flies (Kalugina 1980). These seven dipteran lineages included disparate mouthpart modifications for passive and active filter feeding, net sieving, collecting, and mandible-assisted chewing, indicating that they were dominantly microvores. Microvory in nematocerous Diptera is typically achieved by the pumping of water currents into a specialized mouthpart filter or sieve for capture of small particulate matter such as diatoms, protists, ostracods, and a variety of other microorganisms.

The Jurassic also witnessed the appearance of major lineages of teleost fish, frogs, crocodilians, and aquatic birds (Cohen 2003). These lineages represent evolutionary novelties that may have been conducive to key innovations, mostly increased predation in freshwater settings, which in turn may have resulted in the disappearance of large-bodied branchiopods and other slow moving crustaceans from many lacustrine settings (Webb 1979; Cohen 2003). Since the Jurassic, these taxa seem to have been displaced to more marginal habitats, such as saline lakes and vernal pools, characterized by low diversity of predators. Also, the coincidence of increased predation and infaunalization of the lacustrine benthos may be significant. As indicated by Vermeij (1987), the infaunal environment typically is regarded as a haven from predation and, therefore, infaunalization may be regarded as an adaptive response to increased predation.

Relatively little is known about aquatic vegetation during the Jurassic. The dominance of charophytes is apparent, with porocharaceans and nitellaceans occurring in Early to Middle Jurassic Chinese basins (Wang et al. 1976), probably reflecting accommodation to ephemeral lakes (Martín-Closas and Serra-Kiel 1991). By the Late Jurassic, two charophyte families underwent diversification, the Characeae and the Clavatoraceae, which were associated with oligotrophic and alkaline lakes (Martín-Closas and Serra-Kiel 1991). This may have resulted in the displacement of porocharaceans to higher latitudes and brackish-water settings (Martín-Closas 2003). Nonflowering vascular plants were represented by relatives of *Azolla* ferns along littoral zones (Cohen 2003). An incipient colonization of ponds by ferns also is apparent by the Late Jurassic (Martín-Closas 2003), particularly the Hymenophyllaceae (filmy ferns), that preferred hydric habitats (Hennequin et al., 2008). Lacustrine phytoplankton retained its ancestral condition, with Chlorococcales remaining dominant (Martín-Closas 2003).

Beginning toward the end of the Early Jurassic, and culminating during the Middle to Late Jurassic, a distinctive, fluvio-lacustrine ecosystem is recognized in Eurasia. This ecosystem represents a continuation of earlier, similar, Late Triassic ecosystems, but is characterized by a suite of physical, chemical, and biological features that were distinct from other contemporaneous and later ecosystems (Table 11.1). The overwhelmingly Jurassic biotas that occupy this ecosystem are the "Assemblage B" of Sinitshenkova and Zherikhin (1996), characterized by a detritivore-based food web, in which primary production consisted of coarse and fine detritus and dead benthic algae. These sources of food were channeled to filter-feeding and shredding invertebrates, particularly insects, but also crustaceans, mollusks, and bryozoans (Table 11.1 and Fig. 11.6). Although this biota persisted into the Early Cretaceous, the geochronologic acme of this community type was during the Middle to Late Jurassic.

A prime example of an Assemblage B community is the *Mesoleuctra–Mesoneta* assemblage at Ust'-Balei, in Transbaikalian Russia, representing a lacustrine deposit from uppermost Lower Jurassic strata (Sinitshenkova and Zherikhin 1996). The *Mesoleuctra–Mesoneta* assemblage was more productive, through the fixation of organic carbon by chemotrophic and autotrophic organisms, than those from coexisting Assemblage A lakes. However, the *Mesoleuctra–Mesoneta* assemblage was considerably less productive than Assemblage C lakes of the Early Cretaceous (Table 11.1 and Fig. 11.6). This assemblage type may have occurred in several Gondwanan sites, although documentation is poor. The dominant biotal features of the *Mesoleuctra–Mesoneta* assemblage at Ust'-Balei was an epibenthic fauna that consisted dominantly of mayfly and stonefly taxa, the absence of chaoborid dipteran larvae, and the general presence of some algae, bivalves, and fish. Deposits containing an Assemblage B biota are associated with lignitic and coal-bearing strata, paleobotanical indicators suggesting oxygen depletion (Samylina 1988), and a setting in which microbial activity was strongly suppressed. At Ust'-Balei, the *Mesoleuctra–Mesoneta* assemblage inhabited an aquatic environment similar to a modern, disaerobic peat lake wherein bacterial metabolic activity is limited by water acidity (Kuznetsov 1970).

Jurassic lacustrine deposits are present in North America as well (see review of ichnologic literature above), but unlike those in Eurasia, they have been less studied in a paleoentomological context, typically lacking body fossils, notably insects. Deposits such as the deep, graben-fill deposits of the Late Triassic (Theismeyer 1939) and the more laterally persistent, epicontinental strata of the Late Cretaceous–Early Paleogene temporally bracket the Middle Jurassic (Callovian) Sundance and Late Jurassic (Tithonian) Morrison Formations. The Morrison Formation evidently included a series or large, relatively shallow alkaline lakes, most of which were intermittent and lacked significant freshwater input due to water limitation within an arid, subtropical belt (Turner and Fishman 1991; Demko and Parrish 1998; Engelmann et al. 2004). Although much is known of the vertebrates of landscapes surrounding Morrison lakes, little is understood of their aquatic invertebrate faunas. Lacustrine insects are unknown, and the only significantly studied invertebrates are lacustrine ostracods (Schudack 1998) and bivalves occurring in associated fluvial, floodplain and pond environments (Good 2004).

The Sundance Formation perhaps provides the sole exception of a Jurassic, North American lacustrine biota on par with numerous Eurasian examples of the same period (Fig. 11.7). The Sundance Formation occurs along the central-northern Wyoming and central-southern Montana border, and provides paleoentomologically the best documented Jurassic lacustrine ecosystem in North America (Santiago-Blay et al. 2001; Grimaldi and Engel 2005). In particular, the thinly laminated, interbedded paper shales of the Hulett Sandstone Member provide considerable evidence for a modestly diverse lacustrine fauna. The deposit was formed from

Table 11.1 Biological features of Mesozoic lakes before and after the Mesozoic Lacustrine Revolution (MLR) based on aquatic insect data. Modified slightly from Sinitshenkova and Zherikhin (1996), with brown indicating more detritivore-based and green more herbivore-based lacustrine assemblages

	Pre Mesozoic lacus trine revolution lake structure		Post Mesozoic lacustrine revolution lake structure		
Assemblage Type[a]	A	B	C	D	E
Age:	Upper Lower J—Lower K	Upper Lower J—Lower K[a]	Lower K[a]	Lower K	Lower K
1. Algal production	Low	Low	High	?Moderate	High
2. Macrophyte production	Very low	Moderate	Low	Low	Low
3. Allochthonous detritus	Low	High	Low	?Low	?Variable
4. Turnover rate	Low	High	High	High	High
5. Microbial activity	Low	Low, suppres-sed by antibio-tic leaf litter	Moderate, high in deep-water zone	Unknown	?High
6. Dominating trophic chain	Detritivorous	Detritivorous	Herbivorous	Herbivorous	Herbivorous
7. Trophic web complexity	Low	Low	High	Low	Moderate
8. Dominating strategy	K	K	?r	?r	r
9. Shredders[b]	Common	Common	Uncommon	?Uncommon	?Uncommon
10. Scrapers[b]	Common	Common	Uncommon	Uncommon	Uncommon
11. Grazers[b]	Rare	Rare	Common	Common	Common
12. Filtrators[b]	Very rare	Rare	Uncommon	Common	Common
13. Planktonivores[b]	Moderately common	Rare	Very abundant	Very abundant	Very abundant
14. Predators[b]	Common	Common	Common	Rare	Common
15. Modern analogues	Cold, clear-water oligo-trophic lakes	None	None	Unknown	None
16. Ecosystem type	Montane; oligotrophic to ultraoligotrophic	Hypotrophic (non-acid dystrophic)	Pseudoligo-trophic (productive nonsaprobic)	?Mesoligo-trophic	?Pseudoligo-trophic.

The vertical line separating Assemblages B and C indicates the timing of the MMLR transition

[a] The five assemblages (A–E) are further detailed in Sinitshenkova and Zherikhin (1996)

[b] Macroinvertebrate functional feeding groups (after Merritt and Cummins 1984)

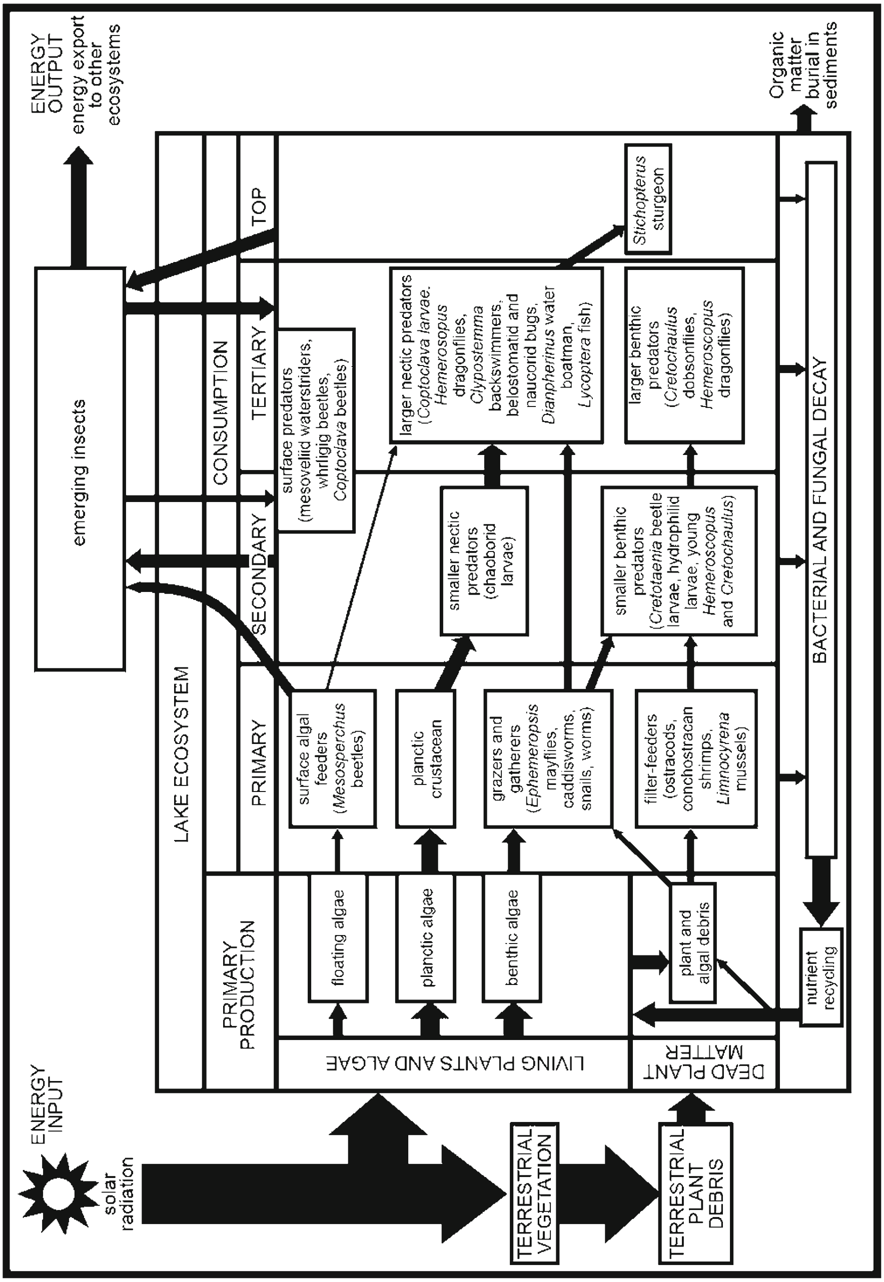

Fig. 11.6 Trophic structure reconstruction for primary producers and arthropods of a Middle Jurassic hypotrophic lake (Zherikhin and Kalugina 1985). This lake represents the *Mesoleuctra–Mesoneta* biotal assemblage typifying Lake Ust'Balei, in the Irkutsk Region of northern Siberia, Russia. This trophic reconstruction corresponds to the Type B lake biotal assemblage of Sinitshenkova and Zherikhin (1996). See Assemblage B in Table 11.1 for additional physical, chemical and biological details. Redrawn, with modification, from Sinitshenkova and Zherikhin (1996)

freshwater to brackish water input and includes locally a back-barrier shoal and tidal inlet consistent with a more estuarine environment during certain time intervals (Uhlir et al. 2006; Stone and Vondra 2013). Vertebrate footprints and bone material have been found in other strata of the Sundance Formation. The biota of the Hulett Sandstone Member consists of pollen, land-plant fragments, aquatic insects, and a leptolepid fish, presumably of continental provenance (Fig. 11.7a–p). The insects are modestly diverse, consisting minimally of about 15 species, and include a variety of typically freshwater nepomorph heteropterans, especially notonectids, corixids, belostomatids, and possibly the extinct Enicocoridae. Adephagan beetles include dytiscids and possible parahygrobiids, and elytra assigned to *Holcoptera* are suggestive of a polyphagan lineage (Santiago-Blay et al. 2001; Grimaldi and Engel 2005). Other faunal constituents are very rare caddisfly cases. Whereas much of these strata, particularly those containing the insects, indicate lacustrine deposition, other strata indicate a more marine influence, suggesting harsh, occasionally hypersaline conditions and an uninhabitable benthic environment. Palynomorph and mesofossil land-plant material reveal a xerophytic coastal vegetation of cheirolepidiaceous and araucariaceous conifers and possible gnetaleans indicated by *Eucommiidites* pollen. A similar, approximately coeval lacustrine deposit, the Todilto Formation, occurs in central New Mexico, is less diverse but has a similar depositional environment with periodic influxes of fresh and brackish water alternating with marine incursions from the east, and has a similar lacustrine biota (Bradbury and Kirkland 1966; Anderson and Lucas 1996; Ulmer-Scholle 2005).

11.5.4 Persistence of Previous Trends During the Early Cretaceous

Early Cretaceous lake-margin ichnofaunas have been documented in England (Goldring et al. 2005), Spain (Moratalla et al. 1995; Moratalla and Hernán 2009), Mongolia (Johnson and Graham 2004) and Korea (Kim and Paik 1997; Kim et al. 2002, 2005, 2012a,b,c; Paik et al. 2012; Lockley et al. 2012). Dinosaur (e.g. *Ornithopodichnus*, *Dromaeosauripus*, *Caririchnium*, *Minisauripus*), bird (e.g. *Koranornis*, *Jindongornipes*, *Uhangrichnus*, *Ignotomis*), crocodile, turtle (*Emydiphus*), and pterosaur (e.g. *Pteraichnus*, *Haenamichnus*) tracks are extremely common, in many cases forming megatracksites (Moratalla et al. 1995; Meyer et al. 2001; Moratalla and Hernán 2009; Lockley et al. 2012; Kim et al. 2012a,b,c).

As is the case for their earlier Mesozoic counterparts, Early Cretaceous lake-margin invertebrate ichnofaunas are dominated by shallow-tier striated or nonstriated meniscate, backfilled structures (*Scoyenia*, *Taenidium*), and simple horizontal (*Planolites*, *Palaeophycus*) and vertical simple or U-shaped (*Skolithos*, *Diplocraterion*) features (Zhang 1987; Kim and Paik 1997; Kim et al. 2002, 2005; Johnson and Graham 2004; Goldring et al. 2005). Arthropod trackways (*Diplichnites*), simple grazing trails (*Helminthopsis*, *Cochlichnus*), and branching burrows (*Thalassinoides*) occur locally (Kim et al. 2002, 2005; Goldring et al. 2005).

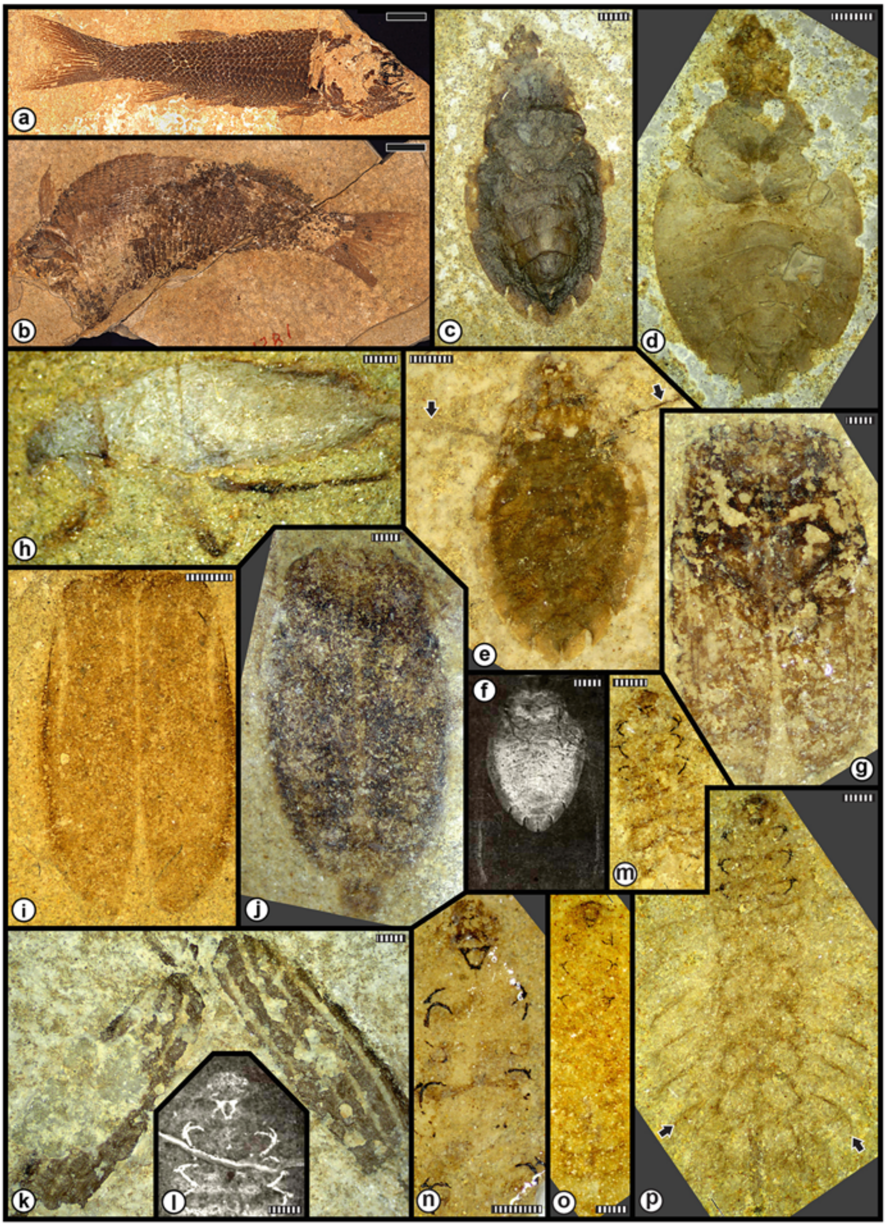

Fig. 11.7 The late Middle Jurassic (Callovian, 165 Ma) Sundance Biota from the lacustrine Sundance Formation, central-northernmost Wyoming and adjacent central-southernmost Montana, United States (Santiago-Blay et al. 2001). (**a**) Leptocerid fish (USNM-597438, Specimen 605); (**b**) Leptocerid fish (USNM-597439, Specimen 1281); (**c**) Hemiptera: ?Belostomatidae (USNM-597440, Specimen 554–39); (**d**) Hemiptera: Belostomatidae (USNM-597441, Specimen 775); (**e**) Hemiptera: Corixidae (USNM-597442, Specimen 1377A); (**f**) Hemiptera: Corixidae (USNM-597443, Specimen 1801); (**g**) Hemiptera: ?Notonectidae (USNM-597444, Specimen 2688B); (**h**) Hemiptera: Enicocoridae (USNM-597445, Specimen 2194); (**i**) Coleoptera: undetermined family (USNM-597446, Specimen 24); (**j**) Coleoptera: undetermined family (USNM-597447, Specimen 2443); (**k**) Coleoptera: (USNM-597448, Specimen 2501); (**l**) (USNM-597449, Specimen 1936B); (**m**) (USNM-597450, Specimen 2398B); (**n**) (USNM-597451, Specimen 2260); (**o**) (USNM-597452, Specimen 2906); (**p**) Coleoptera: (USNM-597453, Specimen 2149). Scale bars: solid, 10 mm; striped, 1 mm

Early Cretaceous examples of fully lacustrine ichnofaunas have been recorded in Spain (de Gibert et al. 1999, 2000, 2016; Buatois et al. 2000a) and Brazil (Buatois and Mángano 1998). Information is sparse, and examples are known from quite different lacustrine settings, further complicating the establishment of general patterns. The Spanish paleolake deposits are carbonates, and their ichnofaunas are dominated by very shallow-tier trails and burrows (*Gordia*, *Cochlichnus*, *Steinsfjordichnus, Cruziana, Helminthoidichnites, Palaeophycus, Treptichnus, Planolites*), with a very minor contribution of arthropod trackways (*Hamipes*) (de Gibert et al. 2000, 2016; Buatois et al. 2000a) (Fig. 11.8a–d). The vertebrate component of the subaqueous biota is represented by the fish trail *Undichna* (de Gibert

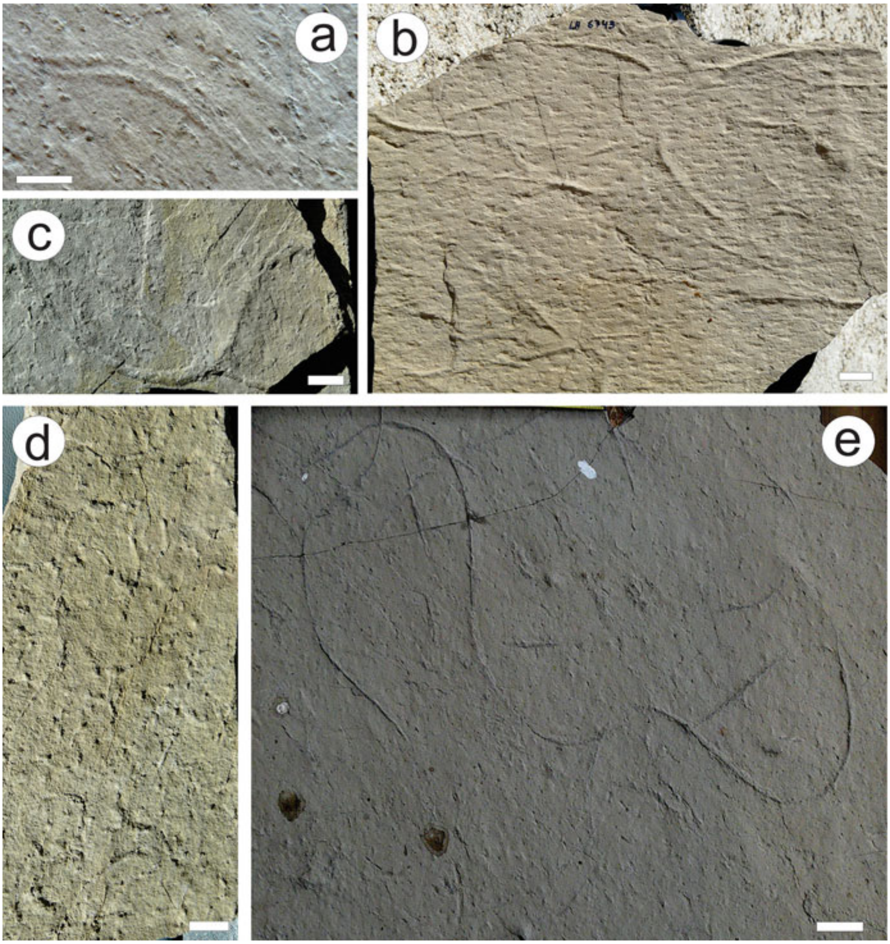

Fig. 11.8 Characteristic trace fossils from Lower Cretaceous fully subaqueous lacustrine carbonate deposits of Las Hoyas, Spain. (**a**) *Cruziana* isp.; (**b**) *Helminthoidichnites tenuis*; (**c**) *Palaeophycus tubularis*; (**d**) Surface containing high density of poorly developed *Treptichnus pollardi*; (**e**) *Undichna unisulca.* All scale bars are 1 cm wide, with the exception of **e**, which is 2 cm long

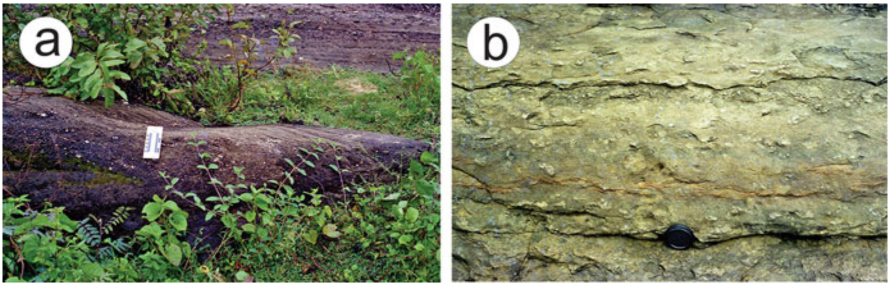

Fig. 11.9 Ichnofabrics from the Lower Cretaceous lacustrine shoreface deposits of the Coqueiro Seco Formation of northeast Brazil. (**a**) General view of cross-bedded pebbly very coarse-grained sandstone (foreground) interbedded with intensely bioturbated fine-grained sandstone (background); (**b**) Close-up of intensely bioturbated sandstone displaying mottled texture. Lens cap diameter is 5.5 cm long

et al. 1999) (Fig. 11.8a–e). In contrast, the Brazilian ichnofauna is derived from intensely bioturbated, lacustrine, clastic shoreface deposits, and displays mottling attributable to *Planolites* (Buatois and Mángano 1998) (Fig. 11.9a–b).

Lower Cretaceous shallow-lake deposits present within the nonmarine Sindong Group of South Korea are useful to illustrate the major characteristics of lacustrine ichnofaunas from this age (e.g. Kim and Paik 1997; Kim et al. 2002, 2005; Paik et al. 2012). In particular, the Jinju Formation has been the object of several ichnologic studies (e.g. Kim et al. 2002, 2005, 2012c). This unit was deposited in a shallow lake periodically affected by immersion and desiccation. The ichnofauna contains a variety of feeding (*Beaconites antarcticus*, *B. coronus*, *Planolites annularis*, *P. beverleyensis*, *Taenidium barretti*), locomotion (*Octopodichnus* cf. *didactylus*, *Diplichnites* ispp., unassigned sauropod trackways), dwelling (*Palaeophycus sulcatus*, *P. tubularis*, *Skolithos magnus*), and grazing (*Cochlichnus anguineus*, *Helminthopsis hieroglyphica*) traces (e.g. Kim et al. 2005). The vast majority of these ichnotaxa are common in the *Scoyenia* Ichnofacies, which is consistent with the lake-margin interpretation for these deposits. The sharply defined margins of the trackways suggest firm substrates. However, Kim et al. (2005) noted that some of the grazing trails may have been emplaced in softgrounds, implying colonization under subaqueous conditions and transition to the *Mermia* Ichnofacies. Potential producers include several groups of dipterans as well as nematodes and spiders. Overall, the Early Cretaceous, South Korean lake ichnofaunas show a similar trace-fossil distribution to those ichnofaunas recorded in shallow-lacustrine deposits of the Newark Supergroup. In both cases, colonization by benthic organisms reflects changes in the degree of consolidation of the substrate as a result of progressive subaerial exposure.

Early Cretaceous lotic and especially lentic insect taxa are derived from the same taxonomic families as those of the Late Jurassic (Martínez-Delclòs et al. 1995; Delclòs et al. 2008). Representatives of this faunal assemblage are a lentic, ephemeropteran fauna that consists of siphlonurids, hexagenitids and mesonetids.

Hexagenitid naiads, as well as ephemeroid naiads, are very common in some Early Cretaceous lentic assemblages (Sinitshenkova 2002), including taxa that produced the bioerosion ichnogenus *Asthenopodichnium* subaqueously in woods (Thenius 1989). Most of the Early Cretaceous mayfly genera did not survive into the Late Cretaceous (Sinitshenkova 2002), and only one lineage, the Australiephemeridae, became extinct at the end-Cretaceous (K-Pg) boundary.

The Early Cretaceous aquatic odonatan fauna is quite different from that of the Jurassic. The diversification of modern anisopteran (dragonfly) and zygopteran (damselfly) lineages appear for the first time. Curiously, the Pseudomyrmeleontidae, interpreted by some as related to the Paleozoic Meganeuroidea, were still present as a relict group. Unlike ephemeropteran assemblages, odonatan assemblages appear to have most of their evolutionary development in lotic habitats. The dominant Early Cretaceous odonatan lineages are the Isophlebioidea, Heterophlebioidea, Calopterygoidea, and other anisopteran clades. Among these lineages are a few specialized types, such as naiads of the Eurasian Hemeroscopidae and Sonidae (Pritykina 1986), which include a morphotype with long legs possessing paddling locomotion and a nectic, predatory existence. By contrast, other taxa, such as the Nothomacromyiidae lacked swimming structures but retained actively cursorial, long legs, indicating predatory pursuit habits. Another ecomorph is represented by the short-legged, burrowing Gomphidae (Bechley 1998). The labial-mask mouthpart structure has been examined for a select few species of these lineages, and no conclusions could be made regarding prey-specific relationships (Sinitshenkova 2002).

Plecopteran family-level diversity increased during the Early Cretaceous. Jurassic plecopteran clades persisted into the Early Cretaceous and were supplemented by the earliest occurrences of several, modern, family-level lineages. All of the modern, plecopteran functional feeding groups were present during the Early Cretaceous, such as collectors and shredders engaged in detritivory, algal herbivory and insect predation. In addition, chresmodids are still present in some lacustrine settings, but probably became competitively excluded by emerging, Early Cretaceous gerrid lineages.

True bugs of the Hemiptera are ubiquitous and diverse throughout the Early Cretaceous, and with the exception of the Shurabellidae, are continuations of Jurassic lineages (Sinitshenkova 2002). By contrast, the Gerridae and Mesoveloidea (water treaders) initially appear during the Early Cretaceous, ecologically supplementing and replacing an earlier convergent ecotype, the orthopteroid Chresmodidae, which had affinities to orthopteroid insects (Martínez-Delclòs et al. 1995). This replacement included larger-sized, surface-skimming gerrids during the Late Cretaceous that approached in size many of the medium-sized Jurassic chresmodids, the latter of which had legspans of up to 16 cm (Labandeira pers. observ.). Corixids, notonectids, mesotrephids and notably large, predaceous belostomatids continued into the Early Cretaceous (Delclòs et al. 2008). Although there are some evolutionary novelties between Jurassic and Early Cretaceous aquatic bug faunas, it appears that all of the Jurassic ecologic feeding types were present during the Early Cretaceous and encompassed surface water and neuston-zone feeders on dead or dying arthropods, nectic algivores, nectic predators and epibenthic predators.

There are minimal taxonomic and ecologic differences between Late Jurassic and Early Cretaceous beetle faunas. Archostematan schizophorids became very rare; the largely aquatic Adephaga retained a similar spectrum of major taxa as before, although the proportions of major lineages change. The major shifts are that the Parahygrobiidae become more abundant; the Coptoclavidae become dominated by a newly emerging, advanced clade, the Coptoclavinae; the Gyrinidae increase in diversity; the Liadytidae become rarer; the Dytiscidae remain rare; and the Haliplidae have their earliest occurrence (Ponomarenko 1969). The dominantly terrestrial Polyphaga are represented by the same families in the Early Cretaceous as during the Jurassic, including the Scirtiidae (marsh beetles), but especially the detritivorous Hydrophilidae, represented by new taxa such as *Cretotaenia*.

Other holometabolous insect clades with aquatic stages include the Megaloptera, Neuroptera (lacewings, antlions, and related forms) and Mecoptera. These clades express a similar pattern of mostly lotic-based diversity, as do their descendants in modern ecosystems. The predaceous larvae of megalopterans, such as the Corydalidae (dobsonflies), neuropterans such as the Osmyloidea (net-winged lacewings and relatives) and the detritivorous mecopteran larvae of the Nannochoristidae occur in Lower Cretaceous deposits of Eurasia and Australia (Zherikhin 1978; Jell and Duncan 1986). These lineages currently reside in the same habitats, although they have been overshadowed by more derived Cenozoic lineages that entered the same aquatic niches.

During the Early Cretaceous, caddisflies experienced major evolutionary novelties, as new family-level lineages emerged, other groups assumed dominance, and a profusion of larval case-making activity ensued. Evidence from adult caddisflies indicate that the earliest Mesozoic caddisflies, necrotaulids, became rare; others, such as the extinct phryganeoid families Dysoneuridae, Vitimotaulidae, and Baissoferidae were common, as were the extant Phyganeoidea, the Calamoceratidae (flat-case caddisflies), Lepidostomatidae (lepidostomatid casemaker caddisflies), Plectrotarsidae (plectrotarsid caddisflies), and Helicopsychidae (snail-case caddisflies) (Sinitshenkova 2002). Of these, the Vitimotaulidae were the most numerically abundant, or at least were common across most Eurasian localities. There was significant differentiation of the Vitimotaulidae at the generic level across Eurasia, and the dominance of particular local genera occurred throughout the region.

An important event in lotic and especially lentic environments was the global diversification of caddis larval-case morphotypes (Sukatcheva 1982). This expansion of domicile morphotypes that used a variety of mineral, plant, and animal resources evidently commenced during the earliest Cretaceous in northern Asia, and penecontemporaneously in Europe, South America and Australia (Sinitshenkova 1999). Circumstantial evidence indicates that the Vitimotaulidae were the dominant fabricators of these cases. In localities where adult body fossils and larval cases are both abundant and diverse, it appears that each case morphotype likely is associated with one adult species. Apparently, each case morphotype was made by an adult species that was restricted to a particular lotic or lentic habitat, partly reflected by use of building materials that were available for case construction. Cases were variously fabricated from conchostracan shells, *Karkenia* ginkgoalean seeds, conifer needles, plant twigs, quartz grains, mica flakes, and other available materials (Sukatcheva 1982).

The dominant lacustrine lineages of the Diptera during the Early Cretaceous were the same as for the Late Jurassic. Planktivorous chaoborids were more abundant but less speciose during the Early Cretaceous when compared to the Late Jurassic, whereas chironomids had an opposite trend. Both groups are represented primarily by adult and pupal fossils; larvae are relatively rare and poorly preserved. This pattern of differential preservation of developmental stages also exists for limoniids, eoptychopterids and other nematocerous fly lineages. Not only compression deposits capture this pattern, but this pattern also is found in amber occurrences, such as Lebanese Amber. In Lebanese Amber the most common families are, in decreasing rank: Chironomidae, Ceratopogonidae, Psychodidae, and Eoptychopteridae (Kalugina 1980). However, in Paleolake Baissa deposits, chaoborids were very abundant and likely were a major food resource for consumers that sustained much of the upper tier of the food-web. One interesting development in Early Cretaceous lakes was the emergence of brachyceran fly larvae, including the Stratiomyiidae (soldier flies), Empididae (dance flies), other asilomorphs, and possibly the Sciomyzidae (snail-eating flies) (Whalley and Jarzembowski 1985).

Arguably, one of the major innovations by the Early Cretaceous is the appearance of aquatic angiosperms which, together with ferns (Schneider et al. 2004), started to replace charophytes as the dominant macrovegetational elements in lacustrine ecosystems (Martín-Closas 2003; Friis et al. 2003, 2010; Gandolfo et al. 2004; Coiffard et al. 2007). The presence of freshwater species representing among the first angiosperms documented in the fossil record is hard to interpret, because it may reflect an initial evolution and diversification in aquatic habitats or a taphonomic bias (Martín-Closas 2003). Regardless of these alternatives, the appearance of angiosperms was an evolutionary breakthrough that may have had a considerable impact on aquatic life in ponds and lakes (Ponomarenko 1998; Friis et al. 2010). Specifically, aquatic angiosperms (Sun et al. 2002; Friis et al. 2003; Dilcher et al. 2007) would have been instrumental in providing substrates for epiphytic organisms, increasing the release of phosphorous by decaying macrophytes, promoting light attenuation, steepening of the vertical temperature gradient, retarding of water flow and enhancing fine-grained sediment deposition, among other processes (Carpenter and Lodge 1986; Granéli and Solander 1988; Ponomarenko 1998; Cohen 2003). Paralleling this pattern, aquatic ferns experienced further diversification (Schneider et al. 2004), but lycophytes remained abundant (Martín-Closas 2003). With respect to phytoplankton, although Chlorococcales were still abundant, the appearance of freshwater dinoflagellates is a major evolutionary innovation which signaled the demise of green algal dominance in freshwater phytoplankton (Martín-Closas 2003; Leliaert et al. 2011).

As with the Triassic and Jurassic, Cretaceous lotic and lentic insect faunas have been divided into distinctive lacustrine assemblages, each characterized by specific dominant and ecologically important insect species occurring in a particular environmental setting (Zherikhin 1978; Sinitshenkova and Zherikhin 1996; Sinitshenkova 1999; Sinitshenkova 2002). For the Cretaceous, 18 such assemblages have been described (Sinitshenkova 2002), one of which is Assemblage 5A, or the *Ephemeropsis melanurus–Hemeroscopus baissicus* Assemblage, whose environmental conditions and trophic structure have been examined in detail (Table 11.1 and Fig. 11.10). This

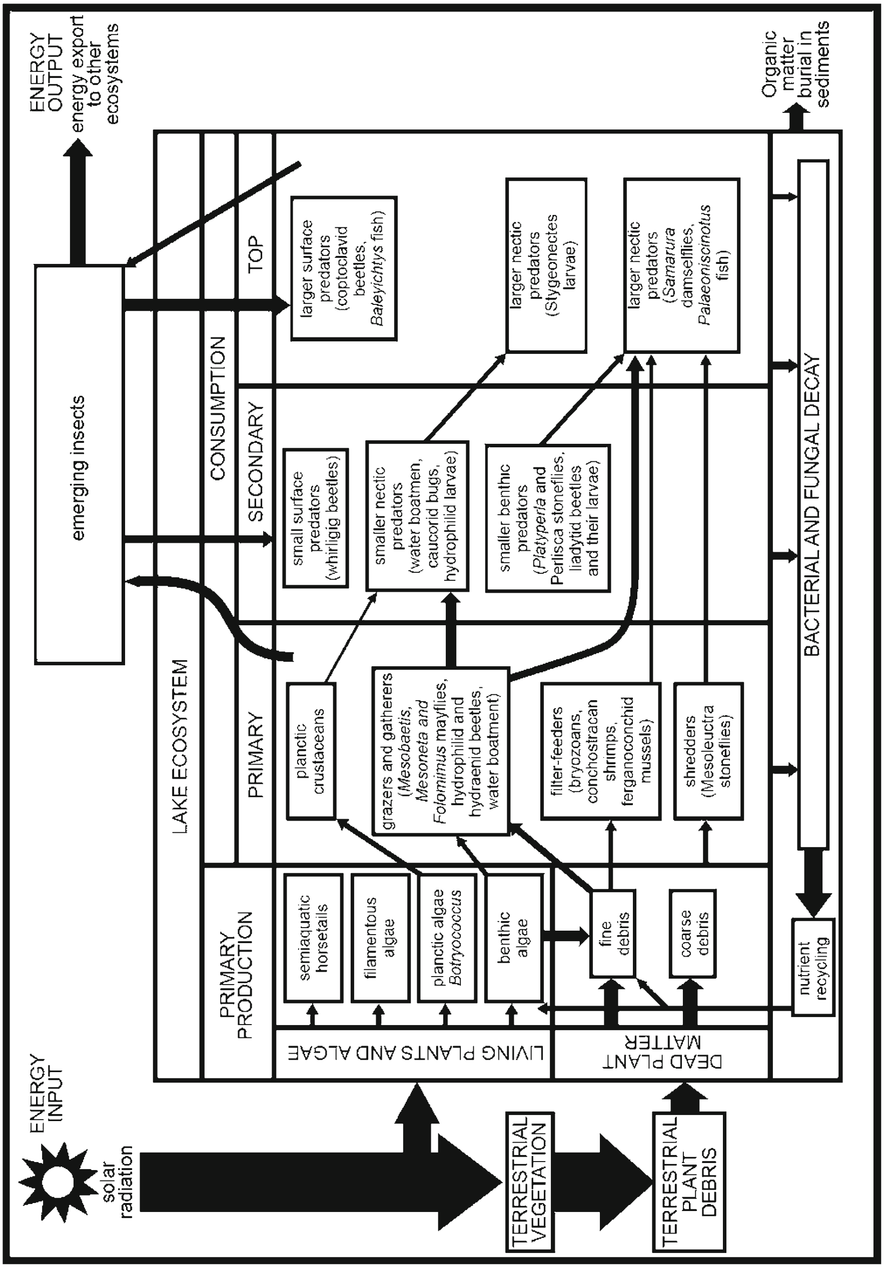

Fig. 11.10 Trophic structure reconstruction of an Early Cretaceous pseudoligotrophic lake (Zherikhin et al. 1999). This lake represents the *Ephemeropsis melanurus–Hemeroscopus bassicus* biotal assemblage typifying Paleolake Baissa in southern Siberia, Russia. This trophic reconstruction corresponds to the Type C lake biotal assemblage of Sinitshenkova and Zherikhin (1996). See Assemblage C in Table 11.1 for additional physical, chemical and biological details. Redrawn, with modification, from Sinitshenkova and Zherikhin (1996)

assemblage, from Paleolake Baissa, occurs in the Zaza Formation, Buryat Republic, in Transbaikalian Russia, and was deposited in a deep, intermontane, meromictic lake. Paleolake Baissa periodically dried out in shallower regions, indicated by mass mortality occurring as dense accumulations of the same instar of large coptoclavid larvae that became locally confined to a few bedding surfaces. Accumulations of chaoborid larvae are present at more widespread event horizons and at small unconformities or possibly diastems separating adjacent beds (Zherikhin et al. 1999).

The *Ephemeropsis melanurus–Hemeroscopus bassicus* Assemblage is more taxonomically and ecologically diverse than earlier Jurassic Eurasian paleolakes. This assemblage includes tetrapods, birds, and osteoglossomorph fish such as *Lycoptera*, and a rare *Stychopterus* sturgeon; phyllopod, conchostracan and ostracod crustaceans, gastropods, bivalves and freshwater bryozoans (Vinogradov 1996). Most of the estimated 1000 species of insects in the fauna are terrestrial and allochthonous in origin (Zherikhin et al. 1999). The autochthonous lacustrine component of the biota consists of ca. 80–120 species of lake residents, and was dominated by the aquatic immatures of odonatans, heteropterans, coleopterans, dipterans and numerous caddisflies (as cases). Insect fossils typically are shed exuviae rather than whole, dead individuals. The surrounding vegetation consisted of *Pseudolarix* forest, a *Podozamites–Czekanowskia* shrubland, and groundcover of horsetails, ferns, and very rare angiosperms of uncertain affiliation (Zherikhin et al. 1999). Although this assemblage represents one of the earliest occurrences of angiosperms in an Eurasian lake deposit, the effect of angiosperms were insignificant, and it was toward the end of the Early Cretaceous, during the Aptian and Albian Stages, during which the role of angiosperms were manifest in terrestrial ecosystems (Labandeira, 2014; Labandeira et al. 2016) and likely in freshwater ecosystems as well.

In most Mesozoic deposits intraspecific links between growth stages, such as naiads and adults in nonholometabolous insects and larvae and adults in holometabolous insects are not possible (Zherikhin and Sinitshenkova 2002). However, in the *Ephemeropsis melanurus–Hemeroscopus bassicus* Assemblage, some larval and adult taxa are associated based on a variety of evidence. Strong associations include the dragonfly adult of the hemeroscopid *Hemeroscopus baissicus* and a very common species of an aeschnidiid naiad, and similarly the hydrophilid beetle adult *Hydrophilopsia baissensis* with the hydrophilid larva *Cretotaenia pallipes*. Adults and larvae of the dobsonfly *Cretochaulus lacustris* and the adephagan beetle *Coptoclava longipoda* are also found in this assemblage, although the latter may be a complex of several species (Zherikhin et al. 1999). It appears that most of the caddisfly cases were constructed by various species of Vitimotaulidae. However, many of these fossils are immature individuals of lentic taxa whose adults are associated with nearby, lotic, especially rhythral, habitats that were allochthonously transported into Paleolake Baissa. The transported lotic taxa are represented by rare odonatans, plecopterans, simuliid dipterans, and nannochoristid mecopterans. These connections between immatures and adults in different aquatic habitats within lakes and rivers indicate a greater autecologic partitioning within species by life stage, as well as among species. This twofold, intraspecific and interspecific subdivision of resources can be interpreted as a maturation of terrestrial aquatic habitats that became more widespread during the Early Cretaceous (Zherikhin et al. 1999).

11.5.5 The Late Cretaceous Biotal Replacement

Ichnologic information from Late Cretaceous paleolakes is remarkably scarce, precluding a detailed discussion. Late Cretaceous examples of lake-margin ichnofaunas are known from the southern United States (Montgomery and Barnes 2012), western Canada (Rylaarsdam et al. 2006), Botswana (Du Plessis and Le Roux 1995), Bolivia (Meyer et al. 2001), China (Zhang 1987), and Korea (Paik et al. 2012; Lockley et al. 2012; Minter et al. 2012). However, most of these studies do not address the ichnofaunas in a comprehensive fashion. As for fully lacustrine deposits, we are aware of only one study documenting Late Cretaceous ichnofaunas in this setting, namely perennial lake deposits in Botswana (Du Plessis and Le Roux 1995).

The crayfish burrow *Camborygma* is present in lake-margin deposits (Montgomery and Barnes 2012), indicating the persistence of this deep tier throughout the Mesozoic. Vertical burrows (e.g. *Skolithos*) and branching structures (e.g. *Thalassinoides*) occur as well (Zhang 1987; Du Plessis and Le Roux 1995). Arthropod trackways (*Lithographus*) have been recorded locally (Minter et al. 2012). Dinosaur and bird tracks preserved along lacustrine paleoshorelines also are known (Meyer et al. 2001; Rylaarsdam et al. 2006; Paik et al. 2012; Lockley et al. 2012). In particular, intense bioturbation by dinosaurs continued to have an impact on the sedimentary fabric of lake-margin deposits throughout the Late Cretaceous (Rylaarsdam et al. 2006).

A complex mosaic of lacustrine deposits is preserved in Upper Cretaceous grabens, whose infill is recorded in the Kalahari Group of Botswana (Du Plessis and Le Roux 1995). The succession includes deposits of ephemeral and perennial alkaline lakes. In both systems, an irregular network of tunnels, showing Y-shaped bifurcations, attributed to *Thalassinoides*, has been recorded (Du Plessis and Le Roux 1995). In the ephemeral lake deposits, these structures are present in sand and mud flats flanking the lake system. In the perennial lake deposits, *Thalassinoides* occurs in fully lacustrine deposits in great abundances, commonly forming intensely bioturbated fabrics, which most likely record less saline conditions in relatively deeper water environments (Du Plessis and Le Roux 1995). In these deposits, *Thalassinoides* commonly occurs in association with vertical shafts that have lateral tunnels, which have been compared with the poorly known vertical burrow *Lennea* (Du Plessis and Le Roux 1995), but this attribution needs further confirmation. In short, the sparse information available suggests continuation in lake-margin environments of the same trends evidenced earlier in this setting. As well, the presence of intensely bioturbated, fully lacustrine deposits resembles similar deposits of the Lower Cretaceous.

Much less is known about Late Cretaceous lacustrine biotas when compared to those of the Early Cretaceous. Most likely this is a reflection of limited outcrop that resulted from the end of the broad extensional-tectonic regime that dominated the mid-Mesozoic continental breakup, which promoted the formation of widespread lacustrine rifts (Cohen 2003). The fossil record of aquatic insects documents mid-Cretaceous extinction of some lineages that were thriving during the Early Cretaceous but are not present during the Late Cretaceous. This event included the extinction of about 20 family- and superfamily-level lineages (Zherikhin 1978; Sinitshenkova and Zherikhin 1996). Of ephemeropterans, none became extinct; for odonatans, the latest meganeuroid lineage, the Protomyrmeleontidae, became extinct, as did the Isophlebioidea and Heterophlebioidea. For plecopterans, the family Oecanthoperlidae is extinguished, as was the Chresmodida, a major Jurassic clade of aquatic Archaeorthoptera. With the exception of the Shurabellidae, apparently no lineage of hemipterans became extinct, as early originating lineages such as corixids, notonectids, belostomatids, and mesoveliids survive to the present day. Coleopterans experienced several major extinctions, such as the Ademosynidae, Parahygrobiidae, Schizophoridae, Coptoclavidae, and Liadytidae. No major extinctions are known for the major lineages of the relatively undiverse neuropteroid groups Megaloptera, Raphidioptera, or Neuroptera, or for the Mecoptera, of which the extant Nannochoristidae is an aquatic representative. For the Trichoptera, major extinctions of family-level taxa were the Dysoneuridae, Necrotaulidae, Baissoferidae, and Vitimotaulidae, the latter of which produced a high diversity of caddisfly case morphologies. The Diptera remained unaffected by the mid-Cretaceous extinction events; evidently the nematocerous Eoptychopteridae and possibly the Hennigmatidae are the only family-level lineages that became extinct (Zherikhin 1978; Sinitshenkova and Zherikhin 1996).

Perhaps more important are the originations of new aquatic insect lineages during the mid Cretaceous, almost all of which survive to the present and essentially form the modern lentic and lotic aquatic insect fauna. Approximately 19 family- and superfamily-level lineages have their first fossil occurrences during the mid Cretaceous, consisting of approximately the same number of lineages that go extinct. For the Ephemeroptera, only the earliest Heptagenoidea is known to occur close to the Early–Late Cretaceous boundary. In odonatans, modern family-level lineages of the Zygoptera (damselflies) may have originated during this interval, but geochronological timing is poorly constrained. No known major lineages of plecopterans originated during the mid Cretaceous. As for hemipterans, the diverse clade Gerromorpha had its earliest major bout of diversification during the mid Cretaceous, including some of the first occurrences of sublineages within the Gerridae, Hydrometroidea (water measurers), probably the Hebroidea (velvet waterbugs and relatives), and the extinct Mesotrephidae. Of coleopterans, only the Haliplidae and Scirtiidae have their earliest occurrences during the mid Cretaceous. Five lineages of the Trichoptera have their first occurrences at this time, including the Hydrobiosidae (pincer-clawed caddisflies), Sericostomatidae (bushedtailed caddisflies), Odontoceridae (mortarjoint casemakers), Calamoceratidae (comblipped casemakers), and Leptoceridae (long-horned caddisflies). The origin of these lineages curiously is associated with a significant decline in case morphotype diversity, as early Cretaceous cases range from 10–15 morphotypes in a typical assemblage, to ca. 5 per assemblage in the Late Cretaceous (Sukatcheva 1991). This decline may be attributable to the disappearance of the diverse Vitimotaulidae which became extinct at this time. Several nematocerous lineages of dipterans with aquatic larvae diversified during the mid Cretaceous, particularly the Ptychopteridae (phantom crane flies), Culicidae (mosquitoes), Chaoboridae (phantom midges), Corethrellidae (frog-biting midges), and Ceratopogonidae (biting midges). Interestingly, while the number of known aquatic insect extinctions and originations for the mid Cretaceous appear to balance out with ca. 20 lineages in each category, the totals of insect herbivore turnover is much greater for the mid-Cretaceous terrestrial realm (Labandeira 2014).

The biologies of these aquatic insect lineages indicate that, whereas the aquatic immatures (naiads, larvae) were well integrated into aquatic ecosystems, the adults became more removed from aquatic habitats than in previous freshwater biotas. For example, whereas the naiads of damselflies were major aquatic predators, their adults preyed on aerially winged insects. The adults of aquatic heteropterans became predators on other aquatic insects (Anderson 1998). Almost all dipteran lineages were comprised of larvae that were aquatic filter-feeders whereas their adults—at least the females—were obligate blood feeders on vertebrates (Labandeira 2002). As the aquatic larvae of caddisflies increasingly became herbivorous, their terrestrial adults targeted angiosperm nectar or similar nutritive sources (Porsch 1958), or lacked feeding capabilities altogether. The disjunction of habitats between immatures (naiads, larvae) and adults increased during the Late Cretaceous, exhibiting an even more profound separation between the life habits of immatures and adults than ever before.

The Late Cretaceous witnessed the continuation of the radiation of aquatic angiosperms and ferns (Martín-Closas 2003; Gandolfo et al. 2004; Schneider et al. 2004), the former showing increased interaction with modern insect families. The shift from gymnosperm-dominated floras to angiosperm-dominated floras was accompanied by a major turnover in their terrestrial insect associates (Labandeira 2014; Labandeira et al. 2016). This transition occurred during the angiosperm radiation, and included episodes of extinction and origination that paralleled a similar pattern characterizing the MLR, although it appears that there is a time shift between the two major events. By contrast, no such pattern is seen in freshwater algal groups. Charophyte assemblages became dominated by the Characeae (Martín-Closas 2003). During the Late Cretaceous, lacustrine phytoplankton displays a similar composition to that of the Early Cretaceous, as indicated by the presence of Chlorococcales and freshwater dinoflagellates (Martín-Closas 2003). However, evidence of diatoms is known from the Late Cretaceous, suggesting early diversification, albeit playing a limited role as lacustrine plankton (Chacón-Bacca et al. 2002). Chrysophytes also are documented from the Cretaceous (Cornell 1979; Adam and Mahood 1981), but as with diatoms, they radiated later in the Cenozoic when they became an important phytoplankton component (Leliaert et al. 2011). In any case, the major changes in the plankton composition involved the diversification of freshwater diatoms and chrysophytes.

11.6 The Aftermath of the Revolution

An examination of the trace- and body-fossil records, as well as the ecological structure of Cenozoic lakes, provides a picture of the aftermath of the MLR, thereby revealing whether additional evolutionary novelties or innovations took place. Interestingly, the biological response to the MLR is not straightforward.

A review of the Cenozoic lacustrine trace-fossil record shows that Cenozoic lake-margin invertebrate ichnofaunas are similar in composition to those of the Late Cretaceous (Table 11.2). Apparently there was minimal effect of the Cretaceous–Paleogene (K-Pg) events on the MLR (see Chap. 12). This is in sharp contrast, for example, with the ongoing rapid diversification of insect nesting structures in paleosols that took place during the Cenozoic (see Chap. 13).

Little is known of complete inventories of bulk aquatic insect faunas from amber and compression–impression deposits during the Late Cretaceous and Paleocene, unlike the significantly better documented terrestrial fossil insect record (Zherikhin and Sinitshenkova 2002; Labandeira 2005b). Perhaps more importantly, paleoecological data indicate that the modern ecologic structure from one, well-documented lake was well established by the early–middle Eocene boundary interval at Paleolake Messel (Fig. 11.12), and resembled in all measured food-web indices that of a variety of modern lake ecosystems (Dunne et al. 2014). This study proposes that earlier, well preserved lake deposits that postdate the MLR but predate Messel (and straddling the K-Pg boundary) also be examined to determine how far back in geologic time modern lacustrine food-web structure extends (Dunne et al. 2014). Until food-web studies that use similar analytical techniques and trophic measurement indices as those used for Messel are applied to well-preserved lake deposits before and after the MLR, analytical detection of the trophic shift left by the MLR may be difficult. Nevertheless, studies of ichnofaunas and insect biotas, particularly those from the Paleogene may provide robust results in lieu of detailed food-web analyses of lake deposits using modern ecological techniques. One particular approach that may be useful is to attempt an associational approach in the freshwater, especially lacustrine realm that has been done for the terrestrial realm (Labandeira et al. 2002; Wilf et al. 2006). In lieu of more complete knowledge of aquatic, arthropod body-fossil faunas during this time interval, analyses of interactions may provide an another approach for detecting the trophic shift toward herbivore-dominated aquatic communities following the MLR.

Ichnofaunas from lake-margin deposits are known from the Paleogene of the western United States (Melchior and Erickson 1979; Lamond and Tapanila 2003; Bohacs et al. 2007; Scott and Smith 2015), Spain (Rossi 1992; de Gibert and Sáez 2009), China (Hsiao et al. 2010), Antarctica (Yang and Shen 1999; Perea et al. 2001), the Neogene of the western United States (Toots 1975; Smith et al. 1982; Squires and Advocate 1984; Scrivner and Bottjer 1986; Lucas et al. 2002), Spain (Rodriguez-Aranda and Calvo 1998; Uchman and Álvaro 2000; Ortí et al. 2003) and Kenya (Laporte and Behrensmeyer 1980; Cohen 1982; Ekdale et al. 1989; Cohen et al. 1991, 1993; Lamond and Tapanila 2003). Shallow-tier, horizontally striated or non-ornamented, meniscate, backfilled structures (*Scoyenia*, *Taenidium*, *Beaconites*), simple horizontal structures (*Planolites*, *Palaeophycus*), vertical burrows (*Arenicolites*, *Polykladichnus*), and striated or non-ornamented branching burrows (*Spongeliomorpha, Labyrintichnus*) are the dominant elements (Toots 1975; Smith et al. 1982; Squires and Advocate 1984; Rodriguez-Aranda and Calvo 1998; Uchman and Álvaro 2000; Ortí et al. 2003; Bohacs et al. 2007; de Gibert and Sáez 2009; Hsiao et al. 2010). The crayfish burrow *Camborygma* has been locally recorded (Hsiao et al. 2010). Vertical burrows with a terminal chamber, ascribed to the ichnotaxon *Liticuniculatus erectus,*

Table 11.2 Summary of ichnologic, paleontologic, and paleoecologic information on the Mesozoic Lacustrine Revolution (MLR)

Evolutionary phases	Aquatic insect body fossils (representative families)[a]	Other benthos	Aquatic plants	Nekton/plankton	Lake-margin trace fossils	Permanently subaqueous trace fossils	Ecosystem characteristics
Pre-Mesozoic Backdrop to Diversification	Dasyleptidae, Protereismatidae, Misthodotidae, Syntonopteridae, Jarmilidae, Oboriphlebiidae, Eraspteriidae, Meganeuridae, Protomyrmeleontidae, Permagrionidae, Kennedyidae, Perlopseidae, Tschekardiperliidae, Palaeonemouriidae	Chelicerates, conchostracans, leperditocopid crustaceans, shrimp-like crustaceans, oligochaetes, bivalves, gastropods, amphibians, reptiles	Charophytes, water-tolerant lycopods, sphenopsids, medullosan seedferns and arborescent marattialean ferns in wetlands; cordaites, noeggeranthialeans, conifers, gigantopterids, and peltasperms in dry settings	Chlorophytes (mostly Chlorococcales), agnathan, acanthodian, placoderm, chondrichthyan, and osteichthyan fish	Arthropod and tetrapod trackways dominant	Superficial grazing trails and shallow-tier feeding trace fossils dominant, fish trails present	Colonization of lake-margin settings by the Silurian-Devonian and of permanently submerged lake bottoms by the Carboniferous. Limited to no colonization of the infaunal ecospace. Poorly developed food webs driven by detritivores and top predators as near-exclusive consumers; herbivory was absent
Early Triassic Denouement	Protomyrmeleontidae, Batkeniidae, Naucoridae, Belostomatidae, Permosynidae, Schizophoridae, Liassophilidae, Tipulidae	Decline in family-level biodiversity. Conchostracans, shrimp-like crustaceans, bivalves, gastropods, oligochaetes, amphibians, reptiles	Charophytes and *Isoetes*-related nonflowering vascular plants	Chlorophytes (mostly Chlorococcales), osteichthyan fish	Arthropod trackways dominant	No data	Persistence of Paleozoic styles of animal–substrate interactions in lake-margin settings. Poorly developed food webs driven by detritivores and top predators as near-exclusive consumers; herbivory was absent

(continued)

Table 11.2 (continued)

Evolutionary phases	Aquatic insect body fossils (representative families)[a]	Other benthos	Aquatic plants	Nekton/plankton	Lake-margin trace fossils	Permanently subaqueous trace fossils	Ecosystem characteristics
Middle-Late Triassic Rediversification	Triassolestidae, Saxonagrionidae, Triadophlebiidae, Siphloneuridae, Euxenoperlidae, Ochteridae, Triassocoridae, Notonectidae, Belostomatidae, Schizophoridae, Ademosynidae, Colymbothetidae, Hydrophilidae, Dytiscidae, Triaplidae, Philopotamidae, Prorhyacophilidae, Nannochoristidae	Biodiversity recovery. Conchostracans, shrimp-like crustaceans, ostracods, kazacharthrans, phyllopods, bivalves, gastropods, oligochaetes, bryozoans, amphibians, reptiles	Charophytes and *Isoetes*- and *Azolla*-related nonflowering vascular plants	Chlorophytes (mostly Chlorococcales), osteichthyes fish	Meniscate trace fossils dominant, crayfish burrows common, reptile trackways and lungfish burrows present	Superficial grazing trails and shallow-tier feeding trace fossils dominant, fish trails present, mid-tier feeding burrows locally present. Vertical dwelling burrows in higher-energy settings	Increase in depth and extent of bioturbation in lake-margin sediments Persistence of Paleozoic styles of animal-substrate interactions in permanent subaqueous lake settings, but incipient colonization of the infaunal ecospace locally. More complex food webs, albeit still driven by detritivores and top predators with herbivory absent
Jurassic diversification and infaunalization	Tarsophlebiidae, Siphlonuridae, Mesonetidae, Epeorominidae, Mesoleuctridae, Siberioperlidae, Chresmodidae, Belostomatidae, Gyrinidae, Mesoveliidae, Shurabellidae, Coptoclavidae, Haliplidae, Liadytidae, Parahygrobiidae, Necrotaulidae, Limoniidae, Chironomidae Eoptychopteridae, Chaoboriodae	Conchostracans, shrimp-like crustaceans, ostracods, phyllopods, bivalves, gastropods, oligochaetes, bryozoans, amphibians, reptiles	Charophytes dominant (radiation of Characeae and the Clavatoraceae), *Azolla*-related nonflowering vascular plants, ferns, porocharaceans and nitellaceans locally	Chlorophytes (mostly Chlorococcales), osteichthyes fish	Meniscate trace fossils dominant, dinoaur trackways present (including trampled surfaces)	Shallow-tier feeding and grazing trace fossils and deeper-tier feeding burrows dominant, fish trails present, mid-tier feeding burrows locally present. Vertical dwelling burrows in higher-energy settings	Persistence of Middle to Late Triassic styles of animal-substrate interactions in lake-margin settings, but with the addition of intense bioturbation by dinosaurs. Widespread occupation of mid tiers in deep lacustrine deposits, but limited sediment reworking.Increase in predation pressures. Initial transformation from detritivore-driven to herbivore-driven trophic networks of the mesolimnion and epilimnion

Early Cretaceous Persistence	Petaluridae, Libellulidae, Hemeroscopidae, Hexagenitidae, Chresmodidae, Clypostemmatidae, Mesotrephidae, Gerridae, Mesoveliidae, Hydrophilidae, Dytiscidae, Coptoclavidae Scirtiidae, Corydalidae Vitimotaulidae, Baissoferidae Calamoceratidae	Conchostracans, shrimp-like crustaceans, ostracods, phyllopods, bivalves, gastropods, oligochaetes, bryozoans, amphibians, reptiles	Aquatic angiosperms and ferns common, charophytes present	Chlorophytes (mostly Chlorococcales), dominant, dinoflgellates, osteichthyan fish	Meniscate trace fossils dominant, crayfish burrows common, dinosaur, pterosaur, bird, reptile and turtle trackways present	Shallow-tier feeding and grazing trace fossils, mid-tier pervasive burrow mottlings, fish trails present	Establishment of the lacustrine mixed layer. Transformation from detritivore-driven to herbivore-driven trophic networks of the mesolimnion and epilimnion
Late Cretaceous biotal replacement	Gomphidae, Petaluridae, Aeshnidae, Libellulidae Coenagrionidae Gerridae, Hebridae, Hydrometridae, Mesotrephidae, Hydrobioscidae, Sericostomatidae, Leptoceridae Culicidae, Ptychopteridae, Chaoboridae Ceratopogonidae	Conchostracans, shrimp-like crustaceans, ostracods, phyllopods, bivalves, gastropods, oligochaetes, bryozoans, amphibians, reptiles	Aquatic angiosperms and ferns dominant, charophytes present.	Chlorophytes (mostly Chlorococcales), and dinoflgellates dominant, osteichthyan fish	Crayfish burrows, and dinosaur and bird trackways present	Deeper-tier feeding burrows present	Persistence of previous trends in styles of animal–substrate interactions

(continued)

Table 11.2 (continued)

Evolutionary phases	Aquatic insect body fossils (representative families)[a]	Other benthos	Aquatic plants	Nekton/plankton	Lake-margin trace fossils	Permanently subaqueous trace fossils	Ecosystem characteristics
Cenozoic Aftermath to MLR	Sieblosiidae, Zacallatidae, Dysagrionidae, Baetidae, Hydrophilidae, Dytiscidae, Hydropsychidae, Leptoceridae, Limnephilidae, Hydroptilidae, Phryganeidae, Culicidae Tipulidae, Cylindrotomidae Chironomidae	Conchostracans, shrimp-like crustaceans, ostracods, phyllopods, bivalves, gastropods, oligochaetes, bryozoans, amphibians, reptiles and mammals	Aquatic angiosperms and ferns dominant.	Chlorophytes (mostly Chlorococcales), and dinoflgellates dominant, freshwater diatoms and chrysophytes, osteichthyan fish	Meniscate trace fossils dominant, crayfish burrows common, insect nests and borings locally, bird and mammal trackways present	Shallow-tier feeding and grazing trace fossils and deeper-tier feeding burrows dominant, fish trails and nests present, mid-tier feeding burrows locally present. Shallow-tier trails in glacial settings. Vertical dwelling burrows in higher-energy settings	Persistence of previous trends in styles of animal–substrate interactions. Strong impact of diatoms starting in early Neogene on the biogeochemical cycling of silica, promotion of more complex trophic webs and probable overall increase of lacustrine productivity

[a] This column provides the more important aquatic forms or inhabitants of wet habitats adjacent to lakes for at least one stage in their life cycle (naiad, larva, adult)

were compared with similar structures produced by decapods (Melchior and Erickson 1979). This is a poorly known ichnotaxon that may elicit comparisons with *Camborygma*. Simple grazing trails (*Archaeonassa*, *Cochlichnus*) are very rare (Smith et al. 1982; de Gibert and Sáez 2009).

In some cases lake-margin deposits are overprinted by a suite of insect nests (*Celliforma, Roselichnus*; Uchman and Álvaro 2000), which are particularly common in Cenozoic terrestrial settings (see Chap. 13). Spectacular examples of surfaces and beds containing several overprinted suites from fully aquatic to transitional and fully terrestrial facies are known from a number of Quaternary localities in Kenya (Scott et al. 2009; Owen et al. 2009). Borings (*Trypanites*, *Sertaterebrites*) and embedment cavities have been documented in lacustrine stromatolites (Ekdale et al. 1989; Lamond and Tapanila 2003; but see Corsetti and Grotzinger 2005 for an alternative interpretation). Evidence of insects capable of burrowing in highly stressed, hypersaline environments of underfilled lakes are observed for the first time in some of the Neogene basins of Spain (e.g. Rodriguez-Aranda and Calvo 1998; Uchman and Álvaro 2000; Ortí et al. 2003).

Vertebrate trace fossils in Cenozoic lake-margin deposits include bird (e.g. *Gruipeda*) and mammal tracks (Scrivner and Bottjer 1986; Yang and Shen 1999; Perea et al. 2001; Lucas et al. 2002; de Gibert and Sáez 2009). A wealth of information has been produced on how vertebrates modify lake-margin surfaces. Large mammals (e.g. hippos) are known to produce trampled surfaces, actively modifying lake-margin landscapes (Laporte and Behrensmeyer 1980; Cohen et al. 1991, 1993; Ashley and Liutkus 2002; Deocampo 2002; Scott et al 2007, 2008) (Fig. 11.11a–c). Additionally, flamingos produce nest mounds and alter lake-margin deposits by trampling and churning wet clayey sediments (Scott et al. 2009, 2012b). These authors documented that these nests may be so compacted that they contribute to the stability of deltaic distributary channels in lake margins, leading to channelization of flow by water diversion around the mounds. Indeed, the impact of flamingos on lake-margin sediments results in the development of a distinctive mounded topography that qualifies as an ichnolandscape (*sensu* Buatois and Mángano 2011a), which can be preserved in the fossil record (Fig. 11.12a–b).

Ichnofaunas from fully lacustrine deposits have been recorded nearly worldwide in Cenozoic deposits. They have been documented from the Paleogene of the western United States (Moussa 1968, 1970; Melchior and Erickson 1979; Loewen and de Gibert 1999; Bohacs et al. 2007; Martin et al. 2010; Scott and Smith 2015), Antarctica (Yang and Shen 1999; Perea et al. 2001), the Neogene of the eastern (O'Brien and Pietraskek-Mattner 1998; Benner et al. 2009; Knecht et al. 2009) and western (Smith et al. 1982) United States, eastern Canada (Gibbard and Dreimanis 1978), Hungary (Babinszski et al. 2003; Magyar et al. 2006; Cziczer et al. 2009), Slovakia (Starek et al. 2010; Hyžný et al. 2015), England (Gibbard and Stuart 1974), Lithuania (Uchman et al. 2008, 2009), Finland (Gibbard 1977), Sweden (Uchman and Kumpulainen 2011), Germany (Walter 1985; Walter and Suhr 1998), Greece (Owen et al. 2011), Turkey (Price and McCann 1990; Uchman et al. 2007), China (Yang 1996), Indonesia (Whateley and Jordan 1989), Thailand (Gibling et al. 1985; Flint et al. 1989), Japan (Allison et al. 2008), Kenya (Feibel 1987) and New Zealand (Lindqvist 1994).

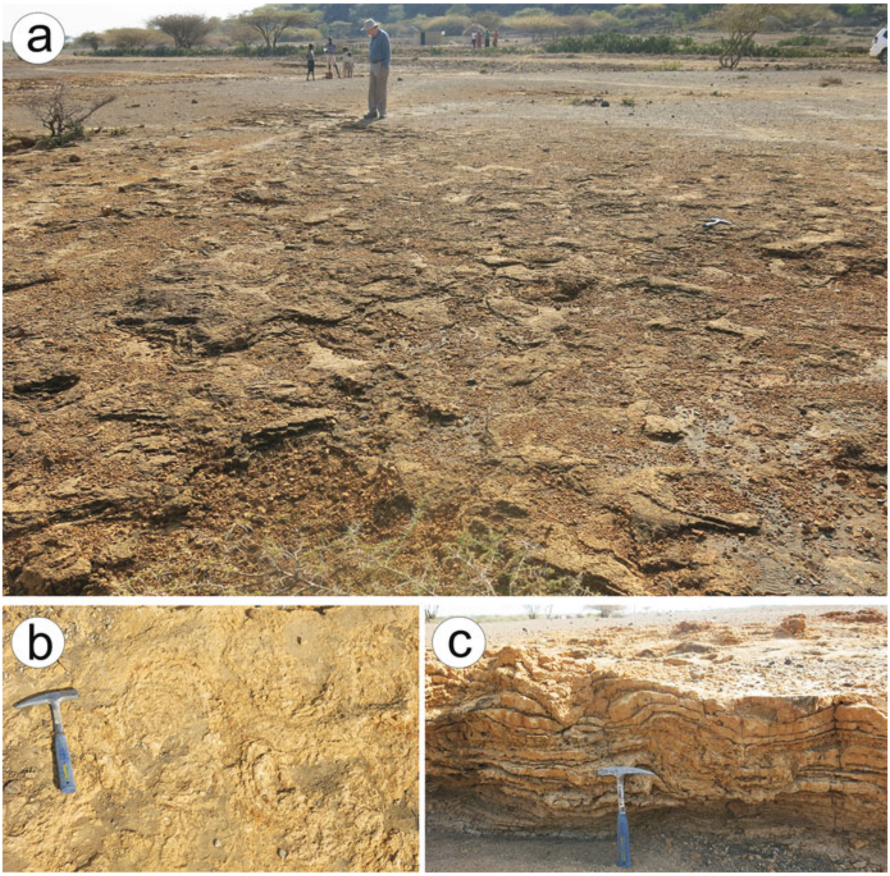

Fig. 11.11 Fossilized trampled surface consisting of a high-density of hippopotamus tracks, Pleistocene, Ilosowuani horst near Logumukum, Lake Bogoria Basin, Kenya. (**a**) General view of the trampled surface; (**b**) Close-up of one of the tracks; (**c**) Cross-section view showing intense disturbance of the primary sedimentary fabric

Ichnofaunas from fully lacustrine, Cenozoic deposits are known from both nonglacial and glacial settings. Nonglacial lake deposits that accumulated under low energy conditions tend to be dominated by a combination of very shallow-tier grazing trails (*Cochlichnus*, *Helminthopsis*), shallow-tier mottlings attributed to *Planolites*, and deeper-tier branching burrows (*Vagorichnus*) (Moussa 1968, 1970; Smith et al. 1982; Gibling et al. 1985; Feibel 1987; Flint et al. 1989; Whateley and Jordan 1989; Yang and Shen 1999; Perea et al. 2001; Bohacs et al. 2007; Uchman et al. 2007; Owen et al. 2011). *Oligichnos limnos*, an ichnotaxon erected by Melchior and Erickson (1979) and suggested to have been made by oligochaetes, needs re-evaluation and may become a junior synonym of *Helminthopsis*. Also, the presence of the bivalve burrow *Lockeia* has been mentioned (Feibel 1987). Interbedded sandstone tempestites and dolomites contain deeper-tier vertical burrows (*Skolithos*, *Arenicolites Polykladichnus*) (Price and McCann 1990; Magyar et al. 2006). Vertical burrows similar to *Trichichnus* have been

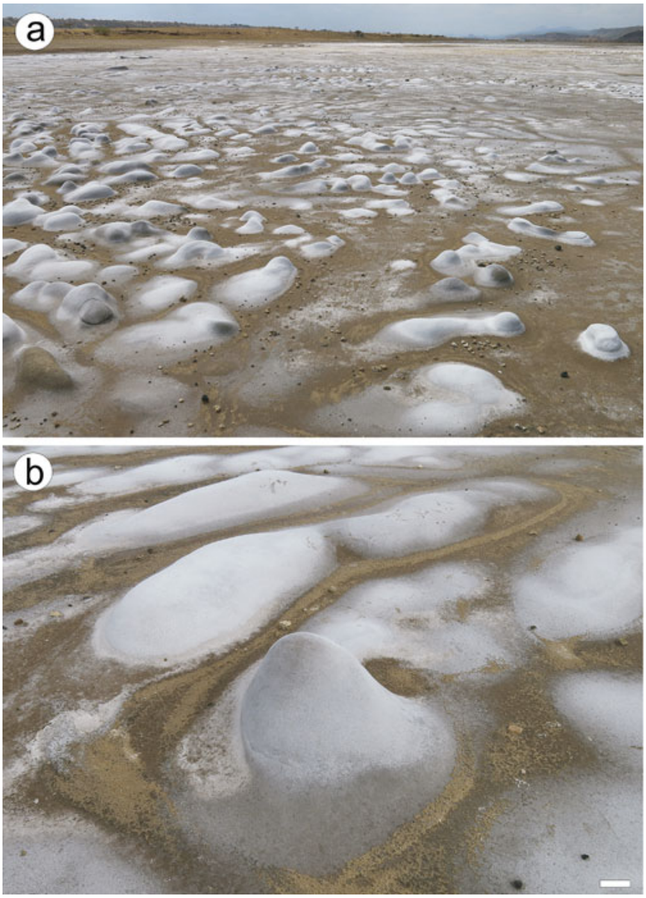

Fig. 11.12 Fossilized flamingo nests, Pleistocene, High Magadi Beds, Lake Magadi, Kenya. (**a**) General view of the nest-bearing surface showing a spectacular biogenic topography (i.e. ichnolandscape); (**b**) Close-up of nests. Scale bar is 10 cm long

mentioned in lacustrine shales (Lindqvist 1994). Burrow systems from long-lived brackish- to freshwater fossil Paleolake Pannon have been attributed a new ichnotaxon, *Egbellichnus jordidegiberti* (Hyžný et al. 2015). These burrows have been interpreted to have been produced by ghost shrimps, indicating that these marine organisms were able to survive for a long time after the closure of the seaway connecting this water body with the central Paratethys sea (Hyžný et al. 2015). Vertebrates are represented by the fish trail *Undichna* (Loewen and de Gibert 1999; Martin et al. 2010) and the fish nest *Piscichnus* (Feibel 1987).

Glacial lakes are dominated by very shallow-tier grazing trails (*Cochlichnus*, *Gordia*, *Helminthoidichnites*) and arthropod trackways (*Glaciichnium*, *Warvichnium*, *Dendroichnites*, *Lusatichnium*), with the branching burrow *Treptichnus* and the conchostracan resting trail *Surculichnus* locally present (Gibbard and Stuart 1974; Gibbard 1977; Gibbard and Dreimanis 1978; Walter and

Suhr 1998; O'Brien and Pietraskek-Mattner 1998; Uchman et al. 2009; Benner et al. 2009; Knecht et al. 2009; Uchman and Kumpulainen 2011). Vertebrates are represented by the fish ichnotaxa *Undichna*, *Broomichnium* and *Piscichnus* (Benner et al. 2009; Uchman and Kumpulainen 2011). The ichnofaunas of Pleistocene glacial lakes are somewhat unusual in that they closely resemble those that are typical of the Paleozoic, displaying a dominance of very shallow-tier ichnotaxa and an underutilized infaunal ecospace. The anachronistic nature of Pleistocene glacial lacustrine ichnofaunas may represent another example of the so-called *déjà vu* effect (Buatois and Mángano 2011b). The dominance of very shallow-tier structures in Pleistocene glacial deposits may reflect very limited burial of organic matter in highly oligotrophic lakes, restricting the habitable zone to a few millimeters below the sediment–water interface.

It should be noted, however, that suppressed bioturbation is not restricted to these types of settings, but also occur in highly productive lakes having oxygenated bottom waters, as evidenced in Lake Turkana (Cohen 1984). In this lake, primary productivity is extremely high toward the lake shore, but phytoplankton populations are markedly less productive offshore. As a result, food content is quite low in offshore lake bottoms and the invertebrate fauna essentially consists of epibenthic detritivores which do not disturb the primary sedimentary fabric. In addition, the lack of sediment mixing results in a redox discontinuity surface very close to the sediment–water interface, further restricting infaunalization (Cohen 1984). This pattern may be regarded as reminiscent of Paleozoic settings displaying limited colonization of infaunal ecospace.

To summarize, a review of the Cenozoic lacustrine trace-fossil record fails to show the appearance of any major evolutionary novelty or innovation from an ichnologic perspective. The spectacular trampled surfaces produced by large mammals that characterize Neogene and modern lake margins were preceded by equally extended and bioturbated surfaces produced by dinosaurs in the Mesozoic. Cenozoic ichnofaunas suggest a continuation of trends that started during the MLR. However, these extensive ichnologic studies need to be linked with examination of body-fossil assemblages from lacustrine and other aquatic environments, particularly during the Paleogene, to more comprehensively document the effects of the MLR. It is notable that, as discussed below, aquatic organisms and ecosystems were better buffered from extinction and ecological reorganization than terrestrial ecosystems during and after the K-Pg crisis (also see Chap. 12). This buffering has multiple sources, including (1), behavioral modifications of lacustrine organisms, including infaunalization, encystment, and planktotrophic larvae that would predispose organisms toward avoiding major environmental vicissitude (Chap. 12); (2), more generalized and less specialized food webs occurring in lakes than for coexisting, surrounding terrestrial communities, at least known for the middle Eocene (Dunne et al. 2014); and (3), the temporally ephemeral nature of lake communities that require considerable dispersal mechanisms for continuity of lake biotas (Cohen 2003), Additionally, the responses to the K-Pg event were variable by the taxonomic group involved, by their occupied habitat, by where they occurred in regional landscapes and in their worldwide distribution, and were variably dampened by the effects of time.

A major effect of the end-Cretaceous global crisis (see Chap. 12) was not only extensive taxonomic extinction and subsequent origination for many non-arthropodan terrestrial lineages, but equally important, trophic pruning of ecosystem structure. On land, the consequences of this event meant the demise of numerous lineages, particularly vertebrates (Archibald and Bryant 1990) and plants (Nichols and Johnson 2008), but this extinction only minimally affected arthropod groups, when evaluated as body-fossil taxa at the family level (Labandeira 2005b). However, when plant–insect interactions are examined at the K-Pg boundary interval, the consequences were important, and hit especially specialized insects such as gallers and leaf miners, while leaving taxa with generalized feeding habits relatively intact (Labandeira et al. 2002; Wilf et al. 2006). In aquatic ecosystems, there was less of an effect (but see Bailey et al. 2005 for possible taphonomic biases). Aquatic insects were minimally affected, at least at the family level (Labandeira 2005b), although there may have been significant changes in food-web structure that persisted well into the Paleogene (Dunne et al. 2014). One important pattern documented for aquatic invertebrates was the differential effects that the K-Pg event had on organisms that inhabited the benthos of water bodies (Twitchett 2006). Detritivorous organisms in or on the sediment were considerably more buffered both from extinction and destruction of their food resources than those trophic networks subsisting on food resources derived from photosynthetic organisms such as algae, diatoms, or aquatic vascular plants (Sheehan and Hansen 1986). This immunity was enhanced for those aquatic invertebrates, such as many detritivorous arthropodan groups, that had planktic immature stages and thus were more able to withstand extinction. For aquatic, especially lentic and lotic–potamic habitats, there was a reduced effect from the end-Cretaceous crisis, particularly for local trophic networks whose dietary resources were not dependent on the herbivory of photosynthetic organisms.

The history of Paleogene insects in aquatic ecosystems is poorly known outside of Central Europe and North America. Most aquatic insect orders have been minimally documented, and many assemblages are woefully deficient in species-level descriptions and revisions. The number of autochthonous lentic taxa is poorly known. Better documented are exceptionally well preserved compression deposits that include the Green River, Messel, Kishenehn, and Menat paleolakes (Nel and Roy 1996; Smith ME et al. 2008b; Greenwalt and Labandeira 2013; Dunne et al. 2014). These well-documented deposits represent only a broad outline of Paleogene aquatic insect history, even though their temporal proximity to the modern fauna should allow easier identification and ecological interpretation of the insect taxa present (Zherikhin and Sinitshenkova 2002). These and almost all Paleogene aquatic taxa are assigned to extant families. The only significant exceptions to this generalization lie within the Odonata, in which the families Sieblosiidae (which disappeared during the Pliocene) and Zacallatidae (Paleogene only) and the subfamilies Dysagrioninae (Paleogene only) and Eodichrominae (Paleogene only) are absent from the modern fauna (Zherikhin and Sinitshenkova 2002). The overwhelming majority of modern lotic and lentic aquatic families extend at least to the Paleogene, and occur in compression and amber deposits. There are many cases of extant aquatic genera extending to the middle Eocene, and apparently living species present in sediments as old as the Eocene (Askevold 1990; Murray 1976; Kluge 1986).

The naiads of ephemeropterans are uncommon in Paleogene compression deposits. Some amber deposits, such as Baltic Amber have provided the overwhelming majority of known mayfly adults. A common, modern epibenthic form, the Baetidae, is virtually absent from Paleogene aquatic faunas. Paleogene odonatan assemblages exhibit minimal similarity with those of today when compared to other aquatic insect lineages (Zherikhin and Sinitshenkova 2002). The relative rarity of Lestidae (spreadwing damselflies), Coenagronidae (narrow-winged damselflies), Corduliidae (emerald dragonflies) and Libellulidae (darner dragonflies) are in stark contrast to the abundance of these lineages in extant aquatic faunas. Naiads are rare in Paleogene aquatic deposits, whereas they are much more common in Neogene faunas, a pattern mirrored by ephemeropterans and attributable to styles of preservation in lacustrine deposits rather than any intrinsic biologic cause.

Paleogene Plecoptera are represented principally by adults in resins and are referable to extant genera. These fossil Plecoptera probably were confined to lotic habitats, consistent with the rarity of their naiad stages in lentic deposits. Apparently, stoneflies do not exhibit any shift in taxonomic proportions between the Paleogene and Neogene (Zherikhin and Sinitshenkova 2002), and display a dominance similar to corixids and notonectids. Aquatic bugs (Hemiptera), unlike paleopterous taxa, are common in Paleogene deposits, where they are often numerically dominant. Similarly, aquatic beetles are diverse in the Paleogene, but are marked by the absence of the algivorous Haliplidae and the overwhelmingly presence of the Hydrophilidae and Dytiscidae, particularly during the Oligocene. Aquatic megalopterans and neuropterans are represented only by extinct genera, and aquatic mecopterans have not been documented.

In contrast to several modern aquatic groups that were uncommon during the Paleogene, the Trichoptera were quite common in local assemblages. All Paleogene taxa have been assigned to modern lineages, many which consist of extant genera (Sukatcheva 1982; Wichard and Weitschat 1996). However, there is a significant difference in family-level dominance between the Paleogene and Neogene assemblages, and in compression versus resin deposits, with the Oligocene being a transitional interval. During the Paleogene, the currently dominant families, the Hydropsychidae (net-spinning caddisflies), Leptoceridae, and Limnephilidae (northern caddisflies) are either rare or absent. Similarly, the diversity of caddisfly cases are rare when compared to the Cretaceous or present-day levels (Zherikhin and Sinitshenkova 2002). Some of these taxa may have colonized floating algal mats (Ponomarenko 1996) or dwelled amid the floating leaves, as appears to be the case for fossils from earliest middle Eocene Paleolake Messel (Lutz 1991).

The Paleogene aquatic dipteran fauna is particularly depauperate in culicids, chironomine chironomids (nonbiting midges), and higher brachyceran taxa. However, the abundance of the enigmatic botfly-like larvae of *Lithohypoderma* continues to elude taxonomic placement and ecologic understanding (Stokes 1978; Sinitshenkova 2002). Culicids (mosquitoes) and brachyceran taxa became more abundant during the Oligocene. Toward the Oligocene–Miocene boundary, the aquatic fauna attained an even more modern cast than in the previously described Paleogene assemblages.

Paleogene aquatic angiosperms continued to be dominant in ponds and lakes, forming diverse assemblages and displaying increased provincialism (Martín-Closas 2003). Aquatic ferns also exhibited further diversification (Schneider et al. 2004), whereas taxonomic turnover within the Characeae took place during the Paleogene (Martín-Closas 2003). Further extinctions and replacements occurred within the charophytes later in the Cenozoic. Aquatic bryophytes became common in shallow lakes and swamps (Mai 1995). The most significant changes, however, are those experienced by lacustrine phytoplankton, essentially by expansion of freshwater diatoms and chrysophytes during the Eocene (Martín-Closas 2003; Wolfe and Edlund 2005; Sims et al. 2006; Leliaert et al. 2011). During the Neogene, diatoms clearly dominated over the Chlorococcales (Martín-Closas 2003; Sims et al. 2006). The overall ecologic impact of the colonization of freshwater bodies by diatoms cannot be overemphasized. In particular, diatoms typically exert a significant effect on the biogeochemical cycling of silica, promote a diversion of other nutrients into other trophic pathways and increase overall lacustrine productivity (Cohen 2003).

One of the most highly investigated Cenozoic lacustrine deposits is the series of four major paleolake basins that form the Green River Formation in the Western Interior of the United States. The Green River Formation is dated from ca. 54.0–43.5 Ma (Smith ME et al. 2008b), and consists of a mixture of open lacustrine, lake-margin lacustrine, shallow playa, carbonate mudflat, fluvial, deltaic and alluvial deposits (Ferber and Wells 1995; Chetel and Carroll 2010; Aswasereelert et al. 2013). The Green River Formation is assigned to Cenozoic Lake Assemblage Type 8 (Zherikhin and Sinitshenkova 2002), dominated by brachyceran fly larvae with few, if any, other aquatic insects (Zherikhin and Sinitshenkova 2002). Green River fossils overwhelmingly preserve land-based organisms, especially plants, insects, and vertebrates, to the near exclusion of autochthonous aquatic organisms (Wilson 1978), which likely was taphonomically modulated by depositional biases favoring terrestrial taxa (Smith, 2000, 2008). The insect fauna is very diverse, consisting of about 26 of the ca. 35 modern recognized orders for the Piceance Creek Basin of the Green River Formation (Pribyl et al. 1996). The apparently under-represented aquatic insect fauna is autochthonous, but only consists of several major lineages of mostly nematocerous Diptera, principally tipulids, cylindrotomids, culicids, chironomids, and the occasional aquatic beetle. In spite of the extensive geographic coverage and numerous fossiliferous strata, there is only minor representation of lotic and lentic fossils from the Green River Formation. Nevertheless, three families of dragonflies are represented (Wilson 1978; Petrulevičius et al. 2007), two families of Hemiptera, two families of beetles, four families of nematocerous Diptera and the enigmatic *Lithohypoderma* “botfly” (Pribyl et al. 1996; Sinitshenkova 2002). The Trichoptera includes the Hydropsychidae, Hydroptilidae (micro caddisflies), Limnephilidae, and Sericostomatidae. The particular reason for such an under-representation of the lentic and lotic fauna, especially when adjacent terrestrial insects are exceedingly abundant by comparison, is likely attributable to the role of size in the formation of live versus death assemblages of insects. In the Green River biota, death assemblages that become incorporated in the fossil record are smaller sized and more robust than live equivalents (Smith 2000). Although the role of size and robustness applies to beetles (Smith 2000), it is unclear if such a relationship also applies to softer-bodied, more gracile insects that are often disarticulated prior to sediment burial.

The taxonomic composition and ecologic structure of Neogene paleolakes is very similar to that of modern lakes (Zherikhin and Sinitshenkova 2002). Many modern aquatic species occur throughout the Neogene. A few extinct insect clades are known, such as the subfamily Electrobatinae of the Gerridae and the coral bug species *Halovelia electrodominica*, both from early Miocene Dominican Amber; the coeval dytiscid genus *Palaeogyrinus* from Germany; several extinct aquatic taxa of the Megaloptera and Neuroptera, including the species *Sialis strausi* from the Pliocene of Germany; and several new caddisfly case morphotypes that are difficult to attribute to potential modern or extinct genera (Illies 1967; Galewski and Glazek 1997; Sukatcheva 1982; Anderson 1998). Throughout the Miocene, these occurrences do not represent any significant change in aquatic insect community characterization, a conclusion buttressed by the similarity of overall lake ecologic structure between the middle Eocene and the present (Dunne et al. 2014), indicated in Fig. 11.13.

There is evidence for an increase in lentic habitats and their biotas at the beginning of the Neogene. This extension is indicated by greater submergent and emergent angiosperm vegetation that increased habitat structural complexity, resulting in an expansion of herbivory, greater constancy of O_2 levels and nutrient cycle stability (Zherikhin

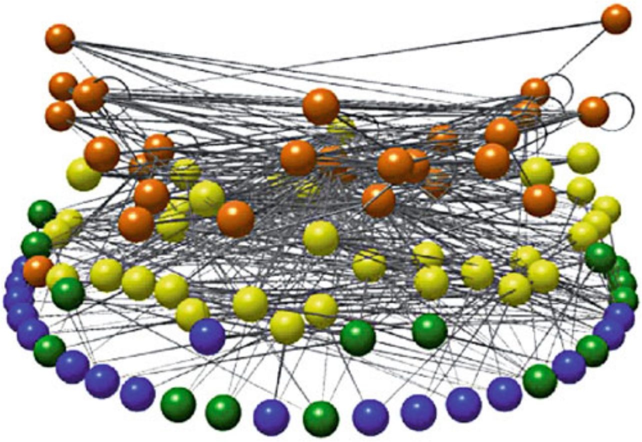

Fig. 11.13 Visualization of the middle Eocene (48 Ma) food web of Paleolake Messel, in central-west Germany, representing a post MLR lake. Spheres designate trophic taxa and lines represent feeding links. A trophic taxon is a species or group of species (in the case of microorganisms) that have links to organisms that consume it and to other organisms that it consumes. Plants have links only to their consumers. Looped links refer to cannibalism. The vertical axis corresponds to short-weighted trophic level, with autotrophic taxa and detritus at the bottom. The colors of nodes indicate the taxonomic assignment of species: green = plants, algae and diatoms; blue = bacteria, fungi and detritus; yellow = invertebrates; orange = vertebrates. This image was produced with Network 3D software (Williams 2010), and reprinted with permission from the Royal Society

1978; Kalugina 1980). Nevertheless, special sedimentary environments occupying spatially small areas could have hosted aquatic communities of distinctive taxonomic composition and ecologic structure. Examples of these biotic microcosms include small bodies of water associated with sinter structures, ponds in asphaltum depressions, karst sinkholes, impact craters, and pits created by subsurface diatreme explosions. Such deposits are typically spatiotemporally ephemeral and constitute a very minor part of the lacustrine record that is represented preferentially toward the recent.

11.7 Discussion

There are four issues about the MLR that necessitate further discussion. The first issue is whether the MLR is indirectly or directly connected to other obvious, major biotic events during the mid Mesozoic, such as the Mesozoic marine, parasitoid, angiosperm, and Cretaceous terrestrial revolutions. The second issue is to what extent did the MLR involve not only a change in the diversity and abundances of participating fossil groups, but also their effect on the sedimentological record through the increased variety of ichnotaxa and bioturbation intensities recorded from well sampled sections. A third issue is how modern lacustrine trophic webs were established. These trophic webs are recorded in a well-examined Paleogene lake deposit, but also should be present in earlier, mid-Mesozoic food webs. Finally, what is the role of behavioral convergence in shaping the aquatic marine and continental trace fossil records, and to what extent should ichnotaxonomic nomenclature be applied across the marine/continental divide to very similar trace fossils that involve convergent morphologies (and presumably behaviors).

11.7.1 Possible Connections to Other Mesozoic, Biotal Revolutions

Other than the MLR, four other, major biotic revolutions occurred during the mid to late Mesozoic: the Mesozoic marine revolution in the marine realm and the parasitoid, angiosperm and Cretaceous terrestrial revolutions in the continental realm. These mid-Mesozoic, global ecologic shifts may have had an effect on the MLR that may be relevant to the development of lacustrine food webs throughout the later Mesozoic. The possible connections among these five prolonged events may shed light on the shift of detritivore- to herbivore dominated ecosystems in lacustrine and other freshwater habitats during the mid Mesozoic.

One of the aspects involved in the Mesozoic marine revolution (see Chap. 9) was the notable increase in mechanical sturdiness and increased robustness of other structural features that promoted the resistance of shells, principally gastropods, to crushing by predators (Vermeij 1977; Stanley 1977). Major structural transformations favored durable shell architecture of molluscan prey, and involved new modes by mostly arthropods and teleost predators of pursuing, capturing, and overcoming the mechanical defenses of their prey. Another aspect of the Mesozoic marine revolution was intensification of marine herbivory, such as grazing on algae at relatively shallow and subsurface depths. Added to the expansion of durophagy and grazing pressure was increased predation in benthic communities that led to infaunalization of many former epibenthic groups, as well as a significant reduction of the sessile life habit (Stanley 2008). The major consequence of these innovations has been the relegation of their certain life forms to extinction or to refugial habitats (Oji 1996), and the occupation of their adaptive zones by competitively superior, new, predatory groups (Vermeij 1977; Stanley 1977). This worldwide marine reorganization has been linked to continental breakup, widening of latitudinal belts, and the emergence of angiosperms on land (Vermeij 1977).

The parasitoid revolution is based on an observation that the first appearances of several major clades of parasitoid insect clades occur primarily during the mid Jurassic (Labandeira 2002). Parasitoids are a distinctive type of carnivore in which a small, invading organism attaches to or lives on or in an animal and slowly feeds on internal tissues and organs of their relatively long-lived but still alive host. The much smaller parasitoid feeds on host such that the most vital organs are consumed immediately before the host dies, followed by its emergence from the host as an adult parasitoid (Vinson and Barbosa 1987). Parasites, by contrast, such as mosquitoes do not kill the host, but use host tissues such as blood to feed on. For insects, the actively feeding parasitoid stage is always a holometabolous larva, overwhelmingly a parasitoid wasp, and less frequently a brachyceran fly. Parasitoids may feed on their hosts internally (endoparasitoids) or externally (ectoparasitoids) and attack arthropod hosts, such as myriapods, arachnids, especially insects, and some vertebrates (Godfray 1994). The earliest appearance of the parasitoid guild was the mid Early Jurassic, during which several clades of parasitoid wasps appear. This was followed and supplemented by more modest brachyceran dipteran diversification and the massive radiation of several parasitoid superfamilies during the Late Jurassic, and continued with the addition of occasional neuropteran, beetle, and lepidopteran parasitoid lineages into the Paleogene (Labandeira 2002).

A major consequence of the parasitoid revolution was the increased complexity of food webs by insertion of a significant more efficient mode of carnivory. This greater efficiency resulted from the targeting of particular species of prey by a host-specific parasitoid using specific chemical, behavioral, visual, and other cues emanating from prey. With the proliferation of the host-specialist, parasitoid feeding guild that originated during the mid Mesozoic, carnivory became considerably more targeted than was the case for food webs earlier in time based solely on diffuse generalist predation patterns (Labandeira 2002). This ecological shift resulted in consumer-driven, top–down regulation of herbivores, rather than bottom–up, resource-driven regulation, based on modern food-web studies (Dunne et al. 2002). In modern ecosystems, parasitoid loads on insect herbivores are elevated (Memmott and Godfray 1993), and are much more efficient at assimilating prey biomass into consumer biomass than either predators such as dragonflies or parasites such as fleas or lice (Eggleton and Belshaw 1992). In lacustrine systems, unionacean and mytilacean bivalves are dispersed in their larval stages as ectoparasites on fish; some copepod and isopod crustaceans are also parasitic on fish, as well as certain flatworms and trematodes (Cohen 2003). One of the major effects of the parasitoid revolution on lake biotas was to further separate immature aquatic stages of insects from their adult terrestrial counterparts. Additional work needs to be done to properly address the importance of parasitoids in lacustrine food webs.

The angiosperm revolution consists of the early, major diversification interval of flowering plants, ranging during the mid Cretaceous from 125 to 90 million years ago (Crane et al 1995). The angiosperm revolution had a major effect on terrestrial ecosystem structure (Wing and Boucher 1998). The emergence of numerous clades of angiosperms over a ca. 35 million-year interval resulted in a major replacement of fern- and gymnosperm dominated floras by angiosperms in most habitats globally (Crane 1987), including aquatic settings (Wing and Boucher 1998).

The Cretaceous terrestrial revolution is directly connected to and may be a consequence of the angiosperm revolution because it encompasses not only the evolutionary radiation of land-dwelling organisms, but involves the replacement of ferns and gymnosperms by angiosperms (Lloyd et al. 2008). Therefore, the comments outlined for the angiosperm revolution are prefatory to the Cretaceous terrestrial revolution. Together with the rapid expansion of flowering plants, the Cretaceous terrestrial revolution includes the diversification of herbivorous and social insects (see Chap. 13), squamates, birds, and mammals (Lloyd et al. 2008). However, these authors (Lloyd et al. 2008) questioned the notion that dinosaur evolution was driven directly by angiosperm diversification. From an ichnologic standpoint, the appearance of trampled surfaces is a direct consequence of the expansion of dinosaur faunas that significantly altered lake-margin landscapes.

Both the Mesozoic marine revolution and the parasitoid revolution provided a greater efficiency in the conversion of prey biomass into consumer biomass. The angiosperm and Cretaceous terrestrial revolutions expanded the amount of photosynthetic biomass created by a new group of primary producers that had a major global impact. The MLR was characterized by increased infaunalization and a major trophic shift from detritivore-based to herbivore-based foodwebs in lacustrine and other terrestrial aquatic ecosystems. However, the detritivore to herbivore shift occurred much earlier in terrestrial ecosystems than in aquatic ones (Vermeij and Lindberg 2000; Miller and Labandeira 2002) – a shift that was already noticeable during the Permian (Labandeira 2006). This is not surprising, as in the continental realm, aquatic ecosystems always have been lagging behind terrestrial ecosystems in other features such as species diversity, trophic relationships, and food-web development (Vermeij and Lindberg 2000; Sinitshenkova 2002). Nevertheless, it is unclear whether there are satisfactory explanations invoking cause-and-effect links among any of these four major revolutions to lacustrine ecosystems.

11.7.2 Secular Changes in Global Ichnodiversity and Bioturbation

A systematic review of the ichnologic record indicates that the MLR is expressed not only by body-fossil data. Ichnologic evidence demonstrates that colonization of freshwater habitats has been a protracted process (Buatois and Mángano 1993a;

Buatois et al. 1998a), with the MLR representing a pivotal point (Cohen 2003) (Table 11.2). Freshwater colonization may have been delayed due to the need to develop complex osmoregulatory systems and innovative styles of reproduction and dispersal (Miller and Labandeira 2002).

Unlocking the evolutionary significance of the lacustrine trace fossil record requires integration of several conceptual and methodological tools. Patterns of change in global ichnodiversity may be misleading, and should not be analyzed in isolation (Buatois and Mángano 2013; see Chap. 16). Mesozoic global invertebrate ichnodiversity in lacustrine environments does not show any significant increase with respect to late Paleozoic levels (Buatois and Mángano 1993a; Buatois et al. 1998a), in contrast to what may have been expected by diversity curves based on body fossils (Labandeira 2005b). Indeed, whereas global ichnodiversity levels for fully lacustrine environments have remained more or less constant since the Carboniferous, global ichnodiversity of lake-margin settings is actually higher in the late Paleozoic than in the Mesozoic. However, it often has been suggested that the Permian ichnodiversity peak reflects at least in part splitting tendencies in arthropod trackway taxonomy (see discussion in Buatois et al. 1998a and Chap. 6). Also, the fact that diversity trajectories for body and trace fossils are markedly dissimilar is not unexpected. The three groups that diversified the most – aquatic insects, aquatic macrophytes, and teleosts – are unevenly represented in the ichnologic record. Aquatic insects are thought to have been widespread tracemakers; some fish (e.g. cichlids) may contribute locally to sediment disturbance (Feibel 1987; Martin et al. 2010; Abbate et al. 2012); and aquatic macrophytes are represented by root structures but technically do not contribute to ichnodiversity. (No formal ichnotaxonomic names are given to root trace fossils.) In addition, it long has been recognized that equating ichnodiversity with biological diversity is fundamentally misleading, and one-to-one correspondences between ichnotaxa and biotaxa is simply not possible (Bromley 1996). This is particularly true for very simple structures (Buatois and Mángano 2011a), which tend to be dominant in lacustrine settings.

However, an evaluation of changes of ichnodiversity that parallel changes in intensity and depth of bioturbation may be illuminating. In both lake-margin and fully lacustrine deposits, an increase in extent and depth of bioturbation long has been recognized (Miller 1984; Buatois and Mángano 1993a; Buatois et al. 1996, 1998a; Miller and Labandeira 2002; Miller et al. 2002) (Fig. 11.14). In lake-margin settings, trace fossils of the *Scoyenia* ichnoguild became more abundant, leading to increased sediment mixing since the Middle Triassic (Buatois et al. 1998a). In addition, a stationary deep crayfish infauna , referred to as the *Camborygma* ichnoguild, was established by the Triassic, further contributing to destruction of primary sedimentary fabric. This is in sharp contrast with the situation of Paleozoic lake-margin deposits, which overwhelmingly are dominated by very shallow-tier trace fossils, mostly arthropod trackways (Buatois and Mángano 1993a; Buatois et al. 1998a; see Chap. 6). Arthropod trackways, although locally present in Mesozoic lake-margin deposits, are never dominant components, and they essentially disappeared from the Cenozoic lacustrine trace-fossil record with the exception of glacial lakes, where they tend to occur in distal facies rather than in lake-margin deposits (Uchman et al. 2009). Seilacher (2008) underscored the importance of bioglue for trackway preservation,

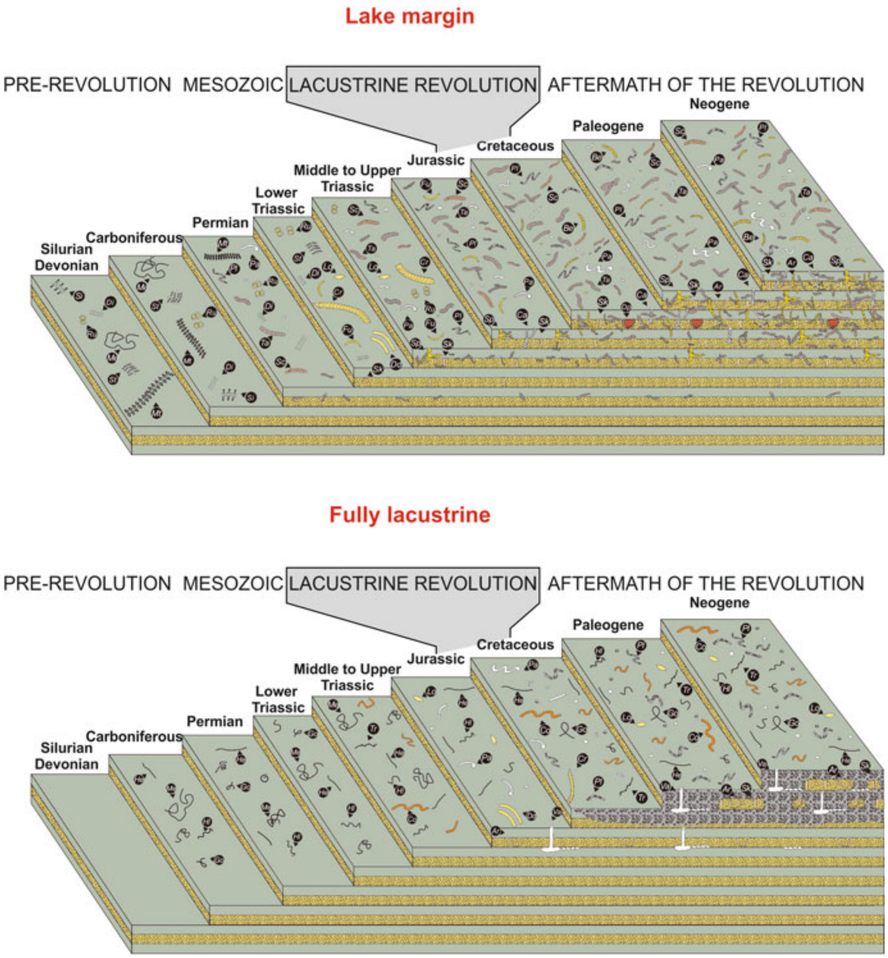

Fig. 11.14 Secular changes in bioturbation in lake-margin and fully subaqueous lacustrine deposits. Note progressive colonization of the infaunal ecospace through time

suggesting that the scarcity of trackways in post-Paleozoic lake-margin deposits may have resulted from the appearance of a bioturbating meiofauna, therefore precluding the formation of coherent biofilms. In any case, it is clear that there is a negative correlation between diversity of shallow-tier trace fossils and intensity and depth of bioturbation. This trend also has been noted for tidal flats, which display high diversity during the late Paleozoic due to a richness of shallow-tier structures and decreased ichnodiversity during the Mesozoic–Cenozoic, with ichnofaunas characterized by deeper-tier structures (Mángano et al. 2002; Mángano and Buatois 2015). This decrease in tidal-flat global ichnodiversity is arguably a taphonomic product resulting from increased colonization of infaunal ecospace (Mángano et al. 2002; Buatois and Mángano 2011a; Mángano and Buatois 2015). A similar argument can be posited to explain the post-Paleozoic decrease in global ichnodiversity in lake-margin deposits.

In fully lacustrine settings, a similar increase in intensity and depth of bioturbation is apparent throughout the Mesozoic, although changes seem to have been slightly more gradual, lagging behind those in lake-margin environments. During the Middle to Late Triassic, assemblages dominated by very shallow-tier grazing trails, not unlike those of the late Paleozoic, were still common (Metz 1995, 1996, 2000; Melchor et al. 2003; Melchor 2004). However, the simultaneous appearance of penetrative trace fossils is evidenced by systems of irregularly branched burrows, most likely produced by oligochaetes or insect larvae (Voigt and Hoppe 2010). The high density of these burrows contributed locally to disruption of the primary fabric, generating patches of intense bioturbation in lacustrine mudstones. Branching burrows occur in Lower Jurassic turbidites as well, reflecting the establishment of the *Vagorichnus* ichnoguild, which represents the activity of a mobile, mid-tier, deposit-feeding infauna (Buatois et al. 1995, 1996). These mid-tier trace fossils persisted in Cenozoic lacustrine deposits (Uchman et al. 2007). Interestingly, although Lower Jurassic turbidites contain many ichnotaxa (e.g. *Cochlichnus*, *Helminthopsis*) common in older deposits, these are more robust and produced infaunally, reflecting penetration into the sediment and unlike those of the late Paleozoic. In the example of the *Vagorichnus*-bearing deposits, the increase in maximum bioturbation depth is not associated with an increase in bioturbation intensity. The decoupling of bioturbation depth and intensity of bioturbation results from the observation that these burrow systems were emplaced at lithologic interfaces without causing major disturbance of the primary sedimentary fabric (Buatois et al. 1995, 1996).

This pattern contrasts with Cretaceous ichnofaunas, which include pervasive mottlings reflecting establishment of a shallow-tier deposit-feeding infauna, referred to as the *Planolites* ichnoguild. The high density of these structures caused major disruption of lacustrine sedimentary fabrics (Buatois and Mángano 1998; Buatois et al. 1998a). These observations may suggest that the establishment of the mixed layer in these settings is a result of the MLR. Although further work needs to be done to detect the exact timing of formation of the mixed layer, sparse data suggest that this sediment zone was already incipiently developed in lake bottoms by the Middle to Late Triassic and well established by the beginning of the Cretaceous. As is the case of lake-margin deposits, the appearance of these active bioturbators was detrimental for the preservation of very shallow-tier structures. In any case, biogenic homogenization of the lacustrine bottom sediments is not a universal phenomenon, as indicated by the dominance of very shallow-tier trace fossils, in pristinely preserved, sedimentary fabrics of other Lower Cretaceous lacustrine deposits (de Gibert et al. 2000, 2016; Buatois et al. 2000a), as well as in modern glaciolacustrine varves (Gibbard and Stuart 1974; Uchman et al. 2009). Studies in other modern lakes, such as the Great Lakes in North America, indicate up to 10 cm of deep reworking by insects, oligochaetes, bivalves, and amphipods (McCall and Tevesz 1982; Miller and Labandeira 2002), suggesting a well-established mixed layer.

The pattern of increased infaunalization during the MLR is empirically well supported, but the underlying causes remain more speculative. As a first approach, the increase in sediment penetration and disruption during the MLR is connected with the expansion and diversification of certain groups of benthic aquatic organisms, most likely dipterans (such as chironomids), which together with oligochaetes, are among the key bioturbators in modern lacustrine settings (McCall and Tevesz 1982; Duck and McManus 1984; Wootton 1988; Evenhuis 1994; Buatois et al. 1998a). At a deeper explanatory level, one may invoke protection from environmental disturbance, escape from predators and increased rates of buried organics as potential causes of infaunalization. It long has been known that burrowing is a key strategy intended to minimize environmental stress, such as salinity variations and sediment disturbance by currents or waves (see Buatois and Mángano 2011a for discussion). However, environmental disturbance may only work as an explanation for infaunalization at a local scale. In a situation such as the MLR, infaunalization occurred globally and no overarching disturbance factor can be associated with this macroevolutionary trait, therefore precluding protection from environmental disturbance as a likely causal factor of infaunalization. In contrast, the link between increased predation pressure and infaunalization seems to be a more robust explanation because the former is considered a driving force in macroevolution, with the infaunal ecospace serving as refugium for predation. As discussed above, the coincidence between increased predation and infaunalization during the MLR is consistent with a causal link. The possibility that infaunalization can be linked to exploitation of increasing amounts of organic matter buried within the sediment cannot be disregarded. Higher quantities of food supply may have resulted from increased eutrophication in lacustrine systems combined with increased delivery of terrestrially derived and aquatic organic matter resulting from macrophyte diversification. Indeed, nutrient availability may be regarded as an overarching factor controlling lacustrine ecospace utilization in deep time (Cohen 2003). The ultraoligotrophic conditions predominant during the early Paleozoic were most likely the key limiting factor preventing colonization of lacustrine bottoms, a situation that started to change during the late Paleozoic, albeit with colonization limited to a narrow inhabitable zone close to the sediment–water interface (Buatois and Mángano 1993a; Buatois et al. 1998a). Finally, it may be argued that invoking complex geobiologic feedbacks between bioturbation and a wide range of abiotic to biotic factors (e.g. Mángano and Buatois 2014) probably is more realistic than strict causal linkage. In the case of the MLR, the timing of events suggests that the interplay of increased predation pressures and food availability may have been the casual drivers forces in lacustrine infaunalization.

To summarize, whereas the Paleozoic is characterized by an increase in global ichnodiversity as a result of the progressive colonization of continental environments (Buatois and Mángano 1993a; Buatois et al. 1998a; see Chap. 6), the ichnologic expression of the MLR is one of increased colonization of infaunal ecospace (Table 11.2). This is reflected by an increase in both degree and depth of bioturbation, although these increases occurred first in lake margins and subsequently in fully lacustrine settings. In addition, the increased intensity of bioturbation lagged behind greater penetration in burrowing depth in both settings. For further evaluation of the evolutionary significance of the MLR, we turn now our attention to trophic webs.

11.7.3 The Establishment of Modern Lacustrine Trophic Webs

Biotic interactions are of fundamental importance to understand ecosystem structure and function in lakes. In particular, deciphering food webs, the complex networks among predators, herbivores, autotrophs, and detritus/deposit feeders is a central issue in reconstructing the biotic dynamics of lakes. Experimental studies show that lacustrine food webs reflect an interplay of both bottom–up and top–down selective pressures. Bottom–up processes involve food/nutrient resource availability and competition for those resources whereas top–down processes involve trophic cascades in which predation and selective consumption are the main regulators of community structure (Carpenter and Kitchell 1993). Various groups of benthic invertebrates, including crustaceans, mollusks, annelids, and larval insects play important roles in mediating energy flow, nutrient cycling, and the ingestion of organic and inorganic detritus and fecal production (reflected to some extent by bioturbation) that is a central component of lacustrine food webs (Charbonneau and Hare 1998; Covich et al. 1999; Voigt and Hoppe 2010). However, from an energetic point of view, the importance of planktonic and nektonic components of the lacustrine food web is probably much greater (Schweitzer et al. 2007).

Accordingly, exploring the timing of the establishment of the modern lacustrine food web and its potential connection with the MLR may yield insights into the evolutionary history of lake ecosystems. There is little known about Early Triassic lakes or their fossils. Late Middle–early Late Triassic Paleolake Madygen, discussed earlier (Voigt et al. 2006), included organisms representing at least five trophic levels (Fig. 11.15). Phytoplankton (of which there is no fossil evidence as yet) and macrophytes (e.g., *Ricciopsis*, *Neocalamites*, and some lycopsids) were presumably the major primary producers. An important external source of food must have been dead

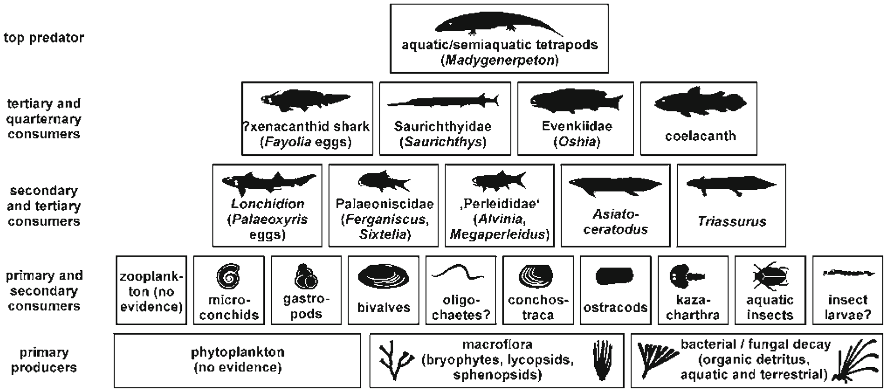

Fig 11.15 Ecosystem of the Madygen Formation of Kyrgyzstan. Trophic levels and their respective constituents as proposed for the Triassic Madygen lake environment. Note the absence of macro herbivores After Voigt et al. (2006, 2016)

organic matter (e.g., plants, insects, tetrapods) transported from the land into lakes. Zooplankton (of which there is no fossil evidence as yet), microconchids, gastropods, bivalves, conchostracans, ostracods, kazakharthrans, certain insects (schizophorid beetles), and wormlike aquatic invertebrates such as oligochaetes or particular insect larvae, based on indirect evidence from trace fossils, are interpreted as primary consumers. These organisms in turn served as food for a variety of fishes including actinopterygians (Palaeoniscidae, "Perleididae"), dipnoans (*Asiatoceratodus*), and durophagous sharks (*Lonchidion*). Four large carnivorous fishes – *Saurichthys*, *Oshia*, a currently unknown xenacanthid (suggested by *Fayolia*-type egg capsules), and coelacanths – can be considered tertiary consumers. The semi-aquatic reptiliomorph *Madygenerpton* may have been the apex predator of Paleolake Madygen. This system shows clear evolutionary innovations when compared to Paleozoic lakes, as it represents among the earliest known record of a well-developed, deep lacustrine infauna (Voigt and Hoppe 2010), and documents a quantitatively important pattern of macrophytic colonization of the shoreline (Moisan et al. 2012a).

Although energy-flow diagrams have not been constructed for a Late Triassic lake, coarse-grained trophic webs have been estimated for the biota of a hypotrophic (low primary production, high O_2) Middle Jurassic lake (Fig. 11.6; Sinitshenkova and Zherikhin 1996), and for a pseudoligotrophic (high O_2 but with an active herbivore guild) Early Cretaceous lake (Fig. 11.10; Zherikhin et al. 1999). These data indicate that there was a major shift in lacustrine productivity and biotal complexity later in the Mesozoic (Table 11.1). However, it appears that these changes likely began during the Late Triassic. The trophic structure of the Jurassic *Mesoleuctra–Mesoneta* Assemblage (Sinitshenkova and Zherikhin 1996) occurred throughout the warm temperate region of Siberia and other Eurasian and perhaps Gondwanan Jurassic localities (Sinitshenkova 2002). In the lowlands at temperate latitudes, particularly in Eurasia, these shallow, hypotrophic (type B) lakes of the Jurassic consisted of depauperate lentic and lotic faunas that allowed high O_2 levels to accumulate, and with a near exclusive trophic emphasis on detritivory (Fig. 11.6). The high abundance of O_2 throughout these hypotrophic lakes, and particularly the benthos, is attributable to the absence of respiring organisms to sufficiently take up the O_2 that was being produced by autotrophic microorganisms (Sinitshenkova and Zherikhin 1996). In addition, Sinitshenkova and Zherikhin (1996) state that these lakes were littered with incoming ginkgoalean and czekanoskialean plant detritus that exerted a negative control on productivity of the lake by having an antimicrobial effect on decomposers, judging by the negative effect that modern *Ginkgo biloba* litter has on modern lake productivity (Samylina 1988). Consequently, productivity in these lakes had two, related features: there was poor development of a detritivore base, in part likely hindered by the dominant terrestrial vegetation of the time that favored buildups of O_2. In addition, there was absence of large, especially vascular, hydric plants that would allow herbivores to expand herbivory, as seen in later Cretaceous lakes (Fig. 11.10). The subsequent changeover is notable, particularly establishment of a guild of grazing herbivorous organisms, present in pseudoligotrophic Paleolake Baissa, a type C lake but also with high O_2 levels, is notable. This shift during the mid Early Cretaceous from a detritivore-based to herbivore-driven food web, occurred in the switch from Type A and B to Type C to E lakes, documented in Eurasia, and is probably the single most important event associated with the MLR. The ecologic structure of Early Cretaceous Paleolake Baissa differs significantly from that of its predecessor lacustrine biotas during the Jurassic (Table 11.1).

The basic trophic structure of Cretaceous Paleolake Baissa was a highly productive, pseudo-oligotrophic lake in which there were relatively low levels of dissolved nutrients supporting an abundant and diverse standing crop of green plants, especially algae. Paleolake Baissa apparently is a lake type without a clear modern analog. The algae was limited by high consumption levels, but promoted a complex, herbivore-based food web within an ecosystem of de-emphasized detritivore food chains (Sinitshenkova 2002). The elevated O_2 levels were sufficiently depressed to allow a diverse, detritivorous insect fauna (Zherikhin et al. 1999) at greater depths in the water column, the hypolimnion. At intermediate depths, in the mesolimnion, but below the surface-water layer of the epilimnion, there was an herbivore community of grazing and algivorous gastropods and insects, including case-bearing caddisflies, which were supported by abundant and diverse benthic, planktonic, and floating algae (Sinitshenkova 2002). Paleolake Baissa was an early lake ecosystem where aquatic invertebrate herbivory played a significant trophic role. Other coeval deposits of similar origin are the lacustrine beds of the Yixian Formation in China (Barrett 2000; Pan et al. 2011) and the Las Hoyas wetland deposits of Spain (Buscalioni et al. 2016 and references therein).

In particular, the Las Hoyas fossil site, which is now interpreted as a freshwater carbonatic, lentic wetland, has been analyzed recently from a trophic-web approach (Buscalioni et al. 2016). According to this study, hydrophytic vegetation is dominated by charophytes and aquatic angiosperms. The large mass of hydrophytic plants allowed the presence of abundant grazers, such as ostracods, gastropods, spelaeogryphaceans, and aquatic insects, pointing to the importance of herbivory in this trophic web, as is the case of Paleolake Baissa. Various worm-like organisms have been regarded as feeding on phytoplankton and zooplankton, whereas unionid bivalves were suspension feeders and crayfish are considered omnivorous scavengers. Some large aquatic insects may have preyed on fish larvae and medium-sized fish consumed various aquatic insects. Buscalioni et al. (2016) also emphasized the importance of insects and fish in lake productivity, which is consistent with data from modern wetlands.

During the Cretaceous, physical and chemical lake conditions exhibit a major shift favoring development of certain lake types based on a variety of physiochemical conditions. These features were increased aridity, greater topography, more unstable and variable lake levels, enhanced variability in annual temperature, greater water-column stratification, and higher water turbidity. Chemical indicators show elevated nutrient levels, a tendency toward alkaline over acidic water *p*H's, and more variable and lower dissolved oxygen levels. These physiochemical shifts provided an opportune environment for biotal changes, such as less allochthonous plant detritus as input, much greater turnover rates, higher microbial activity, and considerably higher algal production, but anomalously, lower macrophyte production. For food-web development, there was a shift from detritivore to herbivore processing of primary productivity (via more intensive levels of herbivory), greater complexity of food webs, and an emphasis from K-selected to r-selected evolutionary strategies. Among benthic insects there was a trophic shift from shredders and scrapers to filter-feeding and live-plant ingesters as the dominant feeding types (Sinitshenkova and Zherikhin 1996).

Finally, a recent examination of the 48 million-year-old deposit of Paleolake Messel, near Darmstadt, in central Germany, produced an exhaustive food-web analysis that was made for 94, well-documented organisms, including amphibious taxa, that constituted the lake portion (Fig. 11.13) of the total food web (Dunne et al. 2014). This study provides valuable information on food webs in the aftermath of the MLR. The Messel lacustrine web was constructed by using highly-resolved, well-documented data of feeding relationships among all taxa. The lacustrine food-web data from Messel indicate an ecologic structure very similar to modern lake webs, and notably, a stability of trophic relationships that were likely in place shortly after the K-Pg extinction (Dunne et al. 2014). However, the fact that Chlorococcales dominated over diatoms in Paleolake Messel represents a departure from the situation in modern lakes.

11.7.4 Behavioral Convergence Between Marine and Continental Benthic Fauna

A comparison between marine and lacustrine ichnofaunas suggests that use of freshwater infaunal ecospace may have been less complete than in marine environments (Miller and Labandeira 2002). In addition, levels of ichnodiversity and complexity of biogenic structures are significantly lower in lakes than in marine settings (Buatois and Mángano 1998). Evaluation of the extent and limitations of behavioral convergence on both sides of the salinity barrier may help to understand evolutionary constraints on the lake colonization process.

Ichnotaxonomic problems undoubtedly prevented an adequate recognition of the similarities and differences between the marine and continental realms. There are two sides to this problem: uncritical use of marine ichnotaxa in continental settings and unsupported erection of new ichnotaxa apparently exclusive to continental settings. Whereas the former has contributed to the overemphasis of behavioral convergence, the latter promoted its lack of appreciation. This is essentially an issue with freshwater, rather than terrestrial trace fossils. The vast majority of the latter (e.g. *Coprinisphaera*, *Termitichnus*, *Vondrichnus*, *Celliforma*, *Eatonichnus*, *Castrichnus, Quirogaichnus*) are exclusively found in paleosols, and their ichnotaxonomic intricacies have been clarified by extremely detailed and solid work (e.g. Genise 2000, 2004; Laza 2006).

Freshwater trace fossils tend to be characterized by relatively simple morphologies, typically including facies-crossing ichnotaxa that occur in marine environments (e.g. *Gordia*, *Helminthoidichnites*, *Cochlichnus*). In contrast, there are many ichnotaxa that are restricted to marine environments, including the typical elements of the *Nereites* and *Zoophycos* Ichnofacies and a considerable number of those in the *Cruziana* Ichnofacies (Buatois and Mángano 2007). Arguably, the best example of this confusion is *Scolicia*. This ichnogenus consists of bilobate or trilobate horizontal structures displaying a complex meniscate backfill and two parallel strings, representing the feeding and locomotion activities of irregular echinoids (Smith and Crimes 1983; Uchman 1995; Bromley et al. 1997), which are restricted to the marine realm. Although *Scolicia* has been the subject of a number of taxonomic revisions and is well understood among ichnologists, surprisingly the name continues to be applied for continental, simple epirelief furrows that lack the complex morphology of this ichnogenus (Turner 1978; Hasiotis 2002, 2004; Lovelace and Lovelace 2012). Less commonly, other typical marine ichnotaxa, such as *Paleodictyon*, *Nereites,* and *Chondrites*, are used for much simpler freshwater trace fossils. Structures included in *Paleodictyon* from freshwater settings (e.g. Archer and Maples 1984; Wu 1985; Pickerill 1990) are quite simple, and do not display the regular pattern that characterizes this ichnogenus in marine turbidites. A feeding trace referred to as *Nereites* in lacustrine turbidites (Hu et al. 1998) lacks the internal, complex backfill structure of this ichnogenus, displaying only superficial similarities with *Nereites*. Feeding traces doubtfully assigned to *Chondrites* in lacustrine deposits (Smith et al. 1982; Kim et al. 2005) may superficially resemble this ichnogenus, although the dichotomous, primary successive branching that is diagnostic of *Chondrites* has never been documented in continental settings.

By contrast, some names that have been introduced for freshwater trace fossils fail to pass ichnotaxonomic validation. The classic example is *Isopodichnus*, a combination of short, bilobate resting traces and more continuous bilobate trails. Although *Isopodichnus* was frequently used in the past for continental bilobate trace fossils, recently its use essentially has been abandoned, following convincing demonstration that it is a junior synonym of *Rusophycus* and *Cruziana* (Bromley 1996). More recently, however, meniscate trace fossils present in continental deposits, previously referred informally as “adhesive meniscate burrows” (Hasiotis 2004), were subsequently included in a new ichnogenus, *Naktodemasis* (Smith JJ et al. 2008). However, *Naktodemasis* clearly falls within the diagnosis of *Taenidium* (Krapovickas et al. 2009; Díez-Canseco et al. 2016), an ichnogenus known from marine environments as well.

Behavioral convergence may also be evaluated by examining categories of ichnodisparity (architectural designs) rather than ichnotaxa. Of the 58 architectural design categories defined for invertebrate bioturbation structures (see Chap. 16), none are exclusive to freshwater settings, six are only present in terrestrial settings (vertical to oblique simple ornamented burrows; isolated, clustered, or interconnected cells; chambers with discrete thick linings; excavated chambers with thin linings undetachable from rock matrix; interconnected chambers and boxworks; and Holes, pits and galleries in walls and fillings), and one is shared by terrestrial and marginal-ichnofaunas (Simple to complex burrows with terminal chambers). Indeed, the only ichnogenus in the latter present in both marine and continental environments is *Macanopsis*, which actually occurs in backshore coastal areas, rather than in fully marine settings.

Freshwater ichnofaunas are represented by twenty architectural design categories, all of which also occur in marine environments: (1) simple horizontal trails (*Archaeonassa, Circulichnis, Cochlichnus, Gordia, Helminthoidichnites, Helminthopsis, Herpystezoum, Mermia*); (2) trails with undulating transverse bars and furrows (*Steinsfjordichnus*); (3) bilobate trails and paired grooves (*Cruziana, Didymaulichnus, Diplopodichnus*); (4) trackways and scratch marks (e.g. *Diplichnites, Hamipes, Keircalia, Lithographus, Siskemia, Stiallia, Stiaria, Tasmanadia, Umfolozia*); (5) bilaterally symmetrical short, scratched impressions (e.g. *Avolatichnium, Rotterodichnium, Tonganoxichnus*); (6) bilaterally symmetrical short, scratched burrows (e.g. *Rusophycus*); (7) passively filled horizontal burrows (*Palaeophycus*); (8) simple actively filled (massive) horizontal burrows (e.g. *Planolites*); (9) simple actively filled (meniscate) horizontal burrows (e.g. *Scoyenia, Taenidium, Beaconites*); (10) simple actively filled (pelletoidal) horizontal burrows (e.g. *Edaphichnium, Sphaerapus*); (11) complex actively filled (meniscate) horizontal burrows (*Scolecocoprus*); (12) horizontal branching burrow systems (*Labyrintichnus, Paracanthorhaphe, Shanwangichnus, Vagorichnus)*; (13) horizontal burrows with horizontal to vertical branches (*Ctenopholeus*, *Treptichnus*); (14) burrows with horizontal spreiten (*Fuersichnus, Rhizocorallium*); (15) isolated and serial almond-shaped burrows (*Calceoformites, Lockeia, Ptychoplasma*); (16) vertical simple burrows (e.g. *Skolithos*); (17) vertical U- and Y-shaped burrows (e.g. *Arenicolites, Diplocraterion*); (18) vertical multiple U- and Y-shaped burrows (*Polykladichnus*); (19) Simple to complex burrows with terminal chambers (*Camborygma, Castrichnus, Katbergia, Macanopsis, Platicytes)*; and (20) mazes and boxworks (*Thalassinoides*, *Spongeliomorpha, Virgaichnus*)

The common feature of this list is that these freshwater biogenic structures collectively represent relatively simple behaviors. Miller and Vokes (1998) categorized trace fossils as incidental and deliberate. Incidental trace fossils are those that record a single or dominant behavioral activity, and typically are structurally simple. Deliberate trace fossils are those that represent restructuring of habitats, modulation of disturbances, and control of food resources, and are typically structurally complex. Freshwater trace fossils tend to fall within the first category. In some cases, the same groups of producers were involved (*Lockeia* produced by both marine and freshwater bivalves). In other cases, true behavioral convergence can be invoked. The U-shaped burrow *Arenicolites* in marine environments is produced by a wide variety of organisms, such as polychaetes, echiuran worms, crustaceans, holothurians, and enteropneusts (e.g. Bromley 1996; Mángano et al. 2002), whereas in freshwater settings insects and oligochaetes are involved (e.g. McCall and Tevesz 1982; Scott et al. 2012a). Amphipods produce U-shaped burrows in both freshwater and marine settings. Behavioral convergence on both sides of the salinity barrier seems to have occurred only with the simplest ethologic types. The most complex architectural categories, such as burrows with helicoidal spreiten, dichotomous branching burrows, and those included within graphoglyptids, do not have a freshwater counterpart. This is clearly illustrated by the contrasting trace-fossils suites present in lacustrine and marine turbidites (Buatois and Mángano 1998).

Although the term "salinity barrier" has been commonly used to contrast the nature of freshwater and marine ichnofaunas, the term is somewhat misleading. Differences between ichnodiversity levels and the degree of morphologic complexity of trace fossils most likely are explained by the stability-time hypothesis developed by Sanders (1968), rather than salinity per se. According to this hypothesis, species diversity – and parallel to this, the degree of complexity of biogenic structures – is a function of environmental stability or predictability of the environment. Because lakes are considerably shorter-lived than oceanic basins, they tend to display lower taxonomic diversity (and ichnodiversity) levels and more simple structures than marine settings (Buatois and Mángano 1998). In addition, this line of reasoning can be applied to understand contrasting ichnodiversity levels in different lakes. For example, lakes from recently glaciated regions exhibit lower diversity levels than those from the long-lived, large, and deep lakes such as Lakes Baikal and Tanganyika (Saunders 1968).

Finally, regardless of the specifics of the MLR and lacustrine ecosystems in general, there are at least two common themes between the macroevolutionary aspects of marine and lacustrine settings. First, the overall trend in increased infaunalization discussed above also took place in marine basins, albeit with very different timing, because infaunalization in lacustrine basins lagged behind the same process in marine settings (Buatois and Mángano 1993a; Buatois et al. 1998a). Second, an analogue of the onshore – offshore pattern recognized in marine communities seems to be apparent in freshwater settings as well. An onshore origination of novelties and subsequent migration or expansion into deeper water has been proposed in marine settings based on body fossils (e.g. Jablonski et al. 1983; Sepkoski and Miller 1985; Jablonski 2005; Sepkoski and Sheehan 1983) and trace fossils (Crimes and Anderson 1985; Bottjer et al. 1988; Jensen and Mens 1999). In freshwater settings, an analogue of the onshore-offshore pattern is indicated by increases in the depth and extent of bioturbation that took place progressively through time, expanding from fluvial and lake-margin settings to permanent subaqueous lacustrine environments (Buatois et al. 1998a). These commonalities between the continental and marine trace-fossil records suggest the existence of recurrent macroevolutionary patterns of animal–substrate interactions through time (see Chap. 16).

11.8 Conclusions

Our review of the trace-fossil and body-fossil histories of the continental aquatic record suggests that the Mesozoic Lacustrine Revolution (MLR) represents a significant evolutionary event for lacustrine ecosystems that took place in a protracted fashion in time and space. Although ichnologic data demonstrate that both lake-margin and fully lacustrine deposits were colonized prior to the MLR, benthic activity essentially was restricted to a very narrow zone at the sediment–water interface, leaving the overwhelming portion of infaunal ecospace empty or underutilized. This situation commenced first in lake-margin environments during the Middle to Late Triassic, as shown by widespread presence of mid-tier meniscate trace fossils and deep-tier crayfish burrows. Colonization of the infaunal ecospace in these deposits resulted in more intense sediment reworking, typically precluding preservation of superficial trace fossils such as arthropod trackways. Although incipient penetration of the substrate in fully lacustrine settings has been recorded locally during the Middle to Late Triassic, ichnofaunas from these settings are typically reminiscent of those from the Paleozoic, suggesting that colonization of lacustrine bottoms was delayed in comparison with lake margins. Deeper penetration into the substrate became more common during the Early Jurassic, but the intensity of bioturbation remained low. The lacustrine mixed layer seems to have become well-established by the Early Cretaceous, as indicated by intense bioturbation mottlings.

The MLR also is recorded by examination of the record of body-fossils, particularly arthropods and angiosperms, and by trophic interactions at both the interorganismic and entire-lake foodweb levels. From an ecosystem perspective, prior to the MLR, lacustrine primary production by microorganisms was low and the depressed level of invertebrate consumption was overwhelmingly detritivorous. After the MLR, lakes are characterized by the appearance of macrophytes and a significantly more robust herbivore guild of microorganisms and increasingly larger arthropods and vertebrates, especially grazers on plants other than microscopic and small algae. This transition occurred during elevated lake oxygen levels, attributable to the insufficiency of detritivorous microorganisms before the MLR and detritivorous plus dominant herbivorous organisms after the MLR to use all available O_2 for respiration. Given this context, the MLR actually represents the incremental trophic shift from a detritivore-based to an herbivore-based lacustrine biota and concomitant food-web adjustments. But this change also represents a shift toward infaunalization that results from predatory escalation, also seen in other parts of the lake environment postdating the MLR. Perhaps related to predatory escalation is the distinct evolution of insect species in which their immature aquatic stages become increasingly more environmentally decoupled from their conspecific, exclusively terrestrially occurring adult stages. Based on the arthropod body-fossil record, this switch took place during the Late Jurassic to Early Cretaceous, but may have had a variable spatiotemporal occurrence in other mid-Mesozoic continents. Information from both trace fossils and body fossils suggests that this shift to more mixed trophic strategy consisting of detritivores, herbivores, predators, and other macroguilds that form animal communities has persisted to the present since initiation of the MLR, as demonstrated by the Paleolake Messel food web.

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Chapter 12
The End-Cretaceous Extinction and Ecosystem Change

Conrad C. Labandeira, Francisco J. Rodríguez-Tovar, and Alfred Uchman

12.1 Introduction

One of the most phenomenal events in the history of Phanerozoic life was the end-Cretaceous (K-Pg) mass extinction, occurring 66.04 Ma ago (Vandenberghe et al. 2012; Husson et al. 2014 for recent calibrations), an event that has been important for the subsequent evolutionary and ecological history of the continental and marine biota. Interest in this event was reignited during the early 1980s, when evidence for extraterrestrial causation was proposed based on several lines of evidence (Alvarez et al. 1980, 1984), later identified with an impact site (Hildebrand et al. 1991). Currently there is near consensus that the K-Pg event was caused by a bolide hitting the carbonate platform in Yucatan, Mexico (but see Schoene et al. 2014), which resulted in a significantly altered global environment, including altered sedimentation patterns (D'Hondt 2005), wildfires (Wolbach et al. 1985), and elevated atmospheric temperatures, and $p\mathrm{CO}_2$ and $p\mathrm{O}_2$ concentrations (Gale et al. 2001;

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Beerling et al. 2002; Schulte et al. 2010). However, the most consequential, long-lasting effects were on organisms, not only immediately after the event, but also throughout the intervening time between the event and today.

In the continental realm, the most obvious group that became extinct were major lineages of non-avian dinosaurs (Sereno 1999), which suffered a sudden fate (Sheehan et al. 2000); the previously declining pterosaurs (Penny and Phillips 2004); and several lineages of birds (Hou et al. 1996, but see Cooper and Penney 1997) that underwent major diversity declines (Gelfo and Pascual 2001). For birds, nine lineages survived that became the progenitors to the 42 extant orders of birds (Jarvis et al. 2014). There was extinction of at least one and probably several major clades of mammals (MacLeod 2005), although 39 lineages continued across the boundary, giving rise to the 25 orders of mammals of today (Bininda-Emonds et al. 2007). The similar style of survivorship of bird versus mammal lineages across the K-Pg boundary is noteworthy. Both major vertebrate lineages seem to support a slow-fuse model (Bininda-Emonds et al. 2007; Jarvis et al. 2014), in which overwhelmingly fewer, nondiverse lineages were present deep in the Cretaceous or earlier. These comparatively few lineages were "triggered" soon after the end-Cretaceous ecological crisis to provide a stunningly rapid cascade of evolutionary diversification within 10–15 Ma into the numerous lineages of birds and mammals that presently occupy virtually every significant continental and marine habitat on the planet.

Other organisms in terrestrial and freshwater habitats suffered considerable losses, including land plants (Johnson 2002; Wilf and Johnson 2004; McElwain and Punyasena 2007), with important regional differences (Askin and Jacobson 1996); bivalves (Hartman 1998; Hartman et al. 2009); crocodyliforms (Brochu 2004); and many avian dinosaurs (Sereno 1999; Retallack 2004). Groups that were minimally or not affected were amphibians (Archibald and Bryant 1990); and non-archosaurian reptiles such as turtles, lizards, rhynchocephalians, amphisbaenians, and choristoderes (MacLeod et al. 1997; Novacek 1999). Major insect lineages were unaffected at the family level (Labandeira and Sepkoski 1993), although ecological relationships with plants were significantly reduced (Labandeira et al. 2002a, b; Wilf et al. 2006; Donovan et al. 2014). Spiders, predators overwhelmingly consuming insects, also were not reduced in family-level diversity (Penney et al. 2003), and appear to track the family-level diversity of insects before and after the event (Penney 2003).

For the marine realm, as in the continental realm, some clades experienced significant or outright extinctions, whereas others did not (D'Hondt 2005). The principle clades that suffered major extinctions at the K-Pg boundary were diatoms (MacLeod 1998); calcareous nannoplankton (Bown 2005); other phytoplankton (MacLeod et al. 1997); benthic and planktic foraminifera (Kuhnt and Collins 1996; Arenillas et al. 2000; Molina 2015); scleractinian corals, particularly colonial taxa inhabiting warmer waters (Rosen and Turnšek 1989); echinoderms (Jeffrey 2001); mollusks such as belemnoids, ammonites (Marshall and Ward 1996) and inoceramid and rudistid clams (Ward et al. 1991; Raup and Jablonski 1993; Lockwood 2003). Vertebrate extinctions included many lineages of teleost fish (Friedman 2009, 2010), mosasaurs (MacLeod et al. 1997), and plesiosaurs (O'Keefe 2001). Apparently, there were minimal levels of extinctions, if any, of radiolaria (MacLeod et al. 1997), dinoflagellates (Gedl 2004); probably ostracods (Brouwers and De Deckker 1993); and brachiopods, which experienced a diversification event during the early Paleocene (MacLeod et al. 1997).

It is evident that these data are overwhelmingly based on identifications and tallies of body fossils, inventoried as either specimens or taxa, which represent diversities or abundances through time. A neglected but crucial aspect toward understanding the K-Pg event and its recovery phase is the collection, analysis, and interpretation of ecological data. When appropriately linked to various types of diversity data and to assessments of phylogeny based on paleobiological occurrence data and molecular phylogenies, ecological data can yield insights into mechanisms and patterns that may not be evident solely from a focus on taxonomic affiliations or occurrence tallies in particular habitats. In this contribution, we attempt to fill this void by providing two approaches toward understanding the ecology of the K-Pg extinction in both the continental and marine realms. For the continental realm, we will employ the system of analyzing damage types (DTs), that record distinctive plant–insect interactions throughout the K-Pg event to the late Paleogene (Labandeira et al. 2007). This approach has resulted in a fuller understanding of the patterns and processes during this tumultuous interval in terrestrial earth history. From a different branch of paleoichnology, we employ sedimentologically based tools for understanding marine organism–sediment relationships and behavioral correlates, mainly based on detailed ichnofabrics from studies of polished sections and examined burrow fills, including isotopic composition studies, which yields a better understanding of organism response to changes in the marine realm.

12.2 Evolutionary and Ecological Dynamics of the K-Pg Event and Its Recovery

There are two basic aspects to the generation of new lineages and their associated ecologies during a major mass-extinction crisis. The initial phase involves lineage-sorting processes inherent in the extinction, whereas the subsequent phase molds the selected lineages within the context of newly created ecospace.

12.2.1 Selectivity and Sorting During the Mass Extinction

The effect of the K-Pg event on the evolutionary trajectory of life has been examined extensively, particularly for marine mollusks (Jablonski 1989, 2001, 2005). The K-Pg mass extinction resulted in dramatic decreases in standing diversity (Jablonski 2005), although there were other significant patterns that have been recorded related to lineage selectivity and its consequences on affected taxa (Jablonski and Raup 1995). One of the more important conclusions of these studies has been the central role that mass extinction selectivity plays in favoring certain taxa-specific attributes over others (Jablonski 2001). The targeting of attributes during mass extinctions differs substantively from times of ambient, background extinction rates (Kitchell et al. 1986). In addition to providing dramatic decreases in standing diversity, another pattern resulted in more widely distributed taxa becoming considerably extinction averse compared to taxa with much narrower biogeographic ranges (Jablonski 2005). This extinction differential tends to favor taxonomically higher-ranked taxa for survival over their lower-ranked subordinates. Consequently, there was extinction of species with narrower geographic ranges, many of which were members of more broadly distributed (and temporally persistent) genera.

Perhaps the most important factor for selectivity during mass extinction was the relationship between life habits and feeding biology (Jablonski 2005). Most buffered of all were deposit feeders that occurred in the benthos or on sediment substrates that subsisted on detritus or dead organisms (Arthur and Zachos 1987; Twichett 2006). Deposit-feeding clades suffered much lower extinction levels than those groups occurring in the water column or having more direct trophic links to photosynthetic organisms (Sheehan and Hansen 1986). Consequently, in the marine realm, benthic deposit feeders and scavengers were favored over suspension and filter feeders existing in the water column that were embedded in food webs connected to photosynthetic organisms. For the continental realm, small insectivorous animals and aquatic invertebrates in streams were favored over most large-bodied vertebrates such as dinosaurs (Sheehan and Hansen 1986). Nevertheless, Levinton (1996) suggested that deposit feeders should have suffered extinction levels comparable to organisms more directly linked to photosynthetic organisms. This alternative pattern would be attributable to all dead organic material ultimately originating from more inclusive food chains of primary producers and their herbivores, although the effects would have been separated by a temporal lag of 3–6 months after impact. Contrary evidence is the presence of a local detritivorous earthworm fauna within several thousand years of the K-Pg event that consumed organic material preserved regionally as lignites (Chin et al. 2013). Another life-history source of immunity from extinction was marine organisms that possessed planktic life stages, versus those that do not (Kitchell et al. 1986). Those organisms with planktic life stages, such as many crustaceans with planktotrophic larvae, preferentially survived the K-Pg extinction. A considerably longer effect, resulting from a decrease of organic flux to the sea, were the negative consequences on calcium carbonate production by marine plankton, which took a few million years for the open-ocean ecosystem to be restored to full operational capacity, well into the mid Paleocene (D'Hondt 2005).

12.2.2 Establishing New Lineages and Ecologies During the Recovery

The recovery phase also had interesting evolutionary and ecological dynamics that were separate from the much shorter, preceding extinction phase. One secondary effect, based on a combination of theoretical models (Erwin 2001) and observations

(Jablonski 2001), was the probable lack of an association between the severity of the extinction and the length of recovery. In part, this would have been attributable to the collapse of ecosystems and thus the removal of ecospace that would disallow a rapid, orderly, logistic recolonization of pre-existing habitats. The destruction of ecospace was rebuilt, figuratively and trophically, from the ground up, and the idiosyncratic nature of lineage survivorship suggests that the recovery pattern was not attributable to global trophic principles, but rather represent a summation of lineages resulting from disparate patterns in time and space (McKenna and Farrell 2006), with no single, unifying ecological explanation (Jablonski 2005).

The vagaries of organismic occupation of ecospace during the recovery phase also indicate that origination rates of major lineages are reset at mass extinction episodes, rather than at intervals of background extinction (Jablonski 1989). It is during the recovery phase that entirely novel ecologies are created for surviving lineages (Solé et al. 2002); indicating that mass extinction and subsequent recoveries ultimately are the key intervals for establishing major evolutionary trajectories (Erwin 1998; Krug and Jablonski 2012). Indeed, the effects of the K-Pg event are reflected in current disruptions in the biogeographical distributions and ages of marine bivalve genera (Krug et al. 2009), and in the times of origin of particular extant plant–insect interactions (Labandeira 2005). These patterns indicate an increase in origination rates that followed the K-Pg mass extinctions and eventually reached a peak about 10 my after the event (Kirchner and Weil 2000). Effects of these origination-rate increases persist to the present day. An associated, but opposite, phenomenon is the survival of some lineages that survived the mass extinction event in radically decreased diversity, only to be finally extirpated early within a short-lived recovery (Erwin 2001). Such clades are termed “dead clade walking” (Jablonski 2002), and their early, post-event demise probably involved mismatches among biotic interactions.

12.3 The Continental Perspective of Ecological Disruption and Its Consequences

In this section, the effects of the K-Pg crisis on aquatic and terrestrial communities will be discussed, although the focus will be insects and their associations with plants from floras spanning the K-Pg boundary in the Western Interior of North America (Labandeira et al. 2002a, b; Wilf et al. 2000, 2006; Winkler et al. 2010; Labandeira and Currano 2013; Donovan et al. 2014). The analytical techniques used in these studies were developed during the late 1990’s (Wilf and Labandeira 1999; Wilf et al. 2001; Labandeira et al. 2007), and have expanded in scope to allow examination of plant–insect herbivore dynamics immediately preceding, during, and following the Paleocene–Eocene Thermal Maximum (PETM) floras that occur in the same or nearby basins (Wilf and Labandeira 1999; Wilf et al. 2001; Currano et al. 2008, 2010). Examination of plant-host and insect herbivore dynamics of the PETM studies can be seen as an extension of the K-Pg work, the latter detailed below, particularly as it documents the final stage of recovery from the major effects of the end-Cretaceous ecological crisis.

Parenthetically, it should be noted that study of plant–insect interactions in the fossil record never has been a major theme in paleoichnology. Mainstream paleoichnology has been principally driven by varied studies of the organismic alteration of sediment substrates in the fossil record from a wide variety of continental and marine depositional environments (Bromley et al. 2007). By contrast, much of the recent study of plant–insect interactions, principally herbivory, has targeted well-preserved, angiosperm-dominated fossil floras from several well-studied areas worldwide, including western North America (Wilf et al. 2001, 2006; Labandeira et al. 2002a), western Europe (Wappler et al. 2009, 2012), east Africa (Currano et al. 2011), and southern Patagonia and northern Colombia in South America (Wilf et al. 2005; Wing et al. 2009). The two approaches—sedimentological and plant–insect associational——have allowed for differing collection procedures, statistical protocols, interpretations, research-driven questions, and reference to overarching theory.

12.3.1 Aquatic Communities

The fate of invertebrates in freshwater aquatic communities during the K-Pg event is minimally understood, but is best demonstrated for bivalves, which experienced a major contraction of taxa that survived into the Paleocene (Hartman 1998). Major insect lineages such as mayflies, dragonflies, stoneflies, caddisflies, nematocerous flies, and beetles, which have actively feeding aquatic immatures, did not suffer extinction at the family level above that of the background level (Labandeira 2005), and likely were preferentially buffered against extinction (Sheehan and Hansen 1986). There is virtually no data on survivorship of major freshwater malacostracan lineages across the boundary.

12.3.2 Terrestrial Communities

Terrestrial communities house the bulk of biodiversity in the modern world, and undoubtedly did so during the latest Cretaceous. Most of this biomass occurs as land plants and arthropods, the two hyperdiverse groups that provide macroscopic structure to terrestrial ecosystems. Because of the ecological importance of these two groups and the absence of body-fossil insects near the K-Pg boundary (e.g., Larsson 1975; Pike 1994), a plant–insect associational analysis was conducted across the boundary in the Williston Basin of North Dakota, where abundant, diverse, and well-preserved floras are widespread (Johnson 2002; Labandeira et al. 2002a, b; Wilf et al. 2006; Donovan et al. 2014). When these ecological studies of K-Pg plant–insect interactions (Labandeira et al. 2002a, b) were linked to those of the PETM (Wilf et al. 2006; Currano et al. 2008, 2010; Donovan et al. 2014), the results (discussed below) parallel those found in the evolutionary studies of birds (Jarvis et al. 2014) and mammals (Bininda-Emonds et al. 2007), also occurring within 10 to 15 my after the boundary. Additionally, examinations of K-Pg to PETM floras have been extended to western Europe (Wappler et al. 2009, 2012; Dunne et al. 2012), and the results are suggestive of the pattern in North America. However, a valid test of Williston Basin data in Europe would require a regional, continuous section of well-preserved floras traversing the K-Pg boundary, currently absent, for further progress toward understanding the broader biogeographical extent of this global event.

12.3.2.1 Plants

The change in plant diversity across the K-Pg boundary was once thought to have been gradual (Hickey 1981) or stepwise (Frederiksen 1989), based on megafloral and palynological data, respectively. However, subsequent evidence from more intensely collected sections from the Williston Basin have clearly established a catastrophic extinction pattern (Johnson 2002), equivalent to a 57 % maximum estimate for extinction based on megafloral species-level data (Wilf and Johnson 2004), and a 30 % minimum estimate based on palynological genus-level data (Nichols 2002). These more recent data indicate a major turnover from more highly diverse and warm-adapted late Maastrichtian floras occupying a variety of habitats, to depauperate, cool-adapted early Paleocene floras that largely occupied mire habitats (Johnson 2002).

12.3.2.2 Insect Herbivory

With the possible exception of the Denver Basin to the south, the Williston Basin floral sequence represents the best combination of conditions for an analysis of insect herbivore patterns on floras straddling the K-Pg boundary. These floras are stratigraphically linked to a composite section of 183 m of strata that represent 2.2 my, of which the lower 1.4 my interval is of latest Cretaceous age and the upper 0.8 my interval is of earliest Paleocene age (Fig. 12.1). Within this system of floras, 13,441 specimens representing 380 plant-organ morphotypes were examined from 143 localities derived from 106 discrete stratigraphic levels (Fig. 12.1). Typical of most floras for this time interval, the Williston Basin floras are dominated by dicotyledonous angiosperms (86.3 %), but also include monocotyledonous angiosperms, conifers, cycads, ginkgos, ferns, a horsetail, and bryophytes (Fig. 12.2). The total assemblage represents a variety of fluvially dominated environments, including abandoned channels, sand bars, overbank deposits, ponds, and swamps, which formed a mosaic of distinctive habitats. Additional details are provided in the two reports from this study (Labandeira et al. 2002a, b).

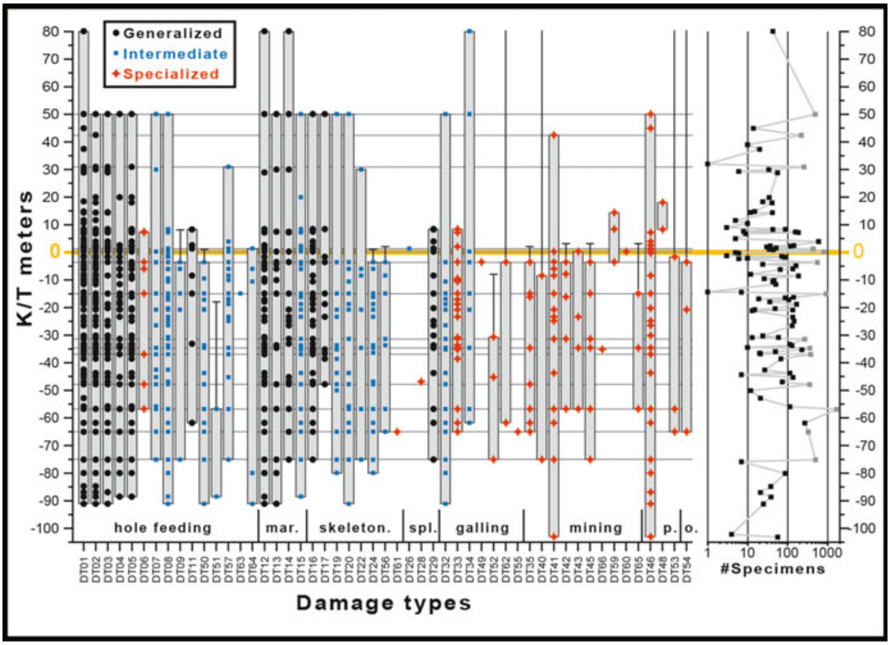

Fig. 12.1 Stratigraphic and sampling data for the 51 insect-mediated damage types from a 183 meter composite section straddling the K-Pg boundary (*orange bar*), from the Williston Basin of southwestern North Dakota. The estimated time duration for this interval is 2.2 million years (my) before present, of which 0.8 my are assigned to the postboundary interval and 1.4 my are allocated to the pre-boundary interval. The Cretaceous strata are within the Hell Creek and Fort Union formations, and the Paleocene strata are entirely within the Fort Union Formation. Placement of the zero datum is at the K-Pg boundary, not the Hell Creek/Fort Union formational contact, because the contact is diachronous with respect to the K-Pg boundary timeline. Depicted are the raw presence/absence data for damage types, categorized by functional feeding group and DT subgroup at bottom, and representing 106 discrete horizons. Eight damage types have single stratigraphic occurrences (*dots*); the ranges of those with multiple stratigraphic occurrences are shown as *vertical shaded bars*, categorized by host specificity from the color scheme at *upper left* (see text). Of the 14 specialized damage types with multiple stratigraphic occurrences that disappear at or below the K-Pg boundary, six (42.9 %) reappear during the latest Paleocene to middle Eocene of Wyoming and Utah. All associations are extant today. Four confidence intervals that exceed our sampling range are shown without end bars. Total specimen frequencies are given at *right*, including all plant organs; note logarithmic scale. The *gray horizontal lines* in the main figure and corresponding *gray squares* at *right* indicate the 14 horizons with more than 200 specimens of identified dicot leaves; meter levels for these floras are: −75.0, −65.0, −56.8, −47.8, −36.9, −31.4, −15.0, −3.6, +0.2, +1.3, +30.9, +42.4, +50.0. Abbreviations: *mar* margin feeding, *skeleton.* skeletonization, *spl.* surface feeding, *p.* piercing-and-sucking, *o.* oviposition. Limitations on graphical presentation cause the flora at +0.2 m, which are Paleocene, to appear within the *orange line* representing the K-Pg boundary. From Labandeira et al. (2002b), reprinted with permission by the National Academy of Sciences

Fig. 12.2 A spectrum of generalized (**c**, **g**, **i**, **j**) and specialized (**a**, **b**, **d**, **e**, **f**, **h**, **i**, **k**) plant–insect associations from the Williston Basin of southwestern North Dakota. Associations range from the earliest Paleocene at upper left, 14.4 m above the K/T boundary, and continue to the older associations of the latest Cretaceous at lower right, 85.5 m below the boundary. All material is from the Denver Museum of Nature and Science (DMNH) or the Yale Peabody Museum (YPM). Following each plant host are, respectively, morphotype number (indicated by the prefixes HC or FU), specimen number, NMNH locality number (loc.), and ± meter distances from the K/T boundary. Damage types are indicated by the prefix DT. Scale bars: *solid*, 1 cm; *backslashed*, 0.1 cm. (**a**) Two linear mines with oviposition sites (*arrows*), following secondary and then primary venation, terminating in a large pupation chamber (DT59) on the dicot *Paranymphaea crassifolia* (FU1), DMNH-20055, loc. 563, +14.4 m. (**b**) Single gall (DT33) on primary vein of *Cercidiphyllum genetrix* (Cercidiphyllaceae, FU5), DMNH-20042, loc. 562, +8.4 m. (**c**) Free feeding (DT26) on *Platanus raynoldsi* (Platanaceae, FU16), DMNH-20035, loc. 2217, +1.3 m. (**d**) Skeletonization (DT51) on a probable lauralean leaf (HC32), DMNH-19984, loc. 2097, −31.4 m. (**e**) Multiple galls (DT33) on *Trochodendroides nebrascensis* (Cercidiphyllaceae, HC103), DMNH-19976, loc. 1489, −33.7 m. (**f**) Initial phase of a serpentine mine (DT45) on *Marmarthia pearsoni* (Lauraceae, HC162), DMNH-7228, loc. 2087, −36.9 m. (**g**) Cuspate margin feeding (DT12, *arrow*) on *Metasequoia* sp. (Cupressaceae, HC35), DMNH-13108, loc. 567, −56.8 m. (**h**) Serpentine leaf mine (DT43) assigned to the Nepticulidae (Lepidoptera) on unidentified Rosaceae (HC80), YPM-6367a, loc. 567, −56.8 m. (**i**) Hole feeding pattern (DT57) on an unknown genus of Urticales (HC81), DMNH-19539, loc. 2203, −56.8 m. (**j**) General skeletonization (DT16) on *Erlingdorfia montana* (Platanaceae, HC57), DMNH-11013, loc. 571, −61.7 m. (**k**) Large scale-insect impressions (DT53) centered on primary veins of *E. montana*, DMNH-18829b, loc. 571, −61.7 m. (**l**) Slot hole feeding (DT08) on an unidentified genus of Platanaceae (HC109), DMNH-18658, loc. 434, −88.5 m. See Labandeira et al. (2007) for descriptions of damage types. From Labandeira et al. (2002b), reprinted with permission by the National Academy of Sciences

Of the examined specimens, 9292 (69 %) were late Maastrichtian and 4149 (31 %) were early Paleocene in age. This breakdown approximately was associated with the Hell Creek Formation, and the Fort Union Formation, respectively, but since the Hell Creek–Fort Union formational contact is diachronous with respect to the K-Pg boundary (the zero datum of Fig. 12.1), some earliest Paleocene floras were within the uppermost Hell Creek Formation. Sampling did not favor either the Paleocene or the Maastrichtian portions of this study, as specimen coverage was approximately equal for any 5-m interval above and below the boundary. In addition, confidence intervals were placed on the tops of ranges for each damage type (or DT) to correct for sampling intensity and to provide estimates for the likely time of extinction for each relevant DT (Labandeira et al. 2002a).

The presence–absence matrix represented 51 DTs from eight functional feeding groups (FFGs): hole feeding, margin feeding, skeletonization, surface feeding, galling, leaf mining, piercing-and-sucking, and oviposition (Figs. 12.1, 12.2, and 12.3). Each DT was categorized as to whether it was a generalized, intermediate, or specialized interaction (Figs. 12.1 and 12.2), but with particular attention to documenting unique host-specialist associations (Fig. 12.3), based on a variety of criteria. Three major patterns resulted from an analysis of the plant–insect interactions dataset. First, generalized DTs are better represented than intermediate and specialized DTs in the Paleocene side, with all generalized DT's crossing the boundary whereas 10 of 16 of the intermediate and 6 of 20 of the specialized cross the boundary. Second, of the 14 Maastrichtian DTs that are represented by large sample size, 10 have a last appearance just below the boundary, indicating extirpation at or just below the K-Pg boundary, a finding buttressed by confidence intervals. Third, after the decrease of the early Paleocene, herbivory increases in both frequency and richness during the later Paleocene. Most of this herbivory is generalized, as the more specialized DTs remain consistently low in frequency and richness. The frequency and richness of insect damage was analyzed throughout the section, and confined to the 14 discrete horizons (Fig. 12.1) and to the most abundant, identifiably dicot leaves to avoid biases in DT sampling on less abundant and poorly preserved non-dicot leaves. These analyses show a decrease in herbivory at the boundary, with the most significant decrease attributed to the intermediate and specialized DTs (data

→

Fig. 12.3 (continued) (**i**) Detail of mine in **h**, showing median frass trail at *upper left*. (**j**) Three aborted leaf mines, two of which have coiled initial phase (loc. 900, DMNH-7325). (**k**) Complete leaf mine with extensive terminal chamber illustrating trail (loc. 900, DMNH-7264). (**l**) Enlargement of terminal mine chamber in **k**, showing path of undulatory frass trail, indicated by *white arrows*. (**m**) Two aborted leaf mines with coiled initial phases (loc. 428, DMNH-7498). (**n**) Enlargement of leaf mine at *upper left* in **m**, showing coiled (*darkened*) initial phase. (**o**) Enlargement of leaf mine at *lower right* in **m**, revealing coiled leaf mine at *lower right* in **k**, indicating coiled (*darkened*) initial phase, and subsequent curvilinear phase along median primary and branching secondary veins (*arrow*). (**p**) Two adjacent leaf mines aborted early in development (loc. 900, DMNH-7313). Abbreviations: *DMNH* Denver Museum of Nature and Science, *YPM* Yale Peabody Museum. Scale bars: 1.0 cm, *solid*; 0.1 cm, *striped*. From Labandeira et al. (2002a), reprinted with permission by the Geological Society of America

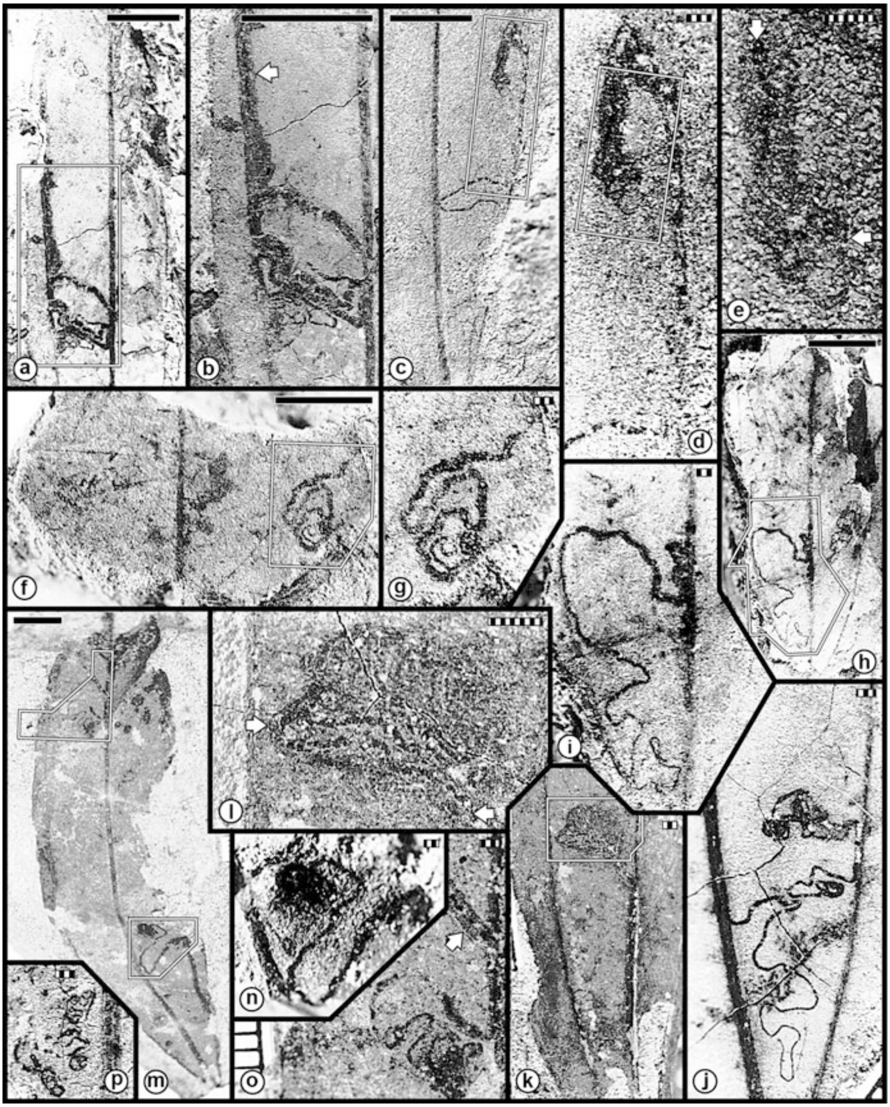

Fig. 12.3 Host-specific association between *Marmarthia pearsoni* (Laurales) and a gracillariid leaf miner (Lepidoptera), from the uppermost Hell Creek Formation. This highly stereotyped damage type, DT45, represents a specialized serpentine miner typically with an initial coiled phase, a subsequent curvilinear trajectory, and modestly expanded terminal chamber. It occurs exclusively on plant host HC162 at YPM localities 900 and 428. (**a**) Near-complete leaf mine following the primary venation (loc. 900, DMNH-7313). (**b**) Enlargement of **a**, with dark colored, medial frass trail detectable at upper left corner, along a primary vein. (**c**) Complete leaf mine with terminal chamber at *upper right* (loc. 900, DMNH-7263). (**d**) Enlargement of latter serpentine phase and terminal chamber of leaf mine in **c**. (**e**) Close-up of terminal chamber displaying dark frass trail (*top arrow*) and chamber edge (*bottom arrow*). (**f**) Fragment of leaf with a portion of leaf mine; note coiled early phase (loc. 900, DMNH-7199). (**g**) Close-up of mine in **f**. (**h**) Complete leaf mine bounded by median and lateral primary veins of plant host, typical for this species (loc. 900, DMNH-20023).

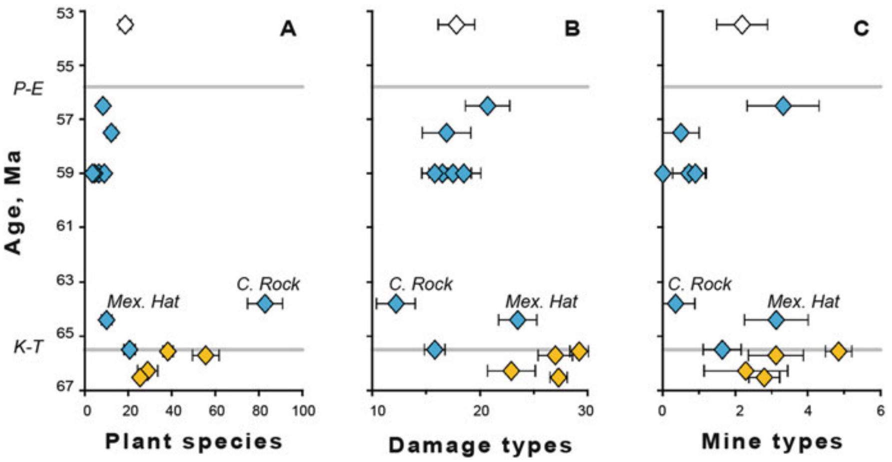

Fig. 12.4 Plant and insect-feeding diversity for bulk floras, standardized to sample sizes of 400 leaf specimens each. *Orange-yellow* data points are Cretaceous floras; *blue* data points are Paleocene floras. *Ma* million years ago. Plant richness (**a**) was standardized by means of rarefaction, with error bars indicating 95 % confidence intervals. Insect damage was standardized by means of random resampling without replacement, with ±1σ error bars around the mean of 5000 iterations, both for (**b**) all damage morphotypes and (**c**) mine morphotypes only. There is a strong negative correlation of plant and insect damage richness for Mexican Hat (*Mex. Hat*) and Castle Rock (*C. Rock*). A separate analysis (not shown in the figure) excluded most external feeding and other generalized damage morphotypes, yielding results nearly identical to (**b**). Abbreviations: *K-T* Cretaceous–Paleogene boundary, *P-E* Paleocene–Eocene boundary. Reprinted from Wilf et al. (2006), with permission from the American Association for the Advancement of Science

not shown; Labandeira et al. 2002a, Fig. 3). The sustained decrease of herbivory above the boundary, and the failure of intermediate and specialized DTs to recover do record a major event affecting insect herbivores, documented in particular for leaf-mining taxa (Donovan et al. 2014).

These results were tested in a subsequent study (Wilf et al. 2006), in which insect feeding damage from 14,999 dicot leaves were examined from 14 latest Cretaceous, Paleocene, and early Eocene sites to understand post-extinction patterns of herbivory, including generalized and specialized forms of interactions (Fig. 12.4). Expectedly, most of the Paleocene sites displayed low richness of plants and insect damage, with two unexpected exceptions in the early Paleocene, both within 1.7 my of the end-Cretaceous extinction. One site from the Denver Basin, Castle Rock, showed exceptionally high plant diversity but virtually no specialized feeding; another site from the Williston Basin, Mexican Hat, conversely exhibited a typically depauperate Paleocene flora but high levels of specialized herbivory. These disparate results indicate that, for about 2 my after the end-Cretaceous extinction, local community structure of plants and insect herbivores remained significantly unbalanced, and did not regain latest Cretaceous levels of herbivory and specialization until much later, during the late Paleocene.

12.3.2.3 Implications for Macroevolutionary Patterns of Specialist Insect Herbivores

The above studies are based on assessments of insect herbivore functional feeding groups and their damage types in floras across the K-Pg boundary, through the Paleocene, and well into the early Eocene. These data may be important for detecting the immediate and longer-term ecological processes of plant–insect interactions after a major environmental perturbation. Given the long lag times toward increased levels of herbivory and host-plant specialization following the K-Pg event, it would appear to support the gradual rather than instantaneous colonization of plant hosts after a major ecological crisis. This pattern also is detected from examination of specialized leaf-mining lineages and their delayed colonization of available plant hosts (Lopez-Vaamonde et al. 2006; Donovan et al. 2014), consistent with the long lead-times to diversification predicted by the resource abundance–dependent diversification hypothesis (Nyman et al. 2012). The post-event fossil pattern also is inconsistent with geologically rapid, synchronous patterns of insects that co-radiate onto their host plants, documented for certain chrysomelid beetles and their burseraceous hosts (Becerra 2003). Alternatively, these data could address the issue of quick, local adaptation to allopatric populations of novel host plants from a broadly distributed specialist species (Rosenzweig 1995; Zvereva et al. 2010).

If host specialists were disproportionately extirpated at the K-Pg mass extinction event, then specialization of insect herbivores could be an evolutionary dead end. A tendency toward lineage phylogenetic stasis has been documented for recent clades of leaf miners (Connor and Taverner 1997; Lopez-Vaamonde et al. 2003), those gallers with more limited host ranges (Hardy and Cook 2010), and some *Dendroctonus* bark beetles (Kelley and Farrell 1998). This especially would be true if the lineages of host-plant specialists are clustered in particular clades vulnerable to a mass extinction (Roy et al. 2009). However, there are good reasons to indicate that some specialized relationships are not evolutionary cul-de-sacs (Colles et al. 2009); counterexamples include doniciine beetles on aquatic reeds (Kölsch and Pedersen 2008) and perhaps other *Dendroctonus* bark beetle taxa (Kelley and Farrell 1998). While host-plant specialization may lead to extinction at times of major ecosystem crises, such as the K-Pg, during other, much more prolonged intervals of background extinction, specialist and generalist herbivore lineages may experience stasis and have bidirectional acquisition of host-plant feeding preferences (DiMichele et al. 2004; Forister et al. 2012; Thompson 2013).

12.3.2.4 Insect Pollination

The data and methods of assessing patterns of insect pollination across the K-Pg boundary are considerably more difficult than that those that evaluate insect herbivory. The palynological record, however, can reveal broad trends in the frequency of zoophilous (insect vectored) versus anemophilous (wind dispersed) pollen. Several examinations have documented a significant reduction of zoophilous pollen at the K-Pg boundary (Frederiksen 1989; Sweet and Braman 2001), indicating a disproportionate extinction of pollen vectored by insects at the boundary. In one study documenting a lineage of dominantly Late Cretaceous zoophilous pollen across the K-Pg boundary, a sole anemophilous palynospecies evidently survived the event in a local section (McIver et al. 1991). Other lines of evidence also indicate the emergence of pollinators immediately after the K-Pg event. One is a fortuitous occurrence of an entrapped stingless bee associated in a flower of its orchid host found in Dominican amber (Ramírez et al. 2007). A molecularly based reconstruction of orchid phylogeny based mostly on this fossil indicated that the time of origin of the insect-pollinated orchid lineage was immediately after the K-Pg event. This result parallels the same time of origin, using a similar method of phylogenetic reconstruction, for nymphalid butterflies (Wahlberg et al. 2009), another major pollinator clade likely originating in the wake of the K-Pg crisis.

12.3.2.5 Blood Feeding on Dinosaur Hosts

Some associations are known from the Late Cretaceous involve live and dead dinosaurs. Perhaps the most intriguing association involves an example of blood feeding between *Culicoides*, the most diverse genus of extant blood-feeding of the mosquito-like dipteran family Ceratopogonidae (biting midges, no-see-ums, punkies) and its inferred live host, the dinosaur *Corythosaurus*. Female ceratopogonids currently are major vectors of arboviruses, parasitic protozoa, and filarial worms that cause diseases such as African Horsesickness, Bovine Ephemeral Fever, Bluetongue Virus, and occasional filariasis, which are associated with acute dermatitis and skin lesions (Lehane 1991). (Male ceratopogonids are nectar feeders and often are pollinators.) Early appearing ceratopogonid lineages occur in Early Cretaceous ambers and include taxa whose modern representatives, such as *Leptoconops* and certain basal species of *Forcipomyia* and *Culicoides* feed on reptiles such as turtles, iguanas and lizards (Wirth and Hubert 1962; Auezova et al. 1990). In particular, these ceratopogonids attack hosts with vulnerable skin regions lacking scales such as eye membranes, the anal vent area, and underbelly of individuals, or alternatively in heavily vascularized regions of the skin that have narrow spaces of exposed skin between thickened scutes (Auezova et al. 1990; Borkent 1995).

An association has been between certain Late Cretaceous species of *Culicoides*—particularly *C. canadensis* and *C. bullus* of Campanian Grassy Lake Amber of Canada and possibly *C. filapalpis* of Coniacian Taimyr Amber of Russia—and dinosaurs (Borkent 1995). This interaction is based on the mouthpart structure of fossil and modern *Culicoides* (Borkent 1995). Those *Culicoides* species with a combination of finely toothed mandibular stylets and coarse, retorsely toothed maxillary stylets indicate feeding on vertebrates, rather than insects (McIver et al. 1991). In addition, the number CO_2 detecting capitate sensillae on the maxillary palps of *Culicoides* species is directly associated with vertebrate host size: those with a greater number of sensillae ($n=29$–74) feed on small hosts such as small birds and small mammals, whereas those species with fewer sensillae ($n=11$–17) feed on large mammals, with some species possessing an intermediate number of sensillae ($n=29$–36) that feed on birds and mammals of intermediate sizes (Rowley and

Cornford 1972; Braverman and Hulley 1979). An examination of the fossil record from both the Late Cretaceous of north-central North America northern Russia indicate that mammals and birds were comparatively small and that the only large vertebrate candidates as hosts were large dinosaurs, such as *Corythosaurus* which possessed exposed integumental surfaces for blood-feeding ceratopogonids that co-occurred with Grassy Lake species of *C. canadensis* and *C. bullus* (Borkent 1995) Both of these and the Russian species of *Culicoides* have several features of mouthpart structure and anatomy that would strongly indicate blood feeding on vulnerable integumental areas of large dinosaurs.

12.3.2.6 Other Interactions

Based on scant evidence, there are other types of interactions that likely were extirpated at the K-Pg boundary. Most of these associations involve plant pathogens, and those involving various relationships with large vertebrates, particularly dinosaurs.

The documented fossil record of plant pathogens is almost nonexistent, with the exception of epiphyllous fungi (Labandeira and Prevec 2014). Mid-Cretaceous floras such as the Dakota Formation display a significant epiphyllous mycota (DT58 on page 15 of Labandeira et al. 2007), and foliar fungi are known from floras spanning the K-Pg boundary of the Williston Basin (Labandeira personal observation), though they have not been characterized other than assignment to DT58. The other major plant-parasitic pathogen groups of viruses, bacteria, and nematodes may have instances of tissue damage in the fossil record (Labandeira and Prevec 2014), but have not been documented formally.

Sediments from approximately the same age as the example of the biting midge and dinosaur parasitism reveal an association between scarab beetles and dinosaur dung rich in conifer fragments (Chin and Gill 1996). Evidence of carrion communities on dinosaur carcasses includes beetle borings in and on bone material from the Campanian of southern Utah and northwestern Montana, and from the Maastrichtian of northwestern Madagascar (Rogers 1992; Roberts et al. 2007). Wasp cocoons associated with decomposing dinosaur eggs were described from middle Campanian to lower Maastrichtian sediments of northern Patagonia, in Argentina (Genise and Sarzetti 2011). These Late Cretaceous associations occur within several million years of the K-Pg boundary likely were extirpated by the demise of their dinosaur hosts.

12.4 The Marine Perspective of Ecological Disruption and Its Consequences

Although the end-Cretaceous mass extinction is one of the best documented events of the Phanerozoic, until recently, there have been few detailed ichnological analyses focusing on this extinction in marine environments (Ekdale and Bromley 1984a;

Savrda 1993; Stinnesbeck et al. 1993, 1996; Keller et al. 1994; Ekdale and Stinnesbeck 1998). This absence of research is a consequence of difficulties inherent in examining discrete trace fossils from lower Danian sediments. However, in Spain and France, the K-Pg boundary transition usually is marked by a 2–3 mm-thick red, iron-rich, boundary layer at the base of several-centimeter-thick interval of dark clay. In most cases, material infilling the earliest Danian trace fossil assemblage is similar in color to that of host Danian strata, precluding any direct, visual, differentiation. Typically, both the latest Maastrichtian and the earliest Danian ichnoassemblages are observed below the K-Pg boundary, and contrast with the light color of Maastrichtian strata. The latest Maastrichtian ichnoassemblage consists of structures filled with sediments that are only slightly darker than the host material, while the earliest Danian forms are filled with a dark-colored matrix similar to marly, lowermost Danian strata that contrast strongly with the light color of the Maastrichtian host rock. In order to analyze the ichnology of the K-Pg transition in Spain and France, one recent, fruitful methodology has been applied in four boundary sections. These methods have focused on detailed ichnofabric analysis based on the study of polished sections and on analyses, including isotopic studies, of material infilling various sedimentary trace fossils (Rodríguez-Tovar et al. 2002, 2004, 2006; Rodríguez-Tovar and Uchman 2004a, b, 2006, 2008).

12.4.1 A Selective Impact Favoring the Deposit Feeding Community

Marine ichnoassemblages recorded in pelagic and hemipelagic, non-turbiditic facies of the K-Pg boundary transition globally are very similar in composition. At one distal, continental shelf deposit in Denmark, the Maastrichtian assemblage consists mostly of *Thalassinoides*, *Zoophycos,* and *Chondrites*, whereas basal Danian sediments are comprised of *Planolites*, *Thalassinoides*, and "small *Chondrites*-like forms" that now are recognized as *Phycosiphon* (Ekdale and Bromley 1984a). In very proximal, continental shelf deposits from Alabama, Savrda (1993) observed that *Thalassinoides*, *Ophiomorpha,* and *Planolites* penetrated estuarine sandy deposits of the lowermost Danian. In shallow neritic settings examined in Mexico, trace-fossil assemblages principally consisted of *Chondrites*, *Ophiomorpha*, *Planolites,* and *Zoophycos* (Ekdale and Stinnesbeck 1998). In sections studied from the south (Agost and Caravaca) and north (Sopelana) of Spain and in southwestern France (Bidart), there is correspondence to open, deep-sea pelagic sedimentation (Fig. 12.5). At these Spanish and French sites, a well-developed, oldest Danian, endobenthic community is recognized, composed typically of *Chondrites*, *Zoophycos*, *Planolites*, *Thalassinoides,* and *Alcyonidiopsis* (Rodríguez-Tovar and Uchman 2004a, b; Rodríguez-Tovar et al. 2011) (Fig. 12.6).

Ichnoassemblages at the K-Pg boundary transition principally consist of *Chondrites*, *Zoophycos*, *Planolites*, *Thalassinoides*, *Ophiomorpha,* and *Alcyonidiopsis* as

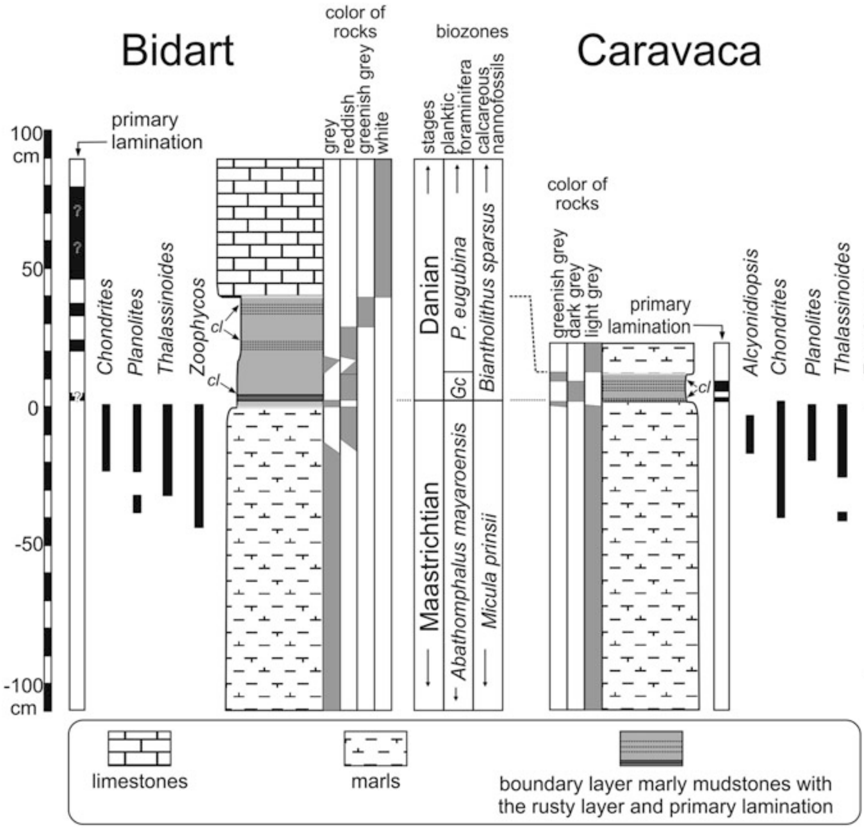

Fig. 12.5 The range of black-filled trace fossils are displayed in stratigraphic sections from Bidart, southwestern France, and Caravaca, southeastern Spain. The trace-fossil infilling is derived from the K-Pg boundary layer. The Bidart lithologic column is after Rodríguez-Tovar et al. (2011). Abbreviation: *cl* base colonization levels in lowermost Danian dark sediments. The planktic foraminiferal zonation and stratigraphic correlation of the Caravaca section is based on Arz et al. (2000) and Arenillas et al. (2004)

the most common ichnotaxa (Figs. 12.5 and 12.6), and are similar to those from other Late Cretaceous, fine-grained, marly sediments (Ekdale and Bromley 1984b). These assemblages reveal the dominance of feeding traces that consist of a variety of behaviors——including domichnia, fodinichnia, pascichnia, and chemichnia——and were produced predominantly by deposit feeders obtaining food from the sediment. This spectrum of feeding ecologies agrees with favorable conditions for detritus- and deposit-feeding tracemakers, associated with the availability of abundant food that was established immediately after the impact event (Morrow and Hasiotis 2007). As mentioned above, deposit-feeding clades were less affected by the extinction than by groups inhabiting the water column or narrowly linked

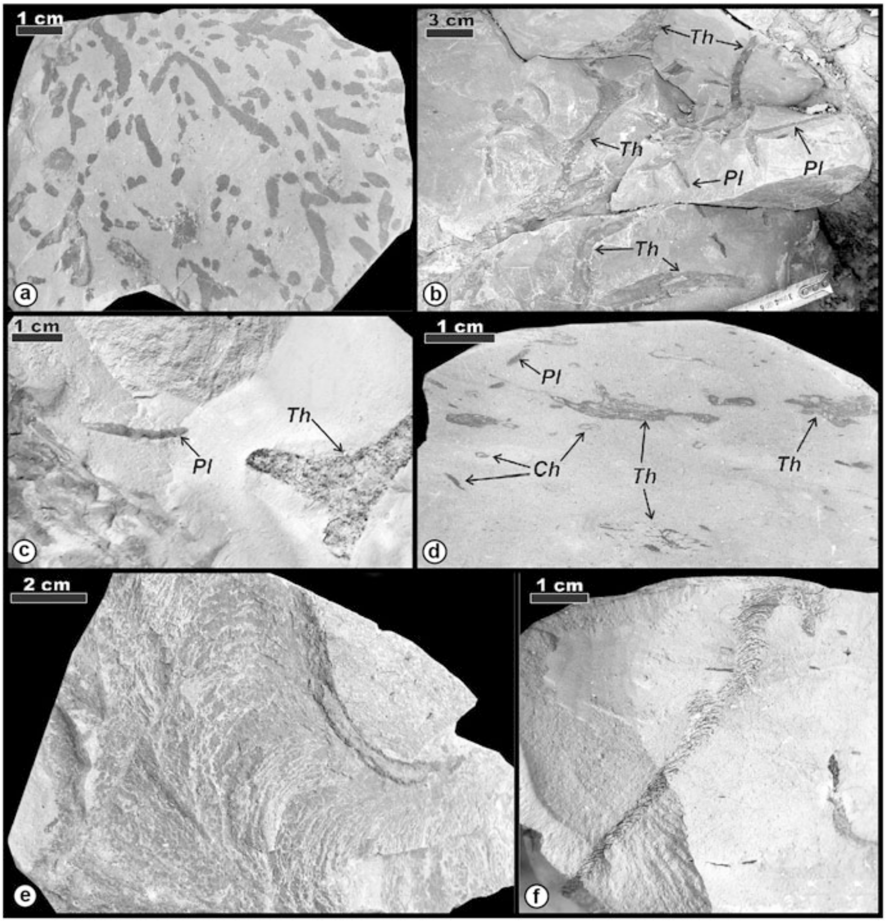

Fig. 12.6 Black-filled, lowermost Danian trace fossils are shown from the uppermost Maastrichtian in stratigraphic sections of Bidart, southwestern France, and Caravaca, southeastern Spain. (**a**) *Chondrites targionii* occurring in a polished section of a horizontal slab, Caravaca section. (**b**) *Thalassinoides* isp. (*Th*) and *Planolites* isp. (*Pl*) occurring in an oblique parting surface, Bidart section. (**c**) *Thalassinoides* isp. (*Th*) and *Planolites* isp. (*Pl*) occurring in a horizontal parting surfaces, Bidart section. (**d**) *Thalassinoides* isp. (*Th*), *Chondrites* isp (*Ch*), and *Planolites* isp. (*Pl*) occurring in a polished section of a vertical slab, Bidart section. (**e**) A lobe of *Zoophycos* isp. in a horizontal parting surface, Caravaca section. (**f**) *Zoophycos* isp. in a vertical section of a parting surface, Caravaca section

trophically to photosynthetic organisms (Arthur and Zachos 1987; Jablonski 2005; Twichett 2006). However, along K-Pg sites along the Gulf Coastal plain, apparently the producer of *Thalassinoides* experienced a significant bout of dwarfism after the boundary, as burrow diameters underwent a significant decrease in earliest Paleocene sediments (Wiest et al. 2015).

Ichnological studies of the K-Pg boundary interval from deep sea turbidite facies are less well known than those from non-turbiditic sediments. In the Uzgruň section of Moravia, in the Czech Republic, *Chondrites intricatus*, *Ch. targionii*, *Ophiomorpha annulata*, *O. rudis*, *Palaeophycus tubularis*, *Planolites* isp., *Phycosiphon incertum*, *Thalassinoides* isp., and *Trichichnus* isp. occur through the boundary interval (Uchman et al. 2005). They occur in the sediments underlying and overlying the boundary, and lack distinct morphological changes. In addition, the trace-fossil diversity pattern at the ichnogenus level does not display significant change through this interval (Uchman 2004, 2007). Interestingly, after a Cretaceous peak, the number of new graphoglyptid ichnogenera in the Paleocene decreased considerably, while the contribution of graphoglyptid taxa in ichnoassemblages of turbiditic sediments increased in general (Uchman 2003). Stratigraphic resolution of these changes is poor, making it very difficult to link these changes precisely to the K-Pg event. However, it is possible that the coincidental the drop of ambient, deep-sea, water temperature during the Paleocene (Barron and Peterson 1991) may have affected the infaunal farming activity of graphoglyptid tracemakers.

12.4.2 Minor Disruption in the Macrobenthic Tracemaker Community

As noted above, in the Spanish and French sections there is a differentiation between pre-event latest Maastrichtian ichnoassemblages, consisting of trace fossils with lighter-hued infillings of *Chondrites*, *Zoophycos,* and *Planolites*, versus post-event, earliest Danian ichnoassemblages of darkly filled structures that contain principally *Chondrites*, *Zoophycos*, *Planolites*, *Thalassinoides,* and *Alcyonidiopsis* (Rodríguez-Tovar and Uchman 2004a, b; Rodríguez-Tovar et al. 2011). These two ichnoassemblages are differentiated by matrix color, nature of the burrow infill material, and isotopic composition. Minor variations between sections, such as the presence or abundance of *Chondrites* and *Zoophycos*, probably have local importance that can be related to differences in feeding strategies of the trace-fossil tracemakers related to food content or site bathymetry.

Similarly, in other K-Pg boundary sections, *Thalassinoides*, *Zoophycos,* and *Chondrites* are representative of the upper Maastrichtian assemblage, while *Planolites* and *Thalassinoides* are dominant in the lower Danian (Ekdale and Bromley 1984a; Savrda 1993). Thus, trace-fossil assemblages do not change significantly across the K-Pg boundary, appearing in lower Danian ichnoassemblages, and by comparison are less abundant and diverse than Maastrichtian ichnoassemblages. Environmental changes associated with K-Pg boundary phenomena apparently did not have a significant impact on macrobenthic tracemakers, and had a minimal effect on the marine macrobenthic tracemaker community at the K-Pg boundary.

12.4.3 An Unfavorable Habitat for Macrobenthic Colonization?

Historically, the rusty, red boundary layer in various K-Pg boundary sections of Spain and France has been considered non-bioturbated, presumably revealing unfavorable environmental conditions that were inhospitable for colonization by organisms. Nevertheless, a detailed analysis does show that the K-Pg boundary layer at the Caravaca section exhibits a highly bioturbated fabric that includes *Zoophycos* and *Chondrites* vertically crossing the boundary layer (Rodríguez-Tovar and Uchman 2008). This boundary interval also is penetrated horizontally by *Chondrites* ramifications. The "unfavorable" conditions displayed by the iron-rich boundary layer evidently did not impede colonization by tracemakers. This important colonization event was related to a repertoire of producer behaviors that was not dependent on substrate features. *Zoophycos* and *Chondrites* tracemakers constructed open, or at least partly ventilated, burrows that accommodated various substrate features, and this was followed by further infaunal colonization of sediment poor in oxygenated pore waters and food (Rodríguez-Tovar and Uchman 2008).

By way of analogy, a recent environmental disaster occurred at Doñana National Park in southern Spain that was caused by the failure of a tailings pond adjacent a pyrite mine at Aznalcóllar, near Sevilla (Rodríguez-Tovar and Martín-Peinado 2009). The sedimentary wedge resulting from the outflow of sedimentary mine waste from the tailings pond, replete with elevated concentrations of pollutants and toxic elements, was colonized within 10 years by the ghost ant, *Tapinoma nigerrima*. *Tapinoma nigerrima* is characterized by aggressive life habits and opportunistic behavior. Notably, the colonized mine-waste substrate was enriched in various pollutants that included mercury, arsenic, lead, thallium, antimony, and iridium, and was characterized by locally elevated heavy elemental concentrations. A comparison of the leaked element abundances from Aznalcóllar with K-Pg boundary sections revealed that in several cases, such as iridium, the values obtained in the polluted soil of Aznalcóllar are higher than those recorded for the K-Pg rusty brown boundary layer (Rodríguez-Tovar and Martín-Peinado 2009). Nests of *T. nigerrima* occurred throughout the tailings layers, and an ant-fashioned biofabric was created from particles within the polluted soil, providing evidence for the irrelevance of substrate structure in determining the ant-generated biofabric in the polluted substrate. The particular response of *T. nigerrima* to the Aznalcóllar disaster is relevant to interpretation of ichnofaunal colonization of the K-Pg boundary event, at least for sections from Spain and France. This relevance is based on similarities between Aznalcóllar soils and the K-Pg boundary layer, such as the presence of strongly anomalous, life-destroying chemical elements.

A similar example recently has been studied in the contaminated marsh area of the Tinto River near Huelva, in southwestern Spain, This marsh is characterized by high soil concentrations of toxic elements, such as copper, zinc, and arsenic (Rodríguez-Tovar and Martín-Peinado 2014). An ichnological analysis revealed the presence of biogenic structures produced by the activity of the earthworm *Lumbricus terrestris* and the beetle *Platystethus*. Colonization of this polluted substrate is possible due to the particular features of the tracemakers: *Lumbricus terrestris* shows a great resistance to elevated concentrations of a number of contaminating elements, whereas *Platystethus* produces traces that are relatively independent of substrate features. These patterns indicate that substrate colonization at Huelva could be comparable to that of *Planolites* and *Thalassinoides* tracemakers immediately after the K-Pg boundary event (Rodríguez-Tovar and Martín-Peinado 2014).

12.4.4 A Relatively Rapid Recovery

Based on observations on microfaunal assemblages, calibrations of the initial recovery of the marine biota associated with the K-Pg boundary were estimated in the range of thousands of years (kyr). The initial recovery of planktic foraminifera was estimated at about 230 kyr (Keller and Barrera 1990), and the early pioneer, calcareous nannoflora appeared approximately 25 kyr after the K-Pg mass extinction event (Lamolda et al. 2005). Approximately ten kyr is proposed for the time involved in restoration of food webs and restructuring of marine ecosystems, a process occurring after the oceans were repopulated by planktonic species with high turnover rates. After an initial, comparatively low occurrence of post-event benthic foraminifera, a subsequent and rapid recovery was found, as complex trophic webs reappeared approximately seven kyr after the K-Pg boundary. During the early phase of the recovery interval, the presence of an epifauna tolerant of low oxygen occurred from 600 to 1200 years after the event (Coccioni and Galeotti 1994).

Two significant observations are important for understanding the response of the macrobenthic tracemaker community to the K-Pg boundary event and their subsequent, comparatively rapid recovery. First is the presence of iron oxide spherules in *Thalassinoides* burrow infillings (Rodríguez-Tovar 2005). A second consideration is physical disturbance resulting from bioturbation of the K-Pg boundary layer (Rodríguez-Tovar and Uchman 2008). Stereomicroscopic and field-emission SEM analyses of *Thalassinoides* at the K-Pg boundary layer from Agost display numerous iron oxide spherules in the infilling material. In addition, the composition, internal texture, morphology, and size of the infilling were similar to the ichnofabric that was confined to other sections of the 2–3 mm-thick, rusty, K-Pg boundary layer (Martínez-Ruiz et al. 1997, 1999). These observations, in conjunction with the homogeneity of the infilling material and the absence of erosional surfaces capping *Thalassinoides* burrows, were interpreted as evidence of rapid colonization by *Thalassinoides* tracemakers, occurring almost contemporaneously with the spherule layer deposit (Rodríguez-Tovar 2005) and by a smaller-bodied species revealed by data from the Gulf of Mexico (Wiest et al. 2015). Subsequently, a detailed analysis of the dark boundary layer from the Caravaca section revealed discrete bioturbation that commenced about 14 mm from the rusty-boundary layer, immediately above the first laminated interval (Rodríguez-Tovar and Uchman 2008). Recently, high-resolution geochemical analyses from the K-Pg boundary at the Caravaca section support the conclusion that the recovery to pre-impact levels of oxygenation was almost instantaneous, with absolute values in the order of 10^2 yr (Sosa-Montes de Oca et al. 2013).

12.4.5 Iterative and Continuous Colonization after the Mass Extinction

The absence of a clear color differentiation between burrow infillings of the earliest Danian ichnoassemblage and the dark, marly, lower Danian host sediments from the K-Pg boundary sections of Spain and France prevented, at least initially, conclusive identification of the colonized stratal horizons and possible assessment of the recovery's initiation. In this context, the analysis of carbon isotope composition of the infill from passively filled burrows became a useful tool (Rodríguez-Tovar et al. 2002, 2004, 2006). A comparison of the $\delta^{13}C$ data from infilled Danian trace fossils in the uppermost Cretaceous sediments in the Agost section allowed for identification and assessment of the relative timing of the macrobenthic colonization phases. This examination distinguished Cretaceous from Danian trace fossils based on isotopic composition, and revealed that different isotopic values from the dark-infilling material could be correlated with those obtained in particular horizons within the Danian marly interval. This analysis provided evidence for different phases of colonization, deployed in succession across the K-Pg boundary interval (Rodríguez-Tovar et al. 2002, 2004, 2006).

A subsequent, detailed ichnofabric analysis of the 7–10 cm-thick, dark Danian boundary layer at the Caravaca section allowed for identification of two bioturbated horizons, separated by two laminated, unbioturbated layers (Rodríguez-Tovar and Uchman 2006). The first laminated layer, 14 mm thick, rests just above the rusty boundary layer. It is overlain by a 26 mm thick, bioturbated horizon, which is covered by a 36 mm thick layer that exhibits convolute lamination. Above, the sediment is again bioturbated (Rodríguez-Tovar and Uchman 2008). From the bioturbated horizons in the dark boundary layer, trace fossils pipe downward continuously to the uppermost horizons of lighter-hued, Maastrichtian sediments. These ichnofossils cross-cut the rusty boundary layer, penetrating up to 90 cm below into Maastrichtian marls. *Zoophycos* and *Chondrites* penetrate up to 90 cm and 35 cm, respectively, below the rusty boundary layer (Rodríguez-Tovar and Uchman 2006, 2008). These data suggest multiple, post-event colonization events.

12.5 Can Trace-Fossil Records Address Biologic Effects of the K-Pg Event?

Although several advantages of trace-fossil data over body-fossil data previously have been discussed (Labandeira 2007), the following eight issues, derived from studies in this contribution, represent utilitarian, recent approaches toward understanding ecological and environmental issues in the deep-time fossil record. These approaches can be applied to both continental and marine trace-fossil records.

12.5.1 Previously Unapplied Analytic Techniques

Trace-fossil data are as eminently amenable to quantification and analysis by a variety of statistical techniques, as are body-fossil data. The quantification of abundant trace-fossil data can be seen as a departure from studies of single, or at most a few specimens of ichnological taxa in previous studies. As well, carbon isotopic analysis, heavy element analysis, and SEM field emission studies provide detailed documentation at local to regional scales of organism–environment relationships before, at, and after the K-Pg boundary. The analytic techniques developed for characterizing plant–insect interactions of entire floras and for understanding the substrate relationships of organisms expand the applicability of trace-fossil approaches to new areas of inquiry.

12.5.2 A Multitude of Data

Plant–insect associational studies of bulk floras or biotas require hundreds to (tens of) thousands of specimens. Such studies also capture data from a multitudinous array of specimens, plant morphotypes, insect damage types, localities, stratal levels, and habitats. As a result, data from plant–insect interactions become ideally suited for examinations of time series originating from bulk-collected floras from multiple stratal horizons. Such data are concordant with modern ecological techniques for examining trends in space, but importantly, the fossil data uniquely offer the opportunity for examining temporal patterns. For example, the effects of the K-Pg event in macroinfaunal habitats of the offshore marine realm in Spain and France took approximately 10^2–10^3 yr, according to recent high-resolution geochemical information (Sosa-Montes de Oca et al. 2013). By contrast, in terrestrial, angiosperm-dominated communities of North Dakota the recovery time was 10^7 yr (Wilf et al. 2006), a difference of approximately 4–5 orders of magnitude.

12.5.3 Unique Ecological Data

The analyses of plant–insect interaction trace fossils are the most successful way of capturing large datasets of trophic data in the fossil record. Because of the absence of interpretable insect body-fossil data in most deposits, plant–insect interactional data can provide trophic data that otherwise would be unavailable. These paleoecological data also can be used as raw input in other approaches recently used in the fossil record, such as the construction of site-specific food webs (Wilf 2008; Dunne et al. 2012), and studies of niche conservatism through time (Solé et al. 2002). Similarly, unique ecological data such as detailed ichnofabric analysis from polished microscopic sections can reveal a variety of specific organism–substrate relationships that are unavailable from more traditional, more macroscopically based ichnological approaches.

12.5.4 Ability to Test and Generate Hypotheses

Because of typically large datasets, trace-fossil data can provide the type and amount of data that are available to test hypotheses established by modern plant–insect interaction theory. Alternatively, trace-fossil data also can generate hypotheses from deep-time trends of plant–insect interactions that are testable using modern data. Specific examples of fossil plant–insect associational data, such as lag times involved in post-event occupation of ecospace, increasingly are becoming important for evaluating hypotheses and concepts that are derived from modern theories. Likewise, in the shallow marine realm, hypotheses regarding the phases of post-event organism colonization of sediment and hardrock substrates can provide evidence for or against the geochronologically instantaneous establishment of burrowing or whether a more prolonged colonization process is involved.

12.5.5 Employing Data from Both the Preserved and "Nonpreserved" Sedimentary Record

An analysis of the material in passively infilled, earliest Danian burrows supports other significant types of data that have been gathered from the sedimentary record for the post-K-Pg recovery event. Collectively, these data provide inferences indicating the prevalent environmental conditions at that time. In some cases, there is recognition of a laterally extensive horizon of colonization if the original layering in sediment was preserved. However, if the initial sediment is not preserved, burrows store the lost sedimentary record, and provide some portion of information. Such information can be used to characterize different phases of colonization and provide an evaluation of the relative time to recovery.

In the terrestrial plant–insect associational record, relevant data can be found in more distant basins. Such basins can provide quantifiable insect damage data that may be closer to the major event boundary of interest. In both the marine and continental records, regionally extensive strata should be intensively explored for collection of data that are unavailable at historically more intensively explored but very local stratigraphic sections.

12.5.6 Data with Enhanced Biostratigraphic Resolution

A consequence of the impact of the K-Pg boundary event on microplankton is the near-complete absence of these groups in the first few centimeters immediately above the K-Pg boundary. The K-Pg event strongly affected diatoms, calcareous nannoplankton, phytoplankton, and planktic foraminifera. Depauperate microplanktic biotas impede a high-resolution biostratigraphy, resulting in doubts about completeness of the sedimentary record or the existence of hiatuses that are biostratigraphically unresolvable. However, in the Agost section, there is the initial appearance of Paleogene planktonic foraminifera located a few centimeters above the K-Pg boundary (Arenillas et al. 2004), calibrated to ~5.7–6.7 kyr later in the K-Pg boundary. The high-resolution (intrasubzone), stable isotope data that were obtained from infill material of trace fossils in the Agost section show a close correspondence with those from the upper Maastrichtian and lower Danian sediments. These data provide evidence for completeness, and the absence of hiatuses within biostratigraphic resolution (intrasubzone) (Rodríguez-Tovar et al. 2006). On land, a similar exploration of the thin and locally present FU0 layer in the Williston Basin, for example, can reveal illuminating patterns of plant–insect interactions at the K-Pg boundary that could be different from the subjacent latest Maastrichtian and superjacent earliest Paleocene strata (Labandeira et al. 2002b).

12.5.7 A Major Role in the Debate on Catastrophic vs. Gradual Extinction

The perennial debate about how catastrophic was the end-Cretaceous mass extinction, include two, highly differentiated and opposite positions of catastrophic versus gradual perspectives (e.g., Smit 1990 vs. Keller et al. 1995, respectively). Catastrophism versus gradualism perspectives still represent an unsolved flash point regarding the biologic consequences of the end-Cretaceous event. This issue, in part, can be related to the presence/absence of several species of microfossils, principally planktic foraminiferans and calcareous nannofossils, immediately below and above the K-Pg boundary, data that has been perceived to support both positions. Maastrichtian taxa found in Danian sediments are considered as totally or partially reworked (e.g., Smit 1990; Pospichal 1994; Henriksson 1996; Molina et al. 1998; Tantawy 2003; Gallala et al. 2009), or as taxa that survived the disaster, but rapidly disappear during the earliest Danian (e.g., Perch-Nielsen et al. 1982; Keller 1988; Keller et al. 1995; Gardin and Monechi 1998; Gardin 2002; Bown 2005).

Within this debate, the sedimentological context of trace fossils is important. For example, the redistribution of microfossils by tracemakers, even immediately below the K-Pg boundary, remains a possibility that has been considered minimally and currently lacks deeper analyses by micropaleontologists and paleoecologists (Thierstein and Okada 1979; Thierstein 1981; Smit and Romein 1985; Pospichal and Wise 1990; Pospichal et al. 1990; Henriksson 1996; Pospichal 1996; Romein et al. 1996; Mai et al. 2003; Bown 2005; Lamolda et al. 2005). Recently, detailed analyses focusing on calcareous nannofossils from the burrow fillings of *Zoophycos*, *Thalassinoides*, *Chondrites,* and their surrounding sediments across the K-Pg boundary transition at the Bidart (Rodríguez-Tovar et al. 2010), and Caravaca (Kędzierski et al. 2011) sections, revealed Danian calcareous nannofossils in lightly-hued Maastrichtian sediments. In these boundary sedimentary sequences, it was only the dark infillings of Danian burrows that piped down across the K-Pg boundary, and conversely, Cretaceous nannoplankton occurred above the boundary layer that was conveyed up onto the seafloor by earliest Danian tracemakers such as *Thalassinoides* through burrow excavation (Rodríguez-Tovar et al. 2010; Kędzierski et al. 2011).

The response of generalized to specialized insect herbivores to their plant-host spectrum after the end-Cretaceous event can provide a terrestrial perspective. Although the terrestrial stratigraphic record is poorer than the marine record at this time, the considerable delay in the recovery of associational diversity and specialization levels to that of the latest Maastrichtian is significant. The presence of lag times from 10^4 to 10^5 orders of magnitude between the rapid response of the marine realm, versus the much more prolonged terrestrial recovery, may hint at differences in ecological structure. The ecological recovery potential and flexibility of the shallow marine realm evidently is considerably greater than that of the terrestrial realm.

12.5.8 Understanding Ecologic and Evolutionary Response to Future Environmental Crises

Uncertainties regarding the effect of the K-Pg mass extinction event on evolutionary and ecological aspects of the biota can be addressed by analogy to the response of modern organisms soon after recent disasters. Although a comparison of paleoenvironmental events with recent examples of environmental crises is rarely applied, nevertheless it is a useful tool (Kuhnt et al. 2005) to understand biotic response to dramatic past, recent, and future environmental change. The response of tracemakers after the K-Pg boundary event as well as those recorded after a drastic environmental disaster occurring at Doñana National Park in southern Spain (Rodríguez-Tovar and Martín-Peinado 2009; Martín-Peinado and Rodríguez-Tovar 2010) – and a parallel crisis associated with the Tinto river marsh at Huelva (Rodríguez-Tovar and Martín-Peinado 2014), in southwestern Spain—indicate that high concentrations of heavy metals accumulated in soils and sediments can be dispersed at geologically ephemeral time scales (Rodríguez-Tovar and Martín-Peinado 2011). These two, recent incidents reveal that a better understanding of significant paleoenvironmental change, either abrupt or extended in time, can have profound consequences for the biota, their lag recovery times, and colonization of previously “uninhabitable” habitats.

Though not discussed in this contribution, related studies relevant to the recovery of plant–insect interactions have been done in real time in defaunation experiments of small, mangrove islands in Florida Bay. These studies have recorded the lag times of recolonization of major plant and insect groups and their associations following complete island defaunation (Simberloff and Wilson 1969). The pattern of the re-establishment of major trophic groups (Simberloff 1976), including generalized and specialized associations of a local biota is relevant to issues such as the return of plant–insect associations after the K-Pg event.

12.6 Conclusions

Based on the results of studies from the terrestrial and marine realm that are detailed in this contribution, there are several major applications of ichnological data, some of which cannot be replicated solely by examination of body-fossil data. For a better understanding of the consequences of major crises in the history of life, such as the K-Pg ecological crisis, the combination of ichnological data with body-fossil and physical data is essential, such as analyses of the diversity and abundance of insect damage on plant hosts in conjunction with various sedimentological and geochemical studies. Integration of such data provides a realistic assessment of organismic response that takes into account all of the major, relevant parameters involved. These features are: (1) the environment in the broadest sense of the term; (2) the organisms themselves; (3) organismic behavior and organism interactions with one another and their environment; and (4) and the temporal dimension that includes event durations and times to recovery. Application of all four aspects of the data provides a more integrative and complete approach toward understanding environment–organism interactions during crucial ecologic crises in the fossil and associated sedimentological record. Moreover, understanding organism response to such events can be put to practical use in approaching similar catastrophes for the future.

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Chapter 13
The Phanerozoic Four Revolutions and Evolution of Paleosol Ichnofacies

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13.1 Introduction

Which is the appropriate scale to analyze how paleosol ichnology reflects major evolutionary events in the history of life? Surely, the scale of the ichnofacies model, which arises from the most elementary aspect of scientific reasoning: to recognize recurrent patterns. Repetitive ichnoassemblages are typical of different periods in the history of life and that they can be grouped in major categories: Seilacherian ichnofacies. Ichnofacies are recurrent associations of trace fossils in time and space, and it is their recurrence that grants the essential, broad scale, data for this evolutionary analysis. Mesozoic ichnoassemblages include or are dominated by crayfish and earthworm trace fossils, whereas insect trace fossils dominate most Cenozoic assemblages (Genise 2016). To ignore these patterns would result minimally in an unacceptable loss of scientific information.

Life on Earth has been evolving since its beginning during the Archean. Accordingly, paleosol ichnofacies, as a reflection of behaviors and ecologic preferences of soil-inhabiting organisms, should also have evolved. As pointed out by MacEachern et al. (2007, 2012), the *Coprinisphaera* Ichnofacies cannot be older

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than the Paleogene when grass-dominated communities appear. What happened, then, with paleosol ichnofacies prior to the Cenozoic? How did ichnofacies evolve? It is impossible to think in static ichnoassemblages from the oldest paleosols-bearing rhizoliths recorded in the Early Devonian to the youngest ones in the Holocene. Alternatively, tracking ichnofacies evolution, an uncommon approach in theoretical ichnology, should allow us a better understanding of evolution of life itself and it would represent a significant contribution of ichnology for its delayed integration with other paleontological disciplines. The idea of major evolutionary changes characterizing the history of life has been designed mostly from data and interpretations provided by paleontological disciplines other than ichnology. Can ichnology, and particularly paleosol ichnology, with its own major evolutionary steps, offer a parallel exploration to the history of life?

On the other hand, which is the influence of soil types on the evolution of paleosol ichnofacies? Much of the major events in life history, such as the end-Permian crisis, the advent of angiosperms during the mid-Cretaceous, or the end-Cretaceous mass extinction, produced no significant changes in the nature of soils. In contrast, it is clear that the increasing complexity of terrestrial ecosystems, from early microbial habitats to the development of complex plant communities, triggered the appearance of the different soil types. Retallack (1992a) proposed that the principal changes of land environments were deployed in a stepwise mode following the origin of different plant formations, from microbial earths to grasslands. Is it possible to use paleosol ichnofacies to test this hypothesis?

In this chapter, we will travel along a two-way road looking at the consequences, if any, that major evolutionary changes had on paleosol ichnofaunas, and vice versa. As a result, we expect to unveil the big picture of the evolution of paleosol ichnofacies accompanying major evolutionary changes in the history of life.

13.2 The Rhizolith Revolution: The Paleozoic Shy Beginning of Paleosol Trace Fossils

The Paleozoic was a very innovative period for history of life (see Chaps. 3–7). It includes the appearance of the first soils bearing subaerial trace fossils (Tables 13.1 and 13.2; Figs. 13.1 and 13.3). Before that, different paleosol features produced mostly by chemical and physical weathering have been recognized in Archean and Proterozoic rocks (Retallack 2001a). These characters would include microbial borings, soil horizons, peds, illuviation argillans, cryogenic cracks, slickensides, nodules, and sepic-plasmic clay microfabrics (Retallack 1992b). These paleosols older than 1 Ga would include Entisols, Inceptisols, Aridisols, Gelisols, Andisols, Vertisols, and Oxisols, whereas "green clays" would have formed in a reducing atmosphere older than 2.2 Ga (Retallack 2001a). Microbial earths would have developed also in terrestrial environments during the Precambrian (Driese et al. 1997).

For various reasons, including the absence of most groups of soil invertebrates that produce preservable traces, paleosol trace fossils are scarce during the Paleozoic.

Table 13.1 Recorded cases of root and invertebrate trace fossils in paleosols

Locality	Formation	Age	Trace fossils	References
Yemen, Ma'rib	Unnamed	Holocene	Root traces	Pietsch and Kühn (2012)
South Africa, Clanwillam	Unnamed	Holocene	Termite earth mounds	Moore and Picker (1991)
South Africa, Western cape	Unnamed	Holocene	Root casts	Cramer and Hawkins (2009)
Sultanate of Oman, Wahiba Sand Sea	Unnamed	Holocene	*Celliforma* *Coprinisphaera* *Rosellichnus* Termite nests	Radies et al. (2005)
USA, San Miguel Island	Unnamed	Holocene	Rhizoconcretions	Stewart and Thorson (1994)
New Zealand, Karikari, and Aupouri Peninsulas	Unnamed	Quaternary (Holocene and Pleistocene)	*Cladichnus* *Planolites* *Skolithos* *Taenidium* Insect burrows Root traces	Gregory et al. (2004)
Spain, Canary Islands	Unnamed	Quaternary (Holocene and Pleistocene)	*Rebuffoichnus guanche* *Rebuffoichnus casamiquelai* *Tombownichnus parabolicus* *Tombownichnus plenus* *Palmiraichnus castellanosi* "Acridian ootheca" Rhizoliths	Alonso-Zarza and Silva (2002), Mikúlaš and Genise (2003), Genise and Edwards (2003), Alonso-Zarza et al. (2008), Meco et al. (2010, 2011), La Roche et al. (2014), Genise et al. (2013a)
Australia	Unnamed	Quaternary (Holocene and Pleistocene)	*Rebuffoichnus casamiquelai*	Lea (1925)
Argentina, Quequén	Unnamed	Late Pleistocene-Holocene	Root traces	Tonello et al. (2002)
Uruguay	Sopas	Late Pleistocene	*Castrichnus incolumis* *Coprinisphaera* *Taenidium serpentinum* Meniscate burrows Rhizoliths	Ubilla (1996), Verde et al. (2007)

(continued)

Table 13.1 (continued)

Locality	Formation	Age	Trace fossils	References
Argentina, Santa Fé	Tezanos Pinto	Late Pleistocene	*Coprinisphaera* Ant nests Root traces	Iriondo and Krohling (1996), Kröhling (1999)
Argentina, Buenos Aires	Buenos Aires	Late Pleistocene	*Barberichnus bonaerensis* *Coprinisphaera* Termite nests	Laza (1995, 2006a), Genise et al. (2000)
Argentina, Buenos Aires and Santa Fé	Luján	Late Pleistocene	*Coprinisphaera* Ant nests	Laza (1995, 1997), Genise et al. (2000)
Namibia	Homeb Silt	Late Pleistocene	*Taenidium* *Termitichnus* Pelletal burrows and chambers	Smith et al. (1993)
Namibia	Sossus Sand (Khommabes Carbonates)	Late Pleistocene	*Taenidium* *Termitichnus* *Digitichnus*	Smith and Mason (1998)
Argentina, Tucumán	Tafí del Valle	Late Pleistocene	*Coprinisphaera*	Fontaine et al. (1995)
South Africa, Still Bay	Waenhuiskrans	Middle and Late Pleistocene	Rhizoliths	Roberts et al. (2008)
Italy, Santo Stefano Island	Villa Giuli	Pleistocene	cf. *Rebuffoichnus* or cf. *Fictovichnus*	Sacchi and Petti (2008)
Canada, Ontario	Pleistocene sands	Pleistocene	Rhizoconcretions	Kindle (1923)
USA, Sapelo Island	Unnamed	Pleistocene	*Taenidium* Root traces	Gregory et al. (2004)
New Zealand, Northland	Unnamed	Pleistocene	Ant burrows Bee burrows Bee cells “*Phoebichnus* look-alike” root system	Gregory and Campbell (2003), Gregory et al. (2009)
Australia	Bridgewater	Pleistocene	*Palmiraichnus*	Zeuner and Manning (1976), Houston (1987)

USA, Washington	Washtucna Soil	Pleistocene	Cicada burrows Root traces	O’Geen and Busacca (2001), Blinnikov et al. (2002)
Ecuador, Quito	Cangahua	Pleistocene	*Coprinisphaera*	Sauer (1955), Clapperton and Vera (1986), Laza (2006b), Sánchez et al (2013)
Brazil, Osorio	Chuí	Pleistocene	*Celliforma* *Coprinisphaera* *Krausichnus* *?Monesichnus* *Palmiraichnus* *Taenidium barretti* *Termitichnus* *Vondrichnus* Rhizoliths Wasp cocoons	Netto et al. (2007)
British West Indies, Cayman Brac	Ironshore	Pleistocene	Rhizoliths	Jones and Ng (1988)
Spain, Mallorca	Unnamed	Pleistocene	Rhizoconcretions	Calvet Rovira et al. (1975), Klappa (1980)
Spain, Ibiza	Unnamed	Pleistocene	Rhizoliths	Klappa (1980)
Kenya, East Turkana	Koobi Fora	Pleistocene	Root traces Root casts	Cohen (1982), Mount and Cohen (1984)
USA, Louisiana	Citronelle	Early Pleistocene	Tree casts	Mossa and Schumacher (1993)
South Africa, Namaqualand	Unnamed	Early Pleistocene	*Planolites* *Skolithos* *Taenidium* *Termitichnus namibiensis* Vertical rhizoconcretions	Miller and Mason (2000)
Tanzania, Olduvai Gorge	Olduvai	Early Pleistocene	Meniscate burrows Rhizoliths Termite and ant traces	Ashley and Driese (2000)

(continued)

Table 13.1 (continued)

Locality	Formation	Age	Trace fossils	References
Argentina, Entre Ríos and Santa Fé	Ensenada	Early Pleistocene	*Coprinisphaera*	Frenguelli (1938)
Spain, Mallorca	Unamed	Pliocene-Early Pleistocene	*Rebuffoichnus*	Mas and Ripoll (2010)
India, Punjab	Boulder	Pliocene-Pleistocene	*Termitichnus* Meniscate burrows	Tandon and Naug (1984)
Argentina, Buenos Aires	San Andrés	Late Pliocene-Early Pleistocene	*Barberichnus bonaerensis* *Coprinisphaera*	Laza (1995, 2006a), Cantil et al. (2013)
Kenya and Tanzania	Laetoli	Late Pliocene	*Coprinisphaera* *Celliforma* *Lazaichnus amplus* Wasp cocoons Termite nests Burrows Root traces	Sands (1987), Ritchie (1987), Darlington (2005), Krell and Schawaller (2011), Darlington (2011)
Argentina, Buenos Aires	Chapadmalal	Late Pliocene	*Coprinisphaera* Ant nests Termite nests	Laza (1995)
Argentina, Buenos Aires	Barranca de los Lobos	Late Pliocene	*Tacuruichnus farinai*	Genise (1997)
Argentina, Jujuy	Maimará	Early Pliocene	*Coprinisphaera*	Laza (2006b)
Argentina, Salta and Jujuy	Piquete	Early Pliocene	*Coprinisphaera*	Alonso et al. (1982)
United Arab Emirates, Abu Dhabi	Unnamed	Early Pliocene	*Rosellichnus arabicus* Ant nests	Genise and Bown (1996)
Argentina, Buenos Aires	Monte Hermoso	Late Miocene-Early Pliocene	*Coprinisphaera*	Laza (1986b)
United Arab Emirates, Abu Dhabi	Baynunah	Late Miocene	*Rosellichnus arabicus* Termite nests	Bown and Genise (1993)
Pakistan	Dhok Pathan	Late Miocene	*Coprinisphaera*-like traces	Retallack (1991a)

Argentina, Neuquén, Río Negro, Chubut and Santa Cruz	Collón-Curá	Late Miocene	*Celliforma* *Coprinisphaera* *Lazaichnus fistulosus* *Fictovichnus sciuttoi* *Rosellichnus patagonicus* *Teisseirei barattinia* Burrows	Frenguelli (1939), Genise and Bown (1996), Laza (1986b), Villafañe et al. (2008), Bedatou (2010), Sarzetti et al (2014)
Argentina, San Luis	Paso de Las Carretas	Late Miocene	*Celliforma* *Coprinisphaera*	Pascual and Bondesio (1981)
Argentina, San Juan	Las Flores	Late Miocene	*Coprinisphaera*	Contreras (1996)
Argentina, Catamarca	Andalhualá	Late Miocene	*Coprinisphaera*	Genise et al. (2000)
Argentina, La Pampa and Buenos Aires	Cerro Azul	Late Miocene	*Attaichnus kuenzelii* *Coprinisphaera* *Quirogaichnus coniunctnus*	Laza (1982, 2006b), Genise et al. (2013b)
Chad	Chad Basin	Late Miocene	*Coatonichnus globosus* *Microfavichnus alveolatus* *Quirogaichnus* *Termitichnus schneideri* *Vondrichnus planoglobus* Root traces	Duringer et al. (2006, 2007)
USA, Oregon	Rattlesnake	Late Miocene	Insect burrows Root traces Root systems	Retallack et al. (2002a)
Perú, Loreto	Pebas	Late Miocene	*Planolites* *Taenidium* Root traces	Rebata et al. (2006)
Spain, Teruel	Unit II	Late Miocene	Cf. *Cellifroma* Root traces	Alonso-Zarza et al. (2012)
USA, Kansas	Ogallala	Middle Miocene-Early Pliocene	*Daimoniobarax nephroides* *Daimoniobarax tschinkeli* Possible dung beetle burrows Root traces	Martin and Bennett (1977), Gobetz and Martin (2006), Yelinek and Chin (2007), Smith et al. (2011)

(continued)

Table 13.1 (continued)

Locality	Formation	Age	Trace fossils	References
Kenya	Maboko	Middle Miocene	Root traces	Retallack et al. (2002b)
USA, Colorado	Pawnee Creek	Miocene	*Beaconites kytosichnus* *B. knestosichnus* *Parowanichnus perirhizaterion* Rhizoliths	Hembree and Hasiotis (2008)
Spain	"Gypsum and grey shales"	Miocene	*Celliforma* *Cellicalichnus* aff. *habari* *Rosellichnus* cf. *arabicus* *Spongeliomorpha* *Labyrintichnus terrerensis* *Taenidium barretti* *Beaconites filiformis* *Polykladichnus aragonensis*	Uchman and Alvaro (2000)
Kenya	Hiwegi (Kibanga Mb.)	Miocene	*Cellicalichnus habari* Root traces Burrows Wasp cocoons	Thackray (1994), Genise (2000)
Kenya	Hiwegi (Fossil Bed Mb.)	Miocene	Root traces Cocoons	Retallack et al. (1995)
Honduras, Tegucigalpa	El Periodista (Member)	Miocene	*Palmiraichnus*	Domínguez-Alonso and Coca-Abia (1998)
Argentina, Santa Cruz	Pinturas	Early Miocene	*Coprinisphaera* *Palmiraichnus* *Skolithos* *Syntermesichnus fontanai* *Taenidium barretti* Burrows Earthworm diffuse boxwork Rhizoliths Root traces	Bown et al. (1988), Bown and Laza (1990), Genise and Bown (1994a), Genise and Hazeldine (1998a), Kramarz and Bellosi (2005), Cosarinsky et al. (2005), Laza (2006b), Bedatou et al. (2007, 2008b), Genise et al. (2008b), Bedatou (2010)

Argentina, Santa Cruz	Santa Cruz	Early Miocene	*Celliforma* *Coprinisphaera* Ant nests	Genise and Bown (1994a), Tauber (1996)
USA, Florida	Tampa	Early Miocene	*Celliforma nuda*	Brown (1935), Genise (2000)
Ethiopia	Bakate	Early Miocene	Termite nests	Bown and Genise (1993)
Germany	Unnamed	Early Miocene	*Celliforma*	Sauer and Schremmer (1969)
Argentina, Neuquén	Puesto Burgos	Late Oligocene-Early Miocene	*Coprinisphaera* Bee cells	Pazos (2011)
USA, Oregon	John Day	Late Oligocene-Early Miocene	*Pallichnus dakotensis* *Edaphichnium lumbricatum* *Taenidium* *Scaphichnium* *Termitichnus* Root traces	Retallack et al. (2000), Retallack (2004)
Spain, Aragón	Sariñena and Uncastillo	Oligocene–Early Miocene	*Coprinisphaera* *Scolicia* Ant nests Bee cells Dung beetle burrows Dung beetle nests and boli Horizontal crawling traces of arthropods Rhizoliths Spider burrows	Hamer et al. (2007)
Spain, Ebro	Solsona	Oligocene	*Taenidium* Vertical ornamented burrows	de Gibert and Sáez (2009)
Germany	Unnamed	Oligocene	*Celliforma*	Schütze (1907)
Argentina, Chubut	Deseado	Oligocene	*Coprinisphaera* *Teisseirei*	Frenguelli (1938), Laza (1986a)

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Table 13.1 (continued)

Locality	Formation	Age	Trace fossils	References
USA, South Dakota	Brule	Oligocene	*Cellicalichnus ficoides* *Celliforma* *Pallichnus dakotensis* Root traces	Retallack (1983, 1984), Genise (2000)
Argentina, Mendoza	Rodados lustrosos	Oligocene	*Coprinisphaera*	Genise et al. (2000)
Egypt, El Fayum	Jebel Qatrani	Oligocene	*Fleaglellius pagodus* *Krausichnus trompitus* *Macanopsis* *Masrichnus issawii* *Scaphichnium hamatum* *Termitichnus qatrani* *Termitichnus simplicidens* *Vondrichnus obovatus* Crayfish? burrows Rhizoliths	Bown (1982), Genise and Bown (1994b)
Czech Republic	Doupov Mountains	Early Oligocene	*Cf. Celliforma* and/or *Rebuffoichnus*	Fejfar and Kaiser (2005)
USA, Colorado	White River	Early Oligocene	*Cellicalichnus ficoides* *Edaphichnium* *Fictovichnus* isp. *Macanopsis* *Pallichnus dakotensis* *Parowanichnus* *Planolites* Backfilled burrows Rhizoliths Wasp cocoons	Retallack (1983), Hembree and Hasiotis (2007)

USA, Montana	Renova	Late Eocene-Early Oligocene	*Steinichnus* *Taenidium* Root traces Wasp cocoons	Sheldon and Tabor (2009), Sheldon and Hamer (2010)
USA, Wyoming	Bridger	Late Eocene	*Celliforma spirifer*	Brown (1934), Genise (2000)
Antarctica, Seymour Island	La Meseta	Late Eocene	*Coprinisphaera*	Laza and Reguero (1990), Laza (2006b)
France	Unnamed	Late Eocene	*Celliforma arvernensis*	Ducreux et al. (1988)
England, Isle of Wight	Bembridge Limestone	Late Eocene	*Fictovichnus sciuttoi*	Edwards et al. (1998), Armenteros and Daley (1998), Genise et al. (2007)
Argentina, Salta	Lumbrera	Middle–Late Eocene	Root traces	Del Papa (2006)
Uruguay	Queguay	Middle Eocene–Middle Oligocene	*Celliforma germanica* *C. spirifer* *C. rosellii* *Fictovichnus gobiensis* *Fictovichnus sciuttoi* *Rosellichnus isp.* Bee nests “Agapostemonini cluster” Rhizoliths	Martínez et al. (1997, 2001), Verde and Genise (2007), Alonso-Zarza et al. (2011)

(continued)

Table 13.1 (continued)

Locality	Formation	Age	Trace fossils	References
Argentina, Chubut	Sarmiento	Middle Eocene–Early Miocene	*Chubutolithes gaimanensis* *Coprinisphaera lazai* *Coprinisphaera murguiai* *Coprinisphaera kraglievichi* *Coprinisphaera kheprii* *Coprinisphaera tonnii* *Feoichnus challa* *Lazaichnus fistulosus* *Pallichnus* *Taenidium* *Teisseirei barattinia* *Tombownichnus pepei* *Tombownichnus parabolicus* Burrows Earthworm diffuse boxwork Root marks Meniscate burrows Pedotubules Rhizoliths Rhizoconcretions	Andreis (1972), Laza (1986a), Bown and Ratcliffe (1988), Genise and Bown (1990), Bellosi et al. (2001, 2002a, 2010), Mikúlaš and Genise (2003), Bellosi and Genise (2004), Genise and Cladera (2004), Genise et al. (2004, 2008b), Krause and Genise (2004), Cosarinsky et al. (2005), Laza (2006b), Bedatou et al. (2007, 2008b). Krause et al. (2008, 2010), Sánchez and Genise (2009), Sánchez et al. (2010b), Bellosi and González (2010), Bedatou (2010)
France, Bouxwiller	Unnamed	Eocene	Cf. *Fictovichnus gobiensis* Cf. *Fictovichnus sciuttoi*	Kuntz (2010, 2012)
USA, Utah	Uinta	Eocene	*Edaphichnium* Ant nests Meniscate burrows Wasp cocoons	Sandau (2005)
Argentina, Chubut	Koluel Kaike	Early–Middle Eocene	*Coprinisphaera* *Feoichnus challa* Root traces	Laza (2006b), Krause and Bellosi (2006), Krause et al. (2008)

Uruguay, Nueva Palmira	Asencio	Early Eocene	*Celliforma* *Coprinisphaera murguiai* *Coprinisphaera kraglievichi* *Corimbatichnus fernandezi* *Elipsoideichnus meyeri* *Krausichnus* *Guerraichnus poligibbus* *Lazaichnus fistulosus* *Monesichnus ameghinoi* *Palmiraichnus castellanosi* *Rebuffoichnus barattinia* *Teisseirei* *Tombownichnus plenus* *Tombownichnus parabolicus* *Uruguay auroranormae* *Uruguay rivasi* Meniscate burrows Root traces Termite nests	Roselli (1987), Genise and Laza (1998), Genise et al. (1998), González (1999), Genise and Verde (2000), Genise and Zelich (2001), Mikúlaš and Genise (2003), Genise et al. (2004, 2008b), Cosarinsky et al. (2005), Laza (2006b), Verde and Genise (2010), Tófalo and Pazos (2010), Bellosi et al. (2016)
USA, Wyoming	Wasatch	Early Eocene	*Camborygma eumekenomos* *Celliforma* *Eatonichnus* *Planolites* *Skolithos* Root traces	Zonneveld et al. (2006), Bohacs et al. (2007), Hasiotis and Honey (2000)

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Table 13.1 (continued)

Locality	Formation	Age	Trace fossils	References
Argentina, La Pampa	Gran Salitral	Early Eocene	*Celliforma germanica* *Celliforma rosellii* *Rosellichnus isp.* *Rebuffoichnus* *Skolithos linearis* *Taenidium barretti* *Teisseirei barattinia* Ornamented burrow fillings Plant traces Rhizoliths	Melchor (2002), Melchor et al. (2002)
Argentina, Jujuy	Maíz Gordo	Late Paleocene–Early Eocene	*Krausichnus trompitus* Root traces	DeCelles et al. (2011)
USA, Wyoming	Willwood	Late Paleocene–Early Eocene	*Camborygma litonomos* *Cylindricum* *Edaphichnium lumbricatum* *Ichnogyrus* *Macanopsis* *Naktodemasis bowni* *Planolites* *Scaphichnium hamatum* *Steinichnus* Cocoon traces Meniscate burrows Pedogenically modified *Camborygma litonomos* Rhizoliths Root traces	Bown and Kraus (1983, 1987), Hasiotis et al. (1993a), Kraus and Hasiotis (2006), Smith et al. (2008a, b, c, 2009)

USA, Utah	Claron	Paleocene-Eocene	*Camborygma eumekenomos* *Camborygma litonomos* *Celliforma* *Eatonichnus uthaensis* *Eatonichnus claronensis* *Fictovichnus* *Parowanichnus formicoides* Wasp cocoons	Bown et al. (1997), Hasiotis and Bown (1996)
USA, Wyoming	Hanna	Late Paleocene	*Camborygma eumekenomos* Root traces	Hasiotis and Honey (1995, 2000)
Argentina, Rocas Coloradas	Peñas Coloradas	Late Paleocene	*Eatonichnus*	Genise et al. (2001a, 2008b)
USA, Wyoming	Unnamed Upper Paleocene unit	Late Paleocene	*Camborygma* Root traces	Hasiotis and Honey (1995)
USA, Wyoming	Fort Union	Late Paleocene	*Camborygma symplokonomos* *Camborygma eumekenomos* *Camborygma litonomos* Root traces Rhizoconcretions	Hasiotis and Honey (2000), Kraus and Hasiotis (2006), Adams et al (2011)
Slovenia	Trstelj	Late Paleocene	Rhizoconcretions	Kosir (2004)
USA, North Dakota	Fort Union, Sentinel Butte Member	Early Paleocene	Undetermined burrows Root traces Stumps	Fastovsky and McSweeney (1991)
USA, Montana	Hell Creek	Late Cretaceous	Root traces	Fastovsky et al. (1989)
Brazil, Bauru Basin	Adamantina	Late Cretaceous	*Coprinisphaera*	Souza Carvalho et al. (2009)
USA, Montana	Two Medicine	Late Cretaceous	*Celliforma* *Fictovichnus sciuttoi* *Skolithos* *Teisseirei* *Tombownichnus*	Martin and Varricchio (2011)

(continued)

Table 13.1 (continued)

Locality	Formation	Age	Trace fossils	References
Romania, Southern Carpathian Mountains	Sânpetru	Late Cretaceous	Burrows Crayfish? burrows Root traces	Therrien et al. (2009)
Romania, Tuştea	Densuş-Ciula	Late Cretaceous	Burrows Root traces	Therrien (2005)
Romania, Vurpăr	Red Continental Strata	Late Cretaceous	Burrows Root traces	Therrien (2005)
Argentina, Rio Negro	Allen	Late Cretaceous	*Fictovichnus sciuttoi*	Genise and Sarzetti (2011)
Argentina, Chubut	Laguna Palacios	Late Cretaceous	*Beaconites* *Cellicalichnus meniscatus* *Cellicalichnus chubutensis* *Loloichnus baqueroensis* *Rebuffoichnus casamiquelai* *Skolithos* *Taenidium* *Tombownichnus plenus* Earthworm diffuse boxwork Insect nests Root traces	Sciutto (1995), Sciutto and Martínez (1996), González (1999), Genise (2000), Bellosi and Sciutto (2002), Bellosi et al. (2002b), Genise et al. (2002a, 2004, 2007, 2008a, b), Mikúlaš and Genise (2003); Genise and Bellosi (2004), Bedatou et al. (2005, 2007, 2008a, b), Bedatou (2010)
Argentina, Chubut	Bajo Barreal	Late Cretaceous	*Pallichnus dakotensis* *Fictovichnus sciuttoi* Earthworms Ichnofabrics Insect traces Meniscate burrows Rhizoconcretions Root moulds	Sciutto and Martínez (1996), Bellosi et al. (2002b), Genise et al. (2007, 2008b), Umazano et al. (2008), Bedatou et al. (2008b), Bellosi et al. (2010), Bedatou (2010)

USA, Alaska	Prince Creek	Late Cretaceous	Root traces	Spicer and Parrish (1987)
France, Albas	Aquitaine Basin	Late Cretaceous	Root traces	Wright et al. (1995)
Gobi Desert, Mongolia	Djadokhta	Late Cretaceous	*Fictovichnus gobiensis* Rhizoliths	Johnston et al. (1996), Loope and Dingus (1999)
USA, Utah	Kaiparowits	Late Cretaceous	*Socialites tumulus* Burrows Root traces	Roberts and Tapanila (2006)
USA, Alabama	Tuscaloosa	Late Cretaceous	*Taenidium serpentinum* Root traces	Savrda et al. (2000)
USA, Arizona	Dakota	Late Cretaceous	*Cellicalichnus dakotensis*	Elliott and Nations (1998), Genise (2000)
Uruguay	Mercedes	Late Cretaceous	*Celliforma spirifer* *Celliforma germanica* *Fictovichnus gobiensis* Bee nests Rhizoliths Wasp cocoons	Veroslavsky and Martinez (1996), Veroslavsky et al. (1997), Tófalo and Pazos (2010), Alonso-Zarza et al. (2011)
Argentina, Santa Cruz	Mata Amarilla	Late Cretaceous	Rhizoliths Stumps	Varela et al. (2012)
South Korea, Kyongsangnamdo	Jinju	Cretaceous	Rhizoconcretions	Kim et al. (2002)
Argentina, Chubut	Castillo	Early Cretaceous	Root traces	Sciutto (1981); Bellosi et al. (2002b)
Argentina, Chubut	Cerro Barcino	Early Cretaceous	Rhizolith balls	Genise et al. (2010a)
Argentina, Chubut	Matasiete	Early Cretaceous	*Palaeophycus* *Planolites* *Taenidium* Root traces	Bellosi et al. (2002b), Paredes et al. (2003, 2007)

(continued)

Table 13.1 (continued)

Locality	Formation	Age	Trace fossils	References
Argentina, Santa Cruz	Bajo Tigre	Early Cretaceous	*Beaconites* *Castrichnus incolumis* *Dagnichnus titoi* *Loloichnus baqueroensis* *Taenidium* Earthworm diffuse boxwork Root traces	Genise (2001), Cladera et al. (2002), Bedatou et al. (2006, 2007, 2008a, b, 2009), Genise et al. (2008a, b), Bedatou (2010)
Argentina, Santa Cruz	Punta del Barco	Early Cretaceous	*Beaconites* *Castrichnus incolumis* *Cellicalichnus meniscatus* *Dagnichnus titoi* *Loloichnus baqueroensis* *Taenidium* Earthworm diffuse boxwork Root traces	Cladera et al. (2002), Bedatou et al. (2006, 2007, 2008a, b, 2009), Genise et al. (2008a, b), Bedatou (2010)
Spain, Soria	Tierra de Lara Group	Late Jurassic-Early Cretaceous	Root traces	Wright et al. (1995)
Argentina, Santa Cruz	Bajo Grande	Late Jurassic	*Beaconites* *Loloichnus baqueroensis* *Taenidium* Earthworm diffuse boxwork Root traces	Cladera et al. (2002), Bedatou et al. (2007, 2008a, b, 2009), Bedatou (2010)

USA, Colorado	Morrison	Late Jurassic	cf. *Ancorichnus* isp. *Camborygma litonomos* *Camborygma eumekenomos* *Camborygma airiokados* *Celliforma* *Coprinisphaera* cf. *Cylindrichum* cf. *Rosellichnus* isp. *Naktodemasis bowni* *Scoyenia* isp. *Steinichnus* "Ant nests" "Bee nests" "Beetle burrows" Cocoons Crayfish burrows Horizontal striated burrow Plant and root traces Quasi-vertical striated burrow Rhizoliths "Termite nests" Vertical burrows Vertical striated burrows	Hasiotis (1993, 1999, 2004), Hasiotis and Demko (1996, 1998), Hasiotis and Kirkland (1997), Hasiotis et al. (1998, 2004), Fiorillo (1999), Demko et al. (2004), Parrish et al. (2004), Bromley et al. (2007)
Iran, Binalud Mountains	Aghounj	Early-Middle Jurassic	*Cellicalichnus antiquus*	Fürsich et al. (2010)
South Africa	Elliot/Clarens	Early Jurassic	*Taenidium* "Termite nests" Root traces	Smith and Kitching (1997), Bordy (2008), Bordy et al. (2004, 2005, 2009), Genise et al. (2005)

(continued)

Table 13.1 (continued)

Locality	Formation	Age	Trace fossils	References
Poland, Holy Cross Mountains	Unnamed	Early Jurassic	*Planolites* *Scoyenia* Arthropod burrows Chambered insect nests Earthworm burrows Radial chambers	Pieńkowski and Niedźwiezki (2008)
Canada	McCoy Brook	Early Jurassic	*Planolites* Burrows Root traces	Tanner (1996)
USA	East Berlin	Early Jurassic	*Palaeophycus striatus*	Gierlowski-Kordesch (1991)
Poland	Zajage	Early Jurassic	*Scoyenia* *Spongeliomorpha* Root traces	Gierlinski et al (2004)
USA, Arizona	Owl Rock	Late Triassic	Crayfish burrows Root traces	Tanner (2000)
USA, Arizona	Chinle	Late Triassic	*Archeoentomichnus metapolypholeos* *Camborygma symplokonomos* *Camborygma eumekenomos* *Camborygma litonomos* *Camborygma araioklados* *Taenidium* *Taenidium serpentinum* *Skolithos* *Naktodemasis bowni* “Bee cells” “Beetle burrows” Inclined burrows J-shaped burrows Rhizoconcretions Root traces	Hasiotis and Mitchell (1993), Hasiotis (1993), Hasiotis et al. (1993b, 2004), Hasiotis and Dubiel (1993a, b, 1994, 1995), Kowaleski et al. (1998), Therrien and Fastovsky (2000), Cleveland et al. (2008), Lucas et al. (2010), Tanner and Lucas (2012)

Argentina, La Rioja	Ischigualasto	Late Triassic	*Taenidium* *Skolithos* Rhizoliths	Melchor et al. (2001), Genise et al. (2001b, 2004)
Antarctica	Lashly	Middle Triassic	Fossil roots Insect? burrows	Retallack and Alonso-Zarza (1998)
Antarctica, Kitching Ridge	Fremeouw	Early Triassic	Burrows Crustacean burrows Root traces	Miller and Collinson (1994), Miller and Smail (1996), Retallack et al. (1996a), Babcock et al. (1998), Miller et al (2001)
Australia, New South Wales	Narrabeen Group	Early Triassic	*Skolithos* Crayfish burrows Earthworm burrows Insect burrows Root traces	Retallack (1976, 1997a)
South Africa	Katberg	Late Permian–Early Triassic	*Katbergia carltonichnus* *Macanopsis* *Scoyenia* *Skolithos* Root traces	Retallack et al. (2003), Gastaldo and Rolerson (2008)
China, Xinjiang Uyghur	Turpan Basin	Late Permian–Early Triassic	Root traces Rhizoliths	Thomas et al. (2011)
Russia, Arkhangelsk Oblast	Salarevo	Late Permian	Root traces	Yakimenko et al. (2000)
Russia, Tetyushi	Urzhumskii, Severodvinskii, and Vyatskii horizons	Late Permian	Root traces	Inozemtsev et al. (2011)
Antarctica, Transantarctic Mountains	Buckley	Late Permian	Root traces	Retallack et al. (1996a)

(continued)

Table 13.1 (continued)

Locality	Formation	Age	Trace fossils	References
USA, New Mexico	Abo	Late Permian	*Scoyenia* Adhesive meniscate burrows Rhizoconcretions	Kessler et al. (2001), Mack et al. (2003)
Antarctica, Victoria Land	Beacon Supergroup	Permian-Triassic	*Skolithos* Root traces	Retallack et al. (1995, 1997)
Antarctica, Prydz Bay	Unnamed	Permian-Triassic	Root traces	Turner (1993)
USA, Kansas	Speiser Shale	Early Permian	Rhizoliths	Hembree et al. (2005)
China, Ghizou	Liangshan	Early Permian	Root traces	Wang et al. (2013)
USA, Nebraska	Lansing-Kansas City Groups	Late Carboniferous	Root traces	Prather (1985)
Russia	Moscow and Mezen Continental-Platform Basins	Late Carboniferous	Root traces	Kabanov et al. (2010)
USA, Pennsylvania	Pottsville	Late Carboniferous	Root traces	Gill and Yemane (1996),Wnuk and Pfefferkorn (1987)
USA, Missouri	Fort Scott	Late Carboniferous	Root mats Root traces	Retallack and Germán-Heins (1994)
USA, Ohio	Glenshaw and Casselman	Late Carboniferous	Millipede burrows Burrows with chambers Root traces	Hembree (2009), Hembree and Nadon (2011)
Australia, New South wales	Seaham	Middle Carboniferous	*Skolithos* Root traces	Retallack (1999a)
England, Bristol	Clifton Down Mudstone	Early Carboniferous	Root traces	Vanstone (1991)
USA, New York	Walton	Late Devonian	Burrows Root traces	Retallack (1985)

USA, Pennsylvania and New York	Catskill	Middle–Late Devonian	Plant and root traces	Driese et al. (1997)
USA, New York	Oneonta	Middle Devonian	Meniscate burrows Rhizoliths	Dunagan and Driese (1999)
UK, Wales	Old Red Sandstone	Middle Devonian	*Beaconites antarcticus* *Taenidium barretti* Root traces	Morrissey and Braddy (2004), Morrissey et al. (2012), Hillier et al. (2008)
Antarctica, Victoria Land	Aztec Siltstone	Middle Devonian	Rhizoconcretions	Retallack (1997b)
Canada, Quebec	Malbaie	Middle Devonian	Plant and root traces	Driese and Mora (2001)
USA, Gilboa	Unnamed	Middle Devonian	Plant and root traces	Driese and Mora (2001)
Norway (Spitsbergen Is.)	Wood Bay	Early Devonian	*Skolithos helicoidalis* Burrows	Blomeier et al. (2003), Volohonsky et al. (2008)
Canada, Gaspé Bay	Battery Point	Early Devonian	Plant and root traces	Driese and Mora (2001), Elick et al. (1998)

Ichnotaxonomy and affinities are included as published, regardless of its reliability. In a few cases, ichnotaxonomy was updated according to recent revisions. Invertebrate cases in the table intended to be all recorded, whereas in the case of root traces is not an exhaustive list

Table 13.2 Paleosol ichnofacies showing trace fossil composition, typical sedimentary environments, and associated plant formations

Ichnofacies	Description	Dominant trace fossils	Sedimentary environments	Vegetation
Scoyenia	Dominated by meniscate structures (feeding and locomotion) both trackways and continuous trails. There is a mix of invertebrate, vertebrate, and plant traces. Invertebrates are mainly detritus-feeders, deposit-feeders, or predators. Vertebrates are predators or herbivorous. Vertebrate traces in this ichnofacies are mainly mammalian and bird tracks. Ichnodiversity of invertebrate traces is usually low, but individual traces can be abundant. Vertebrate footprints may be diverse and abundant.	*Scoyenia*, *Taenidium*, *Beaconites*, *Diplichnites*, *Diplopodichnus*, *Spongeliomorpha*, *Skolithos*, *Fuersichnus*, vertebrate tracks.	Continental low energy deposits with sediments ranging from sandy to argillaceous. Both slightly submerged sediments with periodical exposition to air and subaerial sediments periodically submerged can be represented. Typically transitions between fluvial and lacustrine environments, including floodplains, ponds, lake margins, ephemeral lakes, and humid interdunes.	Little or no vegetation cover. Semi-aquatic vegetation may be present.
Coprinisphaera	Dominant breeding structures of beetles and bees, but traces of other insects such as ants, termites, cicadas, and moths may be present. Meniscate tubes, mammal caves, and rhizoliths can be present. Most common vertebrate structures are rodent burrows. Moderate to relatively high ichnodiversity and abundance	*Coprinisphaera*, *Celliforma*, *Teisseirei*, *Monesichnus*, *Uruguay*, *Palmiraichnus*, *Feoichnus*, *Tombownichnus*, *Lazaichnus*, rhizoliths, vertebrate burrows	Paleosols associated to ecosystems of open herbaceous communities, from dry and cold to humid and warm climate. Paleosols formed in different sedimentary environments including alluvial plains, desiccated floodplains, abandoned fluvial bars, crevasse splays, levees, and vegetated aeolian deposits.	Open herbaceous communities. Mostly grass-dominated habitats.
Celliforma	Dominance of chambers and chambered trace fossils assigned to bees and wasps. Other associated components are rhizoliths, vertebrate coprolites, and large vertebrate burrows. Moderate ichnodiversity, high abundance.	*Celliforma*, *Rebuffoichnus*, *Fictovichnus*, *Pallichnus*, rhizoliths.	Calcretes formed under semiarid (and seasonal) to arid climate. Palustrine carbonates.	Scrubs and woodlands from arid to semiarid environments. Palustrine vegetation or bare soils due to frequent flooding.

Termitichnus	Dominance of chambers and chambered trace fossils attributed to termites. Other components are J-shaped burrows, rhizoliths, large vertebrate burrows, and pelleted burrow fillings. Low to moderately ichnodiversity and abundance.	*Termitichnus*, *Krausichnus*, *Vondrichnus*, *Fleaglellius*, rhizoliths, large vertebrate burrows.	Paleosols of closed forests developed under warm and humid conditions. Moderately developed paleosols on channel-belt deposits.	Closed forests of warm and humid climates.
Camborygma	Dominated by ichnogenera attributed to crayfishes and earthworms. The former are vertical to subvertical burrows, commonly Y-branched, in some cases connected by horizontal burrows, with or without chambers. Rarely breeding structures are present. Earthworm trace fossils are diffuse boxworks, in some cases meniscate, or connected to chambers. Cross-cuttings are very common. Low ichnodiversity, high abundance.	*Camborygma*, *Loloichnus,* *Dagnichnus*, *Cellicalichnus meniscatus*, *Edaphichnium*, diffuse boxworks, rhizoliths.	Paleosols with evidence for a high and fluctuating water table, mostly under warm climates. Paleosols can be formed on different deposits (channel, floodplain, overbank, levee-crevasse splay, gravity flows, loessic, ponds, etc.) and on almost any lithology.	Local marshes, bogs, swamps, or wetlands as a subset of forest, scrub, and open herbaceous communities
Rhizoliths	Associations composed almost exclusively of plant traces, including stumps and any kind of rhizoliths. Usually low ichnodiversity and abundance commonly high.	Root traces, rhizoliths, paleorhizospheres, stump casts.	Different types of paleosols formed on any kind of sedimentary deposit. Indicative of subaerial exposure.	Diverse. Not related to any particular plant formation

Modified from Genise et al. (2000), Buatois and Mángano (2007, 2011) and Melchor et al. (2012)

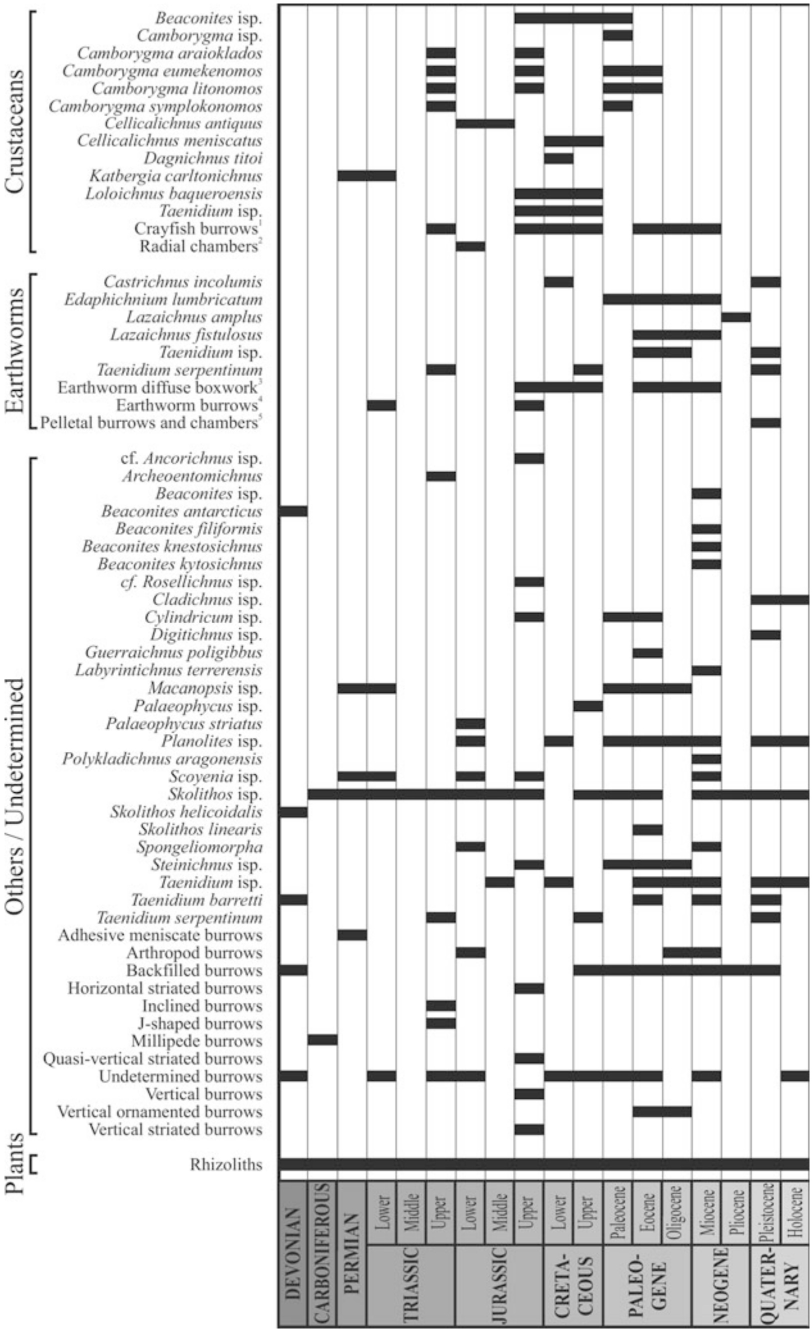

Fig. 13.1 Stratigraphic ranges of crustacean, earthworm, plant, and undetermined trace fossils in paleosols. Figure starts in the Devonian when the first rizholiths are recognized in paleosols. Only reliable attributions to producers in each group are included, whereas trace fossils with nonreliable attributions are included in the group of trace fossils with undetermined affinities. *Numbers* in unnamed trace fossils with reliable attributions indicate consulted references: (1) Bown (1982), Fiorillo (1999), Hasiotis (1993, 1999, 2004), Hasiotis and Demko (1996, 1998), Hasiotis and Kirkland (1997), Retallack (1997a), Tanner (2000), Therrien et al. (2009); (2) Pieńkowski and Niedźwiezki (2008); (3) Bedatou et al. (2005, 2006, 2007, 2008a, b), Bedatou (2010); (4) Pieńkowski and Niedźwiezki (2008), Retallack (1976, 1997a); (5) Smith et al. (1993)

A possible oldest evidence of subaerial trace fossils are drab haloes attributed to filaments of biological soil crusts produced by microorganisms and lichens from the Early Cambrian Flinders Ranges, Australia (Retallack 2008). The Cambrian-Ordovician Grindstone Range Sandstone of Australia shows trackways and resting traces of arthropods (*Diplichnites*, *Selenichnites*), which are interpreted as being produced on the surface of thin and weakly developed paleosols (Retallack 2009). Since Middle–Late Ordovician, soils included liverwort plants, representing low-biomass, high soil-respiration ecosystems (Retallack 1997b). Examples of these conditions would be the red, well-drained, weakly calcareous paleosol of Nova Scotia, which displays small reduction haloes assigned to mold colonies (Boucot et al. 1974), and the Aridisol of the Late Ordovician Juniata Formation from Pennsylvania (Retallack and Feakes 1987; Feakes and Retallack 1988; Retallack 1993, 2001b). However, this evidence was recently criticized based on the depositional environment, evidence for liverworts, and the nature of *S. beerboweri* and its producer, among other issues (Davies et al. 2010) (see Chap. 5).

Undisputed subaerial meniscate trace fossils are younger. They come from the upper Silurian-Middle Devonian Old Red Sandstone of Wales (Morrissey and Braddy 2004; Hillier et al. 2008; Morrissey et al. 2012), the Middle Devonian Oneonta Formation of the USA (Dunagan and Driese 1999), and the Late Permian Abo Formation of the USA (Mack et al. 2003). Also recorded are *Skolithos* from the Early Devonian Wood Bay Formation of Norway (Volohonsky et al. 2008) and the Middle Carboniferous Seaham Formation of Australia (Retallack 1999a). Absence of true assemblages and the paucity of data hamper a more definite inclusion of these assemblages in the ichnofacies model. However, they would be considered herein tentatively as the oldest examples of the *Scoyenia* Ichnofacies. Usually this ichnofacies, indicative of alternative subaerial and subaquatic conditions (Fig. 13.4a), is not recognized as a paleosol one. However, during subaerial exposure the substrate may develop a temporal plant cover producing roots and traces of soil organisms (Genise et al. 2010b; Melchor et al. 2012). Its mention herein responds to its record as the only Paleozoic one indicative of subaerial exposure bearing invertebrate trace fossils. However, for practical purposes, the *Scoyenia* Ichnofacies will not be treated further in this chapter (neither included in Table 13.1), as it has a very different background and approach from the other ichnofacies that occur in post-Paleozoic paleosols (see Chaps. 5, 6 and 12).

Apart from the 9 undisputed cases of Paleozoic paleosols bearing invertebrate trace fossils, other 17 examples show different types of rhizoliths as exclusive trace fossils (Table 13.1, Fig. 13.1). The first assemblage composed only of rhizoliths is Early Devonian (Driese and Mora 2001), in correspondence with the first plant origination event, marked by the advent of lycophytes and sphenophytes, and the first large adaptive radiation of plants (Cascales et al. 2010). This assemblage is recognized herein as the first ichnologic revolution in paleosols (Fig. 13.3). These exclusive rhizolith assemblages, assuming the diversity of different types of rhizoliths is underestimated, are considered herein for practical purposes as cases of a Rhizolith Ichnofacies, a proposal similar to that of Melchor et al. (2012). Its name refers to the initial appearance of rhizoliths, the “Cinderella” of paleosol trace fossils, considering that root traces are largely understudied and unnamed in comparison with animal traces. After future and badly needed research on different root systems and rhizolith branching patterns, the paleoenvironmental meaning of this ichnofacies could be extended greatly. For instance, rhizoliths and root systems constitute indicators of subaerial exposure or vegetation type, but also of drainage conditions in soils and paleosols (Sarjeant 1975; Jenik 1978; Retallack 1988; 2001a). The study of iron oxide-depleted zones around root trace fossils also assists to define several specific categories of drainage conditions in paleosols (Kraus and Hasiotis 2006). In addition, further analyses on the reasons for the absence of associated invertebrate trace fossils in these assemblages will also increase its value. There are about 38 cases of the Rhizolith Ichnofacies occurring along different intervals of the Phanerozoic, even though Table 13.1 is not an exhaustive compendium of all cases recorded from the literature.

Late Silurian and Devonian soils vegetated by the first herbaceous and rhizomatous plants (xeromorphic rhyniophytes), called “brakeland” formations, were represented by stronger developed, well-drained paleosols showing complicated bioturbation patterns (Retallack 1992a, 2001a). By the Early Devonian, root systems of primitive vascular plants were large and stout, reaching 1 m deep (Elick et al. 1998). Rhizome trace fossils in these Entisols consist of dichotomous and fibrous casts and molds presumably produced by trimerophytes. In addition, expansion of swampy vegetation in permanently waterlogged terrains gave way to peaty soils or Histosols (Rice et al. 1995). An old Inceptisol showing large root trace fossils, leaf litter, and spodic attributes was recognized in the Late Devonian of the USA (Retallack 1985). The advent of forested soils represented a change in weathering of soil minerals, and also a renewed step in stability and reduced erosion of landscapes due to deeper penetration of tree roots. Decaying vegetation of these more complex ecosystems probably favored the recycling of nutrients, thus originating new subsurface soil horizons that resulted in the illuviated clay accumulations of Alfisols and Ultisols, or in the iron and organic matter concentrations of Spodosols (Retallack 2001a). The most ancient forest ecosystems are recorded in Middle Devonian reddish Alfisols of Antarctica. These well-drained paleosols bear calcareous rhizoconcretions, ferruginized concretions, and deep and robust root trace fossils surrounded by large drab-haloes, attributed to highly seasonal, warm subhumid environments (Retallack 1997b). Diversity in vegetation communities since the Middle Paleozoic increased weathering rates, which consequently reduced the stability of minerals through the exportation of ions from soil waters and acidizing the rhizosphere (Knoll and James 1987). Root structures diversified anatomically in the Mississipian with the expansion of various forest types (Pfefferkorn and Fuchs 1991). Gill and Yemane (1996) described an ancient Ultisol from the lower Pennsylvanian of the USA, containing deep carbonaceous root trace fossils. A more ancient sandy soil enriched in iron and organic matter (Spodosol) exhibits stout woody root trace fossils probably of conifers (Vanstone 1991). Pennsylvanian calcic Vertisols, Inceptisols, and Alfisols formed in alluvial floodplains of the Appalachian basin bear different root trace fossils (rhizohaloes, rhizocretions, rhizotubules) that vary in depth, representing fluctuating water tables (Hembree and Nadon 2011). Tropical rain forests dominated by large-leaved seed ferns (pteridosperms), are recorded since the

Pennsylvanian (USA), and are represented by kaolinitic Oxisols showing large root trace fossils (Retallack and Germán-Heins 1994).

In sum, the most important soil types were already developed by the Devonian–Carboniferous, as well as most types of plant formations from different environments, from arid herbaceous communities to swampy or forested habitats developed under humid climates. Thus, the paucity of data on paleosol ichnofaunas should respond to other causes, such as the still relatively scarce record of Paleozoic paleosols or to the scarcity of soil inhabiting organisms capable of leaving preservable traces. The latter will be a recurrent issue along this chapter. Most of the recognizable tracemakers of Mesozoic and Cenozoic ichnoassemblages, such as earthworms and crayfishes, have no body fossil record for the Paleozoic, whereas the first holometabolous insects appear at the Mississippian–Pennsylvanian transition (Nel et al. 2007; Béthoux 2008; Wiegmann et al. 2009; Labandeira 2011). In turn, most Paleozoic invertebrate trace fossils in paleosols have been attributed to millipedes (Retallack 1999a, 2001b; Morrissey and Braddy 2004; Hembree 2009). Voigt (2007) analyzed the possible occurrence of insect trace fossils in Permo-Carboniferous basins of North America and Europe.

The Paleozoic records the appearance of the first paleosols bearing subaerial trace fossils. Paleozoic assemblages are composed only of rhizoliths (the Rhizolith Ichnofacies) or in some cases dominated by invertebrate burrows and trackways (the *Scoyenia* Ichnofacies) (Table 13.1). The largest floral extinction, occurred at the end of the Carboniferous (Cascales et al. 2010) is not reflected in changes in paleosols or trace fossil assemblages. This stasis is only interrupted after the end-Permian mass extinction event. The assemblages containing only rhizoliths, which dominate the Paleozoic, are grouped in the Rhizolith Ichnofacies that is recorded extensively from the Devonian along the rest of the Phanerozoic (Table 13.1, Figs. 13.1, and 13.3). The Rhizolith Ichnofacies is a practical concept, to be explored considering three points: (1) the recurrency of paleosols showing only root traces, (2) the dominance of these assemblages in Paleozoic paleosols, and (3) the potential paleoenvironmental significance of different rhizolith morphologies.

13.3 The *Camborygma* Revolution: The Triassic Appearance of Crayfish and Earthworm Trace Fossils

The Late Permian catastrophic loss of plant biodiversity (Ward et al. 2000; Michaelson 2002; Arche and López-Gómez 2005) had an uncommonly long period of recovery in the Triassic. The modification in terrestrial ecosystems was represented by a global change in vegetation corresponding to the appearance and expansion of seed plants and the culmination of widespread coal accumulation (Faure et al. 1995; Retallack et al. 1996b).

In the Southern Hemisphere, this biotic crisis on land is documented in few paleosols from high latitudes that cross the Paleozoic-Mesozoic boundary (Smith 1995; Retallack 1999b; Retallack and Krull 1999). According to Retallack

(2001a), Late Permian–Early Triassic paleosols from Antarctica, South Africa, and Australia record abrupt environmental (e.g., acidification, biological productivity) and paleontological changes, also reflected in the replacement of paleosol types (e.g., Histosols to ferruginized paleosols). In several localities of Antarctica, Late Permian carbonaceous root traces (*Vertebraria*) were replaced by silica or clayey infilled roots (Retallack et al. 2005). Mid-latitude paleosols from China show similar climate controlled, long-term changes, from gleyed, organic-matter rich paleosols indicative of humid conditions, to paleosols with calcic and gypsic concentrations formed in unstable, semiarid environments, through the Permian-Triassic boundary (Thomas et al. 2011). Rhizoliths, root haloes, and root moulds were the only trace fossils observed in these paleosols.

Advanced cone-bearing and seed-producing gymnosperms, along with free-sporing lycopsids and ferns, became the dominant groups in early Mesozoic floras (Niklas et al. 1985; Visscher et al. 2004; Retallack et al. 2011). The major radiation of conifer families (Cephalotaxaceae, Pinnaceae, Taxaceae, Araucariaceae, Podocarpaceae, and Cheirolepidiaceae) occurred during the Triassic in a global scenario of increasing temperature and seasonality (Archibold 1995; Willis and McElwain 2002). By the early Jurassic, the expansion of Cycadales, Bennettitales, and Ginkgoales resulted in a new floristic change at global scale. Eighty percent of plant species were Gymnosperms by the Middle Jurassic (Hallan 1994; Brenchley and Harper 1998).

In spite of the mentioned large-scale vegetational changes, new or particular types of paleosols were not observed in Mesozoic strata. The flora preserved in the Upper Jurassic Morrison Formation illustrates an environment that supported giant sauropods under warm, semiarid to subhumid, seasonal conditions. Floodplains had an herbaceous groundcover mixed with low-growing woody shrubs (ferns, seed ferns, ginkgos, horsetails) adapted to severe droughts (Parrish et al. 2004). Watercourses and lake margins show riparian open-forests of conifers with an herbaceous and shrubby understory (Turner and Peterson 2004; Engelmann et al. 2004). Calcic Vertisols, Aridisols, and Alfisols developed in such scenario with fluctuating water tables (Retallack 1997c; Demko et al. 2004).

The Early Triassic shows the appearance of the first assemblages of paleosol trace fossils that display a moderate diversity of ichnotaxa and trace makers (Table 13.1; Figs. 13.1 and 13.3). Crayfish, earthworm, and other invertebrate burrows, probably some of them produced by insects made their appearance in the geologic record. Nevertheless, the attribution of Early Triassic trace fossils to particular groups of animals was mostly tentative or weakly supported in the different study cases. Retallack (1976, 1997a) mentioned crayfish, insect, and earthworm burrows from the Narrabeen Group of Australia. Among them, earthworm traces, containing fecal pellets, are the most reliable identified ones (Retallack 1976). The body-fossil record of earthworms, as of other soft-bodied organisms, is fragmentary and probably very incomplete to be used as control for the trace-fossil record. Some tentative body fossils of oligochaetes were recorded earlier during the Middle Ordovician (Conway Morris et al. 1982). However, these identifications are uncertain and have been disputed (Humphreys 2003). Unquestionable evidence was presented by Pierce et al. (1990), who described a fossil earthworm embryo

(Oligochaeta: Lumbricidae) preserved with part of its cocoon from beneath a Holocene midden at Potterne, UK. The earliest evidence is not body fossils but rather clitellate cocoons, parataxonomically named *Burejospermum*, *Dictyothylakos*, and *Pilothylakos*, attributed either to Hirudinea or Oligochaeta. These cocoons are diverse and were recorded worldwide from the Late Triassic to the Neogene (Manum et al. 1991; Jansson et al. 2008; Tosolini and Pole 2010). The earliest specimens were described from the Upper Triassic of Greenland (Harris and Rest 1966) and Sweden (Manum et al. 1991). Other records were documented in the Jurassic of Norway (Manum et al. 1991), England (Harris 1961), and Australia (Jansson et al. 2008). Cretaceous cocoons were described from Greenland (Manum et al. 1991), Germany (Manum et al. 1991), Australia, and New Zealand (Tosolini and Pole 2010). Younger material comes from Holocene (post-glacial) deposits from Ontario, Canada (Schwert 1979).

The body-fossil record of crayfishes is more complete. Miller et al. (2001) discussed the difficulties in separating burrows of crayfish from those of small tetrapods in the Lower Triassic Fremeuow Formation of Antarctica. By contrast, Retallack et al. (2003) and Gastaldo and Rolerson (2008) attributed very tentatively, *Macanopsis* and *Katbergia* respectively, from the upper Permian–Lower Triassic interval of the Karoo Basin from South Africa, to crustaceans. The oldest body fossil of Parastacidae is *Palaeochinastacus australianus* (Martin et al. 2008), recorded from the Lower Cretaceous of the Otway Group in Australia. Other body fossil records from the Southern Hemisphere are younger (Sokol 1987; Aguirre-Urreta 1992; Feldmann and Pole 1994). In a recent molecular phylogeny of the Parastacidae calibrated by body fossils, Toon et al. (2010) estimated that the Parastacidae originated around 185 Ma during the Early Jurassic. The oldest Astacidae comes from the Lower Cretaceous of Spain (Garassino 1997). The oldest body-fossil record of possible Cambaridae comes from the Upper Triassic Chinle Formation of USA (Hasiotis and Mitchell 1993; Crandall et al. 2000). Although this particular attribution has been disputed (Rode and Babcock 2003), well documented, reliable crayfish trace fossils included in the ichnogenus *Camborygma*, are recorded from this formation (Hasiotis and Mitchell 1993; Hasiotis et al. 1993b). These trace fossils undoubtedly share with modern crayfish burrows the typical Y branching, longitudinal connecting tunnels, chambers, wall surface texture, and dependence on the water table (Hasiotis and Mitchell 1993; Hasiotis et al. 1993b).

In contrast, the attribution of Late Triassic and Late Jurassic trace fossils from the Chinle and Morrison formations of the USA (Hasiotis 2000, 2003, 2004) to particular groups of insects, such as bees, dung beetles, ants, and termites, among others, and of Early Jurassic trace fossils from the Elliot and Clarens formations of South Africa to termites (Bordy et al. 2004), has been disputed and mostly unaccepted (Engel 2001; Genise et al. 2004, 2005; Grimaldi and Engel 2005; Bromley et al. 2007; Alonso-Zarza et al. 2008; Lucas et al. 2010; Tapanila and Roberts 2012). Undoubtedly, insects would have been conspicuous inhabitants of the Triassic and Jurassic soils and probably many of the simple vertical, inclined, J-shaped, meniscate, or chambered burrows of the Chinle or Morrison Formations belong to them. However, it is hard to unequivocally attribute any trace fossil in a paleosol from these units to a particular group of insects because most of these simple trace fossils lack diagnostic characters. The Chinle and Morrison formations are exceptional in that preserve diverse ichnofaunas, which would contribute significantly to our understanding of ichnofacies evolution and the ichnofacies model. Unfortunately, the lack of ichnotaxonomic treatment of these trace fossils and the brief and poorly documented descriptions reflected in the poor understanding of their affinities and paleoenvironmental significance allow us only a tentative inclusion of these associations in the ichnofacies paradigm (Bromley et al. 2007). The end-Triassic mass extinction event seems to have had little effect on diversity of paleosol ichnofaunas judging by their increase in diversity between the Early and Late Triassic, represented in the Chinle Formation, and the comparable ichnodiversity between the Chinle and Morrison formations (Hasiotis 2000, 2004).

Genise et al. (2008a) proposed that terrestrial crayfishes could be capable of constructing nests, which basically showed two architectures: necked cells attached to parental burrows (*Cellicalichnus meniscatus*) and central chambers surrounded by radiating, short, meniscate tunnels (*Dagnichnus titoi*). The attribution of these structures from the Upper Jurassic and Lower Cretaceous of Argentina to crayfishes were based on their occurrence in the same beds, with abundant crayfish trace fossils (*Loloichnus baqueroensis*) (Bedatou et al. 2008a), and in the case of *Cellicalichnus meniscatus* because its cells are connected to tunnels indistinguishable from the former. In addition, *Dagnichnus* resembles the *bauplan* of thalassinidean calichnia (i.e., small cells or tunnels connected with large chambers or tunnels). There are two outstanding and well described trace fossils from Lower Jurassic paleosols of Poland and Iran that deserve special comment (Pieńkowski and Niedźwiezki 2008; Fürsich et al. 2010). Are these trace fossils the pioneer expressions of larval parental care? Do they represent a major step in the evolution of paleosol ichnofaunas? Pieńkowski and Niedźwiezki (2008) described a trace fossil composed of a central chamber surrounded by radiating cells, resembling the *bauplan* of *Dagnichnus,* from the Lower Jurassic of Sołtyków in Poland. Fürsich et al. (2010) described *Cellicalichnus antiquus*, a trace fossil composed of horizontal tunnels bearing opposite pairs of side branches that are considered breeding cells, from the Lower Jurassic Aghounj Formation of Iran. These authors made a well supported analysis of the affinities of these trace fossils, evaluating the possibilities of bees or bee ancestors, and crayfishes (Genise et al. 2008a; Genise and Verde 2010) as putative producers. They concluded that an insect origin was more likely because its morphology was more similar to that of insect nests than of extant crayfish traces. These cases, which probably have counterparts in the Chinle or Morrison formations, may represent a major acquisition in soil invertebrate behavior, the construction of cells in soils for larval development, regardless their crustacean or insect affinities (Genise 2016; Genise et al. 2008a; Genise and Verde 2010).

The Upper Jurassic and Lower Cretaceous formations of Patagonia, where the most diverse ichnoassemblages are recorded, are clearly dominated by earthworm and crayfish trace fossils (Bedatou et al. 2008a; Bedatou 2010), whereas other ichnoassemblages elsewhere are less diverse. At present, burrowing crayfishes are found in a diversity of soils and vegetation supporting periodical waterlogging.

In South America, crayfishes inhabit swamp, marshes, and mossy bogs occurring in evergreen forests and grasslands (Rudolph 1997; Rudolph and Crandall 2005; Buckup 2003; Noro 2007) (Fig. 13.4b). In North America they live in wet prairies with emergent sedges and grasses, marshes, and swamps (Grow 1981; Huner and Barr 1991; Jordan et al. 2000), whereas in Oceania they inhabit marshes, swamp, peatlands, and wetlands, occurring in grasslands, low shrublands, scrubs, and forests (Lake and Newcombe 1975; Suter and Richardson 1977; Horwitz and Knott 1983, 1991; Richardson 1983; Horwitz et al. 1985; Growns and Richardson 1988; Hamr and Richardson 1994; Richardson and Wong 1995; Whitmore et al. 2000). Accordingly, the *Camborygma* Ichnofacies would be indicative of local marshes, bogs, swamps, or wetlands as a subset of forest, scrub, and open herbaceous communities (Mueller-Dombois and Ellenberg 1974).

In sum, Triassic, Jurassic, and most Cretaceous trace-fossil associations recorded from paleosols of Australia, USA, South America, and Europe include or are dominated by earthworm, crayfish, root, and/or undetermined trace fossils, which in some cases could be produced by unidentified groups of insects (Tables 13.1 and 13.2; Figs. 13.1, 13.2, and 13.3). The Mesozoic record of trace fossils in paleosols is greater than that of the Paleozoic, but it contains fewer and less studied occurrences than those of the Cenozoic. The lack of formally defined Mesozoic paleosol ichnofacies until now reflects this scenario. A new ichnofacies dominated by crayfish and earthworm trace fossils, indicative of paleosols with fluctuating, high water tables and distinctive of wetlands and swamps, may be defined at least tentatively with the database presented herein. This ichnofacies is called the *Camborygma* Ichnofacies, honoring the first ichnogenus named after crayfishes and also the oldest record of crayfishes (Hasiotis and Mitchell 1993; Hasiotis et al. 1993b). The *Camborygma* and Rhizolith Ichnofacies are the dominant paleosol ichnofacies from the Early Triassic to the Early Cretaceous, and represent stasis until the advent of new ichnotaxa and ichnofacies by the Late Cretaceous, the next revolution.

13.4 The *Celliforma* Revolution: The Late Cretaceous Advent of Recognizable Insect Trace Fossils in Paleosols and New Ichnofacies

By the Cretaceous, the Triassic–Jurassic scenario began to change slowly because of the appearance and early diversification of different groups of holometabolous insects capable of constructing preservable and distinct traces in soils (Genise and Bown 1994a). This already “old” observation, put forward almost 20 years ago, is still in force. Ants, bees, some groups of beetles, wasps, and termites that construct preservable and recognizable traces in soils, probably favored by the diversification of flowering plants, appeared by the Cretaceous when their first trace fossils are also recorded (Genise 2016).

The body-fossil record of these distantly related groups of insects began in the Cretaceous, even though there are abundant and impressive Triassic and Jurassic

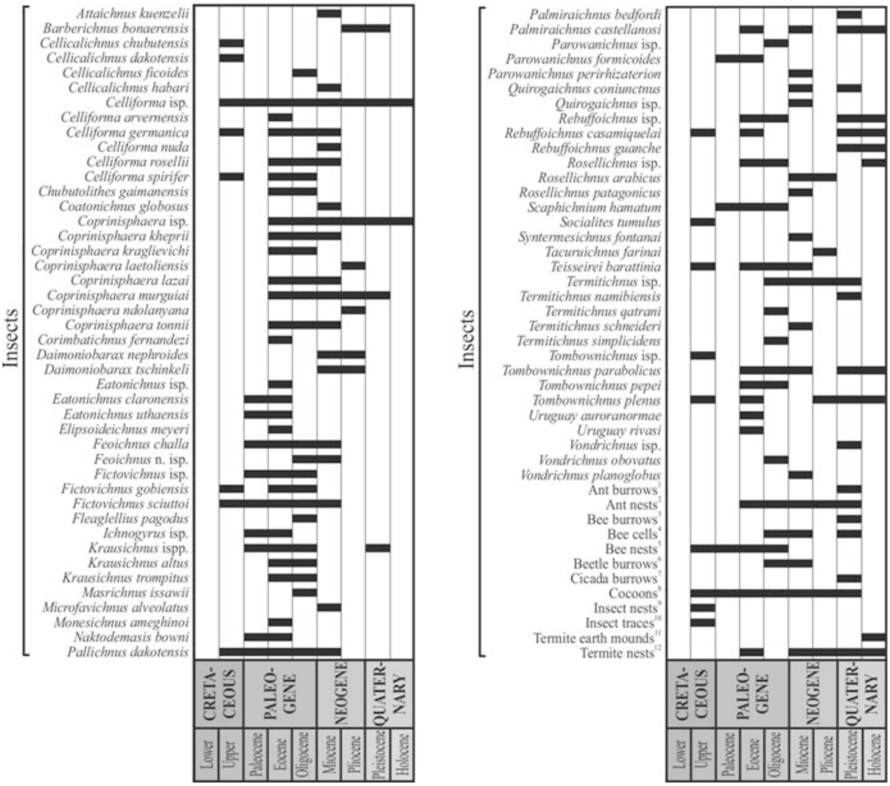

Fig. 13.2 Stratigraphic ranges of insect trace fossils in paleosols. Only reliable attributions to insects are included. *Numbers* in unnamed trace fossils with reliable attributions indicate consulted references: (1) Gregory et al. (2009); (2) Genise and Bown (1994a, 1996), Hamer et al. (2007), Iriondo and Krohling (1996), Kröhling (1999), Laza (1982, 1995, 1997), Sandau (2005), Tauber (1996); (3) Gregory et al. (2009); (4) Hamer et al. (2007), Gregory et al. (2009); (5) Genise and Verde (unpubl.), Verde and Genise (2007), Veroslavsky and Martínez (1996), Veroslavsky et al. (1997); (6) Hamer et al. (2007), Yelinek and Chin (2007); (7) O'Geen and Busacca (2001); (8) Hasiotis and Bown (1996), Hembree and Hasiotis (2007), Netto et al. (2007), Retallack et al. (1995), Sandau (2005), Sheldon and Hamer (2010), Thackray (1994); (9) González (1999), Sciutto and Martínez (1996); (10) Sciutto and Martínez (1996); (11) Moore and Picker (1991); (12) Bown and Genise (1993), Darlington (2005, 2011), Genise et al. (2000), Krell and Schawaller (2011), Laza (1995, 2006a), Radies et al. (2005)

localities bearing fossil insects worldwide (Grimaldi and Engel 2005). Here, it is provided a brief summary of the body-fossil record of common insect producers of trace fossils in Cretaceous–Cenozoic paleosols. The records of Dynastinae (Scarabaeidae) are from the Cenozoic of the USA and Germany, the oldest one of which is *Oryctoantiquus borealis* from the Middle Eocene of the USA (Ratcliffe et al. 2005). There are records of Melolonthinae (Scarabaeidae) from the Cenozoic of Russia, Germany, Czech Republic, and the USA, but the oldest records are from the Lower Cretaceous of Russia: *Cretoserica latitibialis* Nikolajev (1998) and three species of *Lithanomala* Nikolajev (1993) (Krell 2007). The oldest weevils, mostly from the families Nemonychidae and Belidae, come from Late Jurassic deposits of Karatau in South Kazakhstan (Gratshev and Zherikhin 2003; Oberprieler et al. 2007; McKenna et al. 2009; Legalov 2010). The oldest Curculionidae is *Arariperhinus monnei* from the Santana Formation, Brazil (Lower Cretaceous, Aptian-Albian) (Fernandes de Aquino Santos et al. 2011). Other Early Cretaceous weevil fossils come from Sierra del Montsec (Spain), Yixian (China), Bon-Tsagan, (Mongolia), Khetana and Ulya River (Russia), and Santana (Brazil); most of these are members of the Nemonychidae (Gromov et al. 1993; Oberprieler et al. 2007; Fernandes de Aquino Santos et al. 2011). Most families of extant weevils arose by the end of the Cretaceous (McKenna et al. 2009). The oldest termite body fossils are *Baissatermes lapideus* Rasnitsyn (2008) from the Lower Cretaceous (Barremian) of Baissa, Siberia (Engel et al. 2007, 2009) and *Morazatermes krishnai* Engel and Delclòs (2010) from the Lower Cretaceous (Albian) of Spain. Other termites, also recorded from the same deposits but presently known only from the forewings are *Cantabritermes simplex* Engel and Delclòs (2010) and *Aragonitermes teruelensis* Engel and Delclòs (2010) in amber from Teruel, Spain. The oldest undisputed bee is *Cretotrigona prisca* from New Jersey amber, which is closely related to the extant stingless bees (Michener and Grimaldi 1988a; Engel 2000). The precise age of *C. prisca* is still unclear since it was considered initially to be 80 My (Michener and Grimaldi 1988a, b) but later estimated in 70 My (Grimaldi 1999), and still later in 65 My (Engel 2000). Poinar and Danforth (2006) described *Melittosphex burmensis* from the Lower Cretaceous Burmese amber (Myanmar), which was originally considered as a transitional form between crabronid wasps and extant bees. More recently, Danforth and Poinar (2011) proposed that *M. burmensis* was a pollen-collector and accordingly the oldest bee.

The oldest ants are recorded from the Early Cretaceous (Dlussky 1996; Nel et al. 2004; Ward 2007; Perrichot et al. 2008), and are unexpectedly diversified with several distinct genera assigned minimally to two subfamilies (Perrichot et al. 2008). The oldest body-fossil records are *Haidomyrmodes mammuthus* (Sphecomyrminae) (Perrichot et al. 2007) and *Gerontoformica cretacica* (uncertain subfamily) (Nel et al. 2004) from the Lower Cretaceous (Upper Albian) of Charente-Maritime locality (France), and *Haidomyrmex cerberus* (Dlussky 1996), *Sphecomyrmodes orientalis*, *Sphecomyrma* sp. (both Sphecomyrminae), *Burmomyrma rossi*, and *Myanmyrma gracilis* (both uncertain subfamily) from the Lower Cretaceous (Upper Albian) of the Myanmar locality in Burma (France) (Dlussky 1996, Engel and Grimaldi 2006, Ward 2007; Perrichot et al. 2008). Finally, the oldest Aculeata is from the Upper Jurassic of Karatau in Kazakahstan (Central Asia) and was placed in the extinct family Bethylonymidae (Rasnitsyn 1975, 2002). This family probably represents the closest relative and gave rise to all modern aculeates (Rasnitsyn 2002; Brady et al. 2009). Many modern vespoid families diverged in the Late Jurassic and throughout the Early Cretaceous, although few families, including Pompilidae, Mutiliidae, and Sapygidae, may have originated considerably more recently (Brady et al. 2009). The earliest specimens of Sphecidae (Angarosphecidae) appeared during the Early Cretaceous and these were recorded from many localities

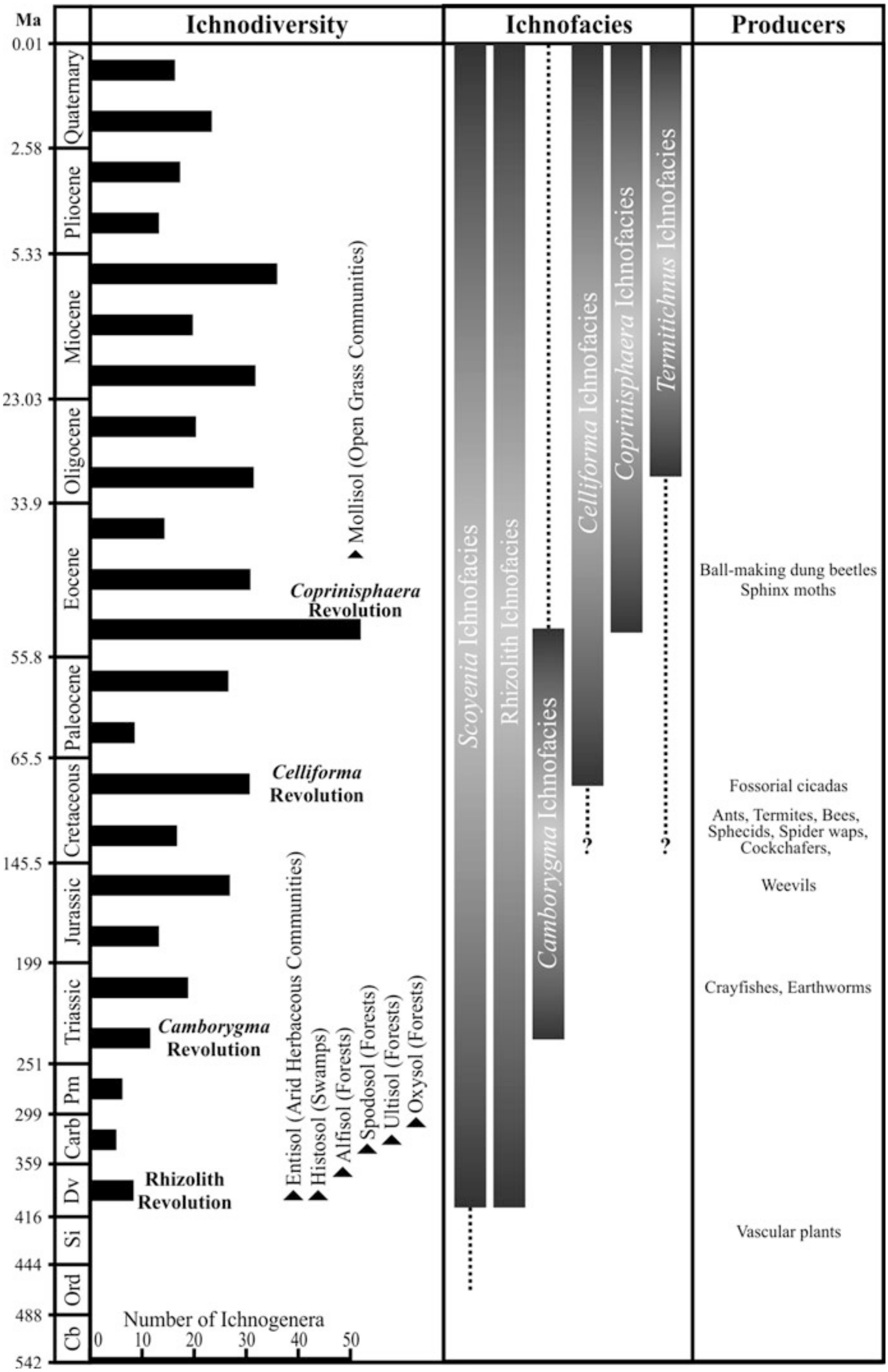

Fig. 13.3 Ichnodiversity of trace fossils in paleosols through the Phanerozoic. To emphasize changes in ichnodiversity, all trace fossils in Table 13.1 are included, independently of the reliability of their ichnotaxonomy and affinities. The *Scoyenia* Ichnofacies is depicted only for the Paleozoic to emphasize that its examples are one of the oldest ichnologic evidence of subaerial exposure and

principally in Eurasia (Spain, Burma, Mongolia, China, Russia, UK, and Transbaikalia) (Evans 1969; Rasnitsyn 1975, 1980, 2000; Darling and Sharkey 1990; Rasnitsyn et al. 1998, 1999; Rasnitsyn and Ansorge 2000; Rasnitsyn and Martinez-Delclòs 2000). The oldest Pompilidae is *Bryopompilus interfector* (tribe Bryopompilini) from the Lower Cretaceous (Albian) amber of Myanmar (Burma) (Engel and Grimaldi 2006).

These phylogenetically unrelated groups of insects, the most common producers of trace fossils in paleosol since the Cretaceous, share a similar behavioral trait. Representatives of these taxa line or construct different parts of their nests, cocoons, or pupation chambers, which are not mere excavations, increasing significantly the potential of preservation (Genise and Bown 1994a). Analogously, insects reinvented several millions of years later, two behavioral acquisitions of Jurassic crayfishes: linings for reinforcing walls and chambers for rearing larvae (Genise et al. 2008a). The need of Jurassic and Cretaceous crayfishes to maintain water for breathing inside their burrows probably favored the acquisition of pelletal linings to increase isolation from soil and retain water within the burrows (Bedatou et al. 2008a). Similar behavioral acquisitions, such as pelletal and fluidized linings, and other features exclusive of insects, such as free-standing walls and organic linings, occur for the first time in Late Cretaceous paleosol trace fossils, such as cocoons, pupation chambers, and nests, which can be attributable to insects. These behavioral traits are recorded for the first time in a few deposits worldwide (Table 13.1; Figs. 13.2 and 13.3).

The advent of flowering plants by the Early Cretaceous was probably one of the greatest innovations, together with the radiation of Triassic seed plant lineages, for Mesozoic continental environments. Examples of paleosols related to primitive angiosperms are known from North and South America. Paleosols of Barremian age are related to the earliest angiosperms in the eastern USA and correspond to Entisols, pink clayey Inceptisols, and coaly Histosols covered by conifers (Retallack and Dilcher 1986; Retallack 2001a). In southern Patagonia

Fig. 13.3 (continued) because they constitute about half of the Paleozoic cases. The *dotted line* indicates that it is recorded up to the Holocene, but these post-Paleozoic cases are not treated herein. The first case of a paleosol bearing only rhizoliths, the rhizolith revolution, took place during the Early Devonian. The Rhizolith Ichnofacies is later extensively recorded along the Phanerozoic. The *Camborygma* revolution, during the Early Triassic, indicates the advent of assemblages dominated or including earthworm and crayfish trace fossils (*Camborygma* Ichnofacies). The last record of this ichnofacies is from the Eocene, but *dotted line* indicates that extant equivalent examples exist. The *Celliforma* revolution, during the Late Cretaceous, is indicated by a rise in the ichnodiversity, which includes records of the first recognizable insect trace fossils in paleosols and the oldest records of the *Celliforma* Ichnofacies. The *Coprinisphaera* revolution, by the early Eocene, is envinced by another rise in the ichnodiversity triggered by the EECO, the appearance and spreading of grass-dominated habitats, and of the oldest cases of the *Coprinisphaera* Ichnofacies. The *Termitichnus* Ichnofacies appeared by the Oligocene in closed forest paleoenvironments. The *Celliforma* and *Termitichnus* ichnofacies could have been originated by the Early Cretaceous due the diversification of its producers by that time. Accordingly, its possible origin is prolonged by a *dotted line*, although there is no record of trace fossils attributable to soil termites, bees, or wasps

(Argentina), the first Barremian–Aptian angiosperms occupied wetlands that were affected by recurrent volcanic ashfalls. They grew on andic and kaolinitic Entisols that supported diverse conifers (Cheirolepidaceae, Podocarpaceae and subordinate Araucareaceae, Cupressaceae), along with Bennettitales, Cycadales, some Ginkgoales, ferns, lycopods, and bryophytes (Cladera et al. 2002; Del Fueyo et al. 2007). Similar, poorly-drained, Aptian environments of the central USA were also occupied by angiosperms, growing on Entisols and Histosols of lowlands and coastal-marine settings (Retallack and Dilcher 1981). Apparently, Early and mid Cretaceous angiosperms were early-successional colonizers (Retallack and Dilcher 1986). Detailed sedimentologic and ichnologic information from Upper Jurassic–Lower Cretaceous continental successions of southern Patagonia (Argentina) indicates that terrestrial environments, paleosols and associated trace fossils show no changes with the appearance of angiosperms. Lithofacies association and paleosol types of the pre-angiosperm Late Jurassic Bajo Grande Formation are similar to those of the post-angiosperm Aptian Bajo Tigre Formation (Cladera et al. 2002; Bedatou et al. 2009).

According to Retallack (1986, 1991b) the significant modification on the weathering pattern produced by the expansion of angiosperms since the Cretaceous (Knoll and James 1987) had no consequences on soils since Jurassic paleosols are similar to those of the early Paleogene. However, the diversification of termites, related to the radiation of angiosperms, may have caused a change in Oxisols (Schaefer 2001) through the incorporation of oval pellets rich in gibbsite, Fe-oxides, and charcoal, along with elongate burrows filled with these microaggregates (Eschenbrenner 1986; Schaefer 2001). Thus, it is probable that proliferation of termites introduced a modification of soils in tropical ecosystems. Nevertheless, most of middle and Late Cretaceous examples of new insect trace fossils suggest no comparable changes in paleosols in temperate regions. In any case, the appearance of flowering plants had little effect on soil types, which remained mostly the same since the Carboniferous.

The record of the third revolution, mostly Late Cretaceous in timing (Table 13.1; Figs. 13.2 and 13.3), includes *Fictovichnus gobiensis* from the Djadokhta Formation of Mongolia (Johnston et al. 1996); *Cellicalichnus dakotensis* from the Dakota Formation of the USA (Elliot and Nations 1998); *Pallichnus dakotensis* and *Fictovichnus sciuttoi* from the Bajo Barreal Formation of Argentina (Genise et al. 2007); *Cellicalichnus chubutensis* and *Rebuffoichnus casamiquelai* from the Laguna Palacios Formation of Argentina (Genise et al. 2002a), and *Fictovichnus sciuttoi* from the Allen Formation of Argentina (Genise and Sarzetti 2011). Particularly interesting are the first records of assemblages of the *Celliforma* Ichnofacies in the Mercedes Formation of Uruguay (Alonso-Zarza et al. 2011) and the Two Medicine Formation of the USA (Martin and Varricchio 2011). The former assemblage is composed of *Celliforma spirifer*, *C. germanica*, *Fictovichnus gobiensis*, and rhizoliths, whereas the latter is composed of *Fictovichnus sciuttoi*, *Rebuffoichnus* isp, and *Skolithos* isp. It is possible that other cases mentioned previously also may represent examples of the *Celliforma* Ichnofacies, such as that of the Allen Formation (Genise and Sarzetti 2011). However the lack of recorded assemblages composed of different ichnotaxa or carbonate-rich paleosols preclude their inclusion until more evidence is recovered to understand the complete paleoenvironmental significance of this ichnofacies. Even when some of these ichnogenera, such as *Fictovichnus*, *Pallichnus,* or *Rebuffoichnus,* are also representatives of the *Coprinisphaera* or *Celliforma* Ichnofacies (Genise et al. 2000, 2010b), when they do occur in associations dominated by earthworm or crayfish traces (i.e., Laguna Palacios Formation), they can be considered more likely as secondary participants of the *Camborygma* Ichnofacies, rather than indicators of Cretaceous examples of the *Coprinisphaera* or *Celliforma* Ichnofacies. The same is true for North American formations, like Claron and Willwood, in which insect trace fossils like *Parowanichnus*, *Eatonichnus*, *Celliforma*, *Naktodemasis*, and wasp cocoons are associated with crayfish and earthworm traces (Bown and Kraus 1983, 1987; Bown et al. 1997; Hasiotis and Bown 1996). The *Celliforma* ichnofacies is indicative of calcretes developed under arid or semiarid conditions and palustrine carbonates (Fig. 13.4c, d).

The presence of the *Termitichnus* Ichnofacies during the Cretaceous is a possibility considering that termites were already diversified by this period. However, there are no cases recorded of associations of termite nests for the Mesozoic, with the exception of those structures described by Bordy et al. (2004) from the Jurassic of the Karoo Basin, which probably deserve a different interpretation (Genise et al. 2005; Alonso-Zarza et al. 2008). Two cases of trace fossils attributed to social insects, including termites, require a brief analysis. Genise et al. (2010a) described rhizolith balls from the Lower Cretaceous Cerro Barcino Formation of Argentina, and discussed their affinities, such as self-induced and localized overgrowth of secondary and tertiary rootlets, crayfish feeding chambers, and termite or ant chambers for agricultural purposes. Tentatively, they were assigned to ant fungus gardens, the oldest evidence of insect agriculture, which would represent an important element of the Cretaceous revolution. The other case, *Socialites tumulus*, described by Roberts and Tapanila (2006) from the Upper Cretaceous Kaiparowits Formation of the USA, was interpreted as an ant or termite nest. However, the morphology may also resemble bioturbated stump casts or megarhizoliths. In any case, both records do not qualify as Cretaceous examples of the *Termitichnus* Ichnofacies.

In sum, bee cells and nests, putative ant and termite nests, coleopteran pupation chambers, and wasp cocoons are the Late Cretaceous pioneer trace fossils that signal another great change that would undergo paleosol ichnofaunas during the Eocene, the fourth revolution (Tables 13.1 and 13.2; Figs 13.2 and 13.3). The increase of ichnodiversity; the appearance of the first recognizable, constructed or lined, insect trace fossils in paleosols included as secondary components of the *Camborygma* Ichnofacies; and the first record of the *Celliforma* Ichnofacies, also are keystones of the third revolution in paleosol ichnofaunas. The possibility of the oldest physical evidence of sociality and insect agriculture is equally significant from an evolutionary viewpoint. According to the body-fossil record, Early–mid Cretaceous records of the *Celliforma* Ichnofacies could be expectable. The lack of them could be an artifact or it could correspond to the absence of some behaviors related to wall construction in the earliest representatives of the involved groups.

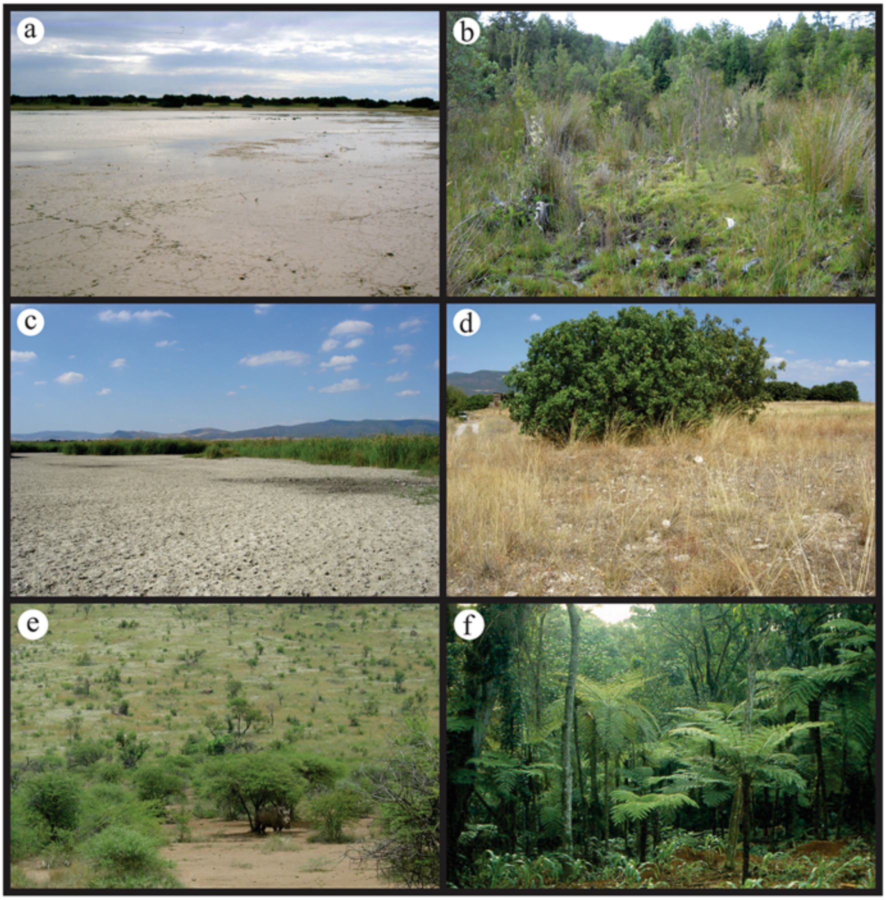

Fig. 13.4 Modern analogous environments of the six paleosol ichnofacies. (**a**) *Scoyenia* Ichnofacies. Drying ephemeral lake deprived of vegetation in Bajo de los Huesos, Chubut, Argentina. Note several vertebrate trackways in the foreground, and some dessiccation cracks in the lower right corner; (**b**) *Camborygma* Ichnofacies. Wetland in a glade of an evergreen forest at Rucapihuel, Chile. Note the soil flooded by the rise of water table in the *center* of the figure. (**c**) and (**d**) *Celliforma* ichnofacies at Las Tablas de Daimiel, Spain. Bare soil in a palustrine environment rich in carbonate (**c**), and carbonate rich soil supporting sparse vegetation. The calcrete was broken and exposed to the surface by plowing. (**e**) *Coprinisphaera* Ichnofacies. Savanna dominated by grasses at the Pilanesberg National Park, South Africa. Bare soil produced by trampling of the rhino (at the *center*) and other large mammals is optimal for bee nesting. Large size herbivores like this provide dung for coleopteran brood balls. (**f**) *Termitichnus* Ichnofacies. Closed forest of warm and humid climate in Misiones, Argentina. Tall trees, with interlocking crowns and understory of tree ferns

13.5 The *Coprinisphaera* Revolution: The Paleogene Explosion of Insect Trace Fossils Related To Grass-Dominated Habitats

The end Cretaceous mass extinction event seems to have had little effect on paleosol ichnofaunas (Fig. 13.3), although the Paleocene record is comparatively scarce for an accurate evaluation. One of the most significant floristic changes related to this biotic crisis was the extinction of several species of evergreen angiosperms and the subsequent predominance of conifers and deciduous angiosperms in the early Paleogene vegetation (Retallack 2001a).

In South America, particularly in Central Patagonia, the Late Cretaceous successions end with a clear dominance of earthworm and crayfish trace fossils, as in most Mesozoic units, and with the appearance of a few insect trace fossils (Genise et al. 2002a, 2004; Bedatou et al. 2008a). For the same region, the Paleocene–Eocene Rio Chico Group shows scarce trace fossils, including the appearance of the first trace fossil attributable to cicadas, *Feoichnus challa*, in the Koluel Kaike Formation of Patagonia (Krause et al. 2008, 2010). The earliest body fossils of true cicadas (Cicadoidea) are from the Triassic of Russia, France, and Australia (Shcherbakov 2008). These specimens are included in the family Tettigarctidae (hairy cicadas). However, the distinct fossorial forelegs of Cicadoidea nymphs apparently were present only by the mid Cretaceous, in amber from New Jersey (Grimaldi and Engel 2005). In South America, body fossils of hairy cicadas also are known from the Lower Cretaceous of Brazil (Lefebvre et al. 1998; Shcherbakov 2008). The earliest record of the family Cicadidae is from the Paleocene (ca. 60 Ma) of North America (Cooper 1941). Another ichnogenus, *Eatonichnus*, attributable to dung beetles (Bown et al. 1997; Krause et al. 2007; Sánchez et al. 2010a), is recorded for the first time from the Peñas Coloradas Formation in Patagonia (Genise et al. 2001a) and the Claron and Colter formations in the USA (Bown et al. 1997). Few recognizable earthworm burrows and doubtful crayfish trace fossils are recorded from the Rio Chico Group (Krause et al. 2007; unpub. data).

In contrast, in North America, crayfish burrows (*Camborygma*) are still abundant in Upper Paleocene–Lower Eocene units of Wyoming (Hasiotis and Honey 1995, 2000; Smith et al. 2008b) and Utah (Hasiotis and Bown 1996). The most diverse Paleocene assemblage is from the Willwood Formation (Bown and Kraus 1983, 1987; Hasiotis et al. 1993a; Smith et al. 2008a, b, c, 2009) and from the Paleocene–Eocene Claron Formation (Hasiotis and Bown 1996; Bown et al. 1997), both of which are Cenozoic cases of the *Camborygma* Ichnofacies. The evidence that supports this assumption is: (1) the abundance of *Camborygma* and *Edaphichnium* in the former deposits, (2) the abundance of *Camborygma* in the latter deposits, and (3) the paleosols exhibiting fluctuating water tables. In those assemblages, recognizable insect trace fossils are associated with crayfish and earthworm ones, as in the Upper Cretaceous deposits of Patagonia. The Paleocene–Eocene Thermal Maximum (PETM) produced the reduction in size and an increase in diversity of trace fossils in the Willwood Formation of USA (Smith et al. 2009).

In both Patagonia and the Western Interior of the USA, crayfish trace fossils are mostly absent in younger deposits. In South America, soil crayfishes are at present restricted to humid environments of Chile and Brazil (Bedatou et al. 2008a). Earthworm trace fossils, although less recorded, are similarly present in Cenozoic trace-fossil assemblages from younger units. Earthworms and crayfishes inhabit modern South and North American soils, indicating that at a global scale the end Cretaceous mass extinction had little direct effect on these organisms (Figs.13.1 and 13.3), even though regionally they displayed changes in their geographic distribution (Bedatou et al. 2008a). In sum, the end Cretaceous mass extinction (see Chap. 14), a major event in the history of life, was less important for paleosol ichnofaunas than previous events, as the rising and diversification of angiosperms during the Early Cretaceous, and later events, such as the origin and diversification of grass-dominated habitats during the Middle-Late Eocene cooling trend after the EECO. The fossorial habit of invertebrate soil organisms could have favored its survival in critical episodes, such as proposed for fossorial vertebrates (Archibald and Bryant 1990; Sheehan and Fastovsky 1992; MacLeod et al. 1997; Robertson et al. 2004; Longrich et al. 2012).

The last major step in the evolution of plant communities and soils took place during the middle Paleogene–early Neogene with the expansion of new, fast-growing monocot plants: the grasses. Grass-dominated habitats (Fig. 13.4e) are high-productivity ecosystems associated with dry or nonhumid habitats (subhumid to semiarid) of different continents, currently occupying 40 % of global land surface (Anderson 2006). However, grasses can also grow in less favorable conditions and environments, such as highly seasonal and tropical, cool temperate, high-mountain prairies, salt marshes, and are successional after periodic fires. Grass-dominated habitat expansion promoted significant changes in biota, favoring development of large vertebrates (grazers) on ground and diverse soil invertebrates, despite of the development as a defensive strategy of chemically harmful effects on mammals, insects, mites, and fungi (Retallack 2001a). As a consequence of changes in their rooting system and soil biota, grassland soils acquired particular characteristics in their soil aggregates, such as coarse granular or near-mollic to very fine-granular or crumb ped structure. Other diagnostic character of these new soils is a dark surface horizon rich in nutrients (mollic epipedon), displaying evidence of intense activity of burrowing invertebrates, such as fecal pellets of earthworms (Retallack 2001a). These features defined a new type of soil: the Mollisol. The appearance of a granular surface horizon in Oligocene-Miocene paleosols of the USA was considered a proxy for grasslands, which replaced and displaced wooded shrublands and dry woodlands (Retallack 1990). Fossil Mollisols present abundant, short and fine root traces. Desert grasslands, bunch grasslands, and rangelands developed in the latest Eocene–early Oligocene in NW and central USA (Retallack 2001a, 2009). The first short (sod) grassland Mollisols with fine crumb peds and dense and fine rhizoliths appeared by the early Miocene (19 Ma) in the USA and Kenya. Both examples occurred in dry climates based on the presence of shallow, calcic horizons (Retallack 2004; Retallack et al. 1995).

Twenty millions years before, a set of particular factors converged in Central Patagonia (Argentina) to trigger the formation of more ancient grass-dominated habitats. Main factors were probably a wetter climate and soils formed in fresh volcanic ashes. In addition, the effect of herbivorous mammals and associated dung beetles would also have contributed to the spread of these habitats. Paleosols of the Sarmiento Formation formed in pyroclastic mudstones composed of dacitic–rhyolitic glass shards (61–99 %) and andesine plagioclase (Bellosi 2010). The distinctive properties of this acid, low bulk-density volcaniclastic material benefited plant growth and rooting by providing high fertility, rapid weathering, a high moisture-holding capacity, and elevated macroporosity resulting in an appropriate medium for the extension of root hairs in a well-aerated medium (Nanzyo 2002). The appearance of the oldest grass-dominated habitats and grasslands is matter of debate and controversial evidence (Genise 2016). The first documented grass-dominated habitats for South America are middle Eocene (39 Ma) and occur at Gran Barranca in the middle Eocene-lower Miocene Sarmiento Formation of Patagonia. This proposal is supported by paleosols and loessic deposits (Bellosi and González 2010), phytoliths (Zucol et al. 2010; Sánchez et al. 2010c) and density and diversity of dung beetle brood balls (Sánchez et al. 2010b). The only thorough and comparative phytolith analysis of *Coprinisphaera* and bearing paleosols (Sánchez et al. 2010c) showed that grasses were the second dominant group after palms, as expectable for grassy savannahs with palms or palm groves (Cabrera 1971). The oldest dung beetles attributable to ball-making species are Eocene (Krell 2007). Morphology and behavior of dung beetles reflect a strong adaptation to exploit mammal excrement in open-grass habitats (Halffter and Edmonds 1982; Hanski and Cambefort 1991). African savannahs show the greatest diversity of dung beetles, whereas South American forests show a large diversity because of the Quaternary extinction of large mammals (Halffter 1991). Trace fossils of the Sarmiento Formation are clear examples of the *Coprinisphaera* Ichnofacies, indicating open-herbaceous communities (Genise et al. 2000). High density (40–100 balls/m^2), abundance and diversity in sizes and ichnospecies of *Coprinisphaera*, indicating a large number and diversity of dung beetles (Sánchez et al. 2010b), reflect the middle Eocene appearance of open-grass habitats (Bellosi et al. 2010), coincident with the increase of diversity and size of mammals (Woodburne et al. 2014). Probably the appearance of grass-dominated habitats was diachonous in different continents through the middle Paleogene–early Neogene. Those of Gran Barranca were probably similar to the present Chaco landscapes of northern Argentina (Cabrera 1971), represented by a mosaic vegetation composed of grassy savannahs with palms and palm groves, and forest in patches and riverbanks. Such a paleolandscape is concordant with all sedimentologic, pedologic, paleontologic, and ichnologic evidence for Gran Barranca.

A possible still older evidence for a wooded grass-dominated habitat, developed at lower latitudes, is represented in the renowned lower Eocene Asencio Formation of Uruguay. The precise age of this unit is unknown because of the lack of datable organisms or rocks. However, the lateritic character of the soils triggered by the Early Eocene Climatic Optimum, the presence of abundant large *Coprinisphaera* that can be only related with large mammals, and the age of the underlying and overlying formations, indicate that this formation is early Eocene in age (Genise et al. 2004; Bellosi et al. 2004, 2016). The Asencio Formation represents not only the oldest example of the *Coprinisphaera* Ichnofacies, but also one of its best examples because of the diversity of the ichnoassemblage. The presence of a grass-dominated habitat is indicated by the extraordinary development of the *Coprinisphaera* Ichnofacies and the record of Ultisols (González 1999), developed under a warm and seasonal-humid climate. When analyzed with more resolution, the Asencio Formation comprises two alternating ichnoassemblages which correspond to the different ichnofabrics recognized either in the duricrusts or in nodular beds Bellosi et al. (2016). The duricrusts, representing drier periods and shallower layers of the soil, bear ichnoassemblages dominated by *Palmiraichnus*, *Teisseirei*, and secondarily *Rebuffoichnus*. In turn, the nodular beds, representing wetter periods and deeper layers of the soil, bear more diverse ichnoassemblages including all ichnotaxa recorded for the formation. Previous and current research shows that the Asencio ichnofauna is composed of traces of cicadas (*Monesichnus*), dung beetles (*Coprinisphaera*), bees (*Palmiraichnus*, *Elipsoideichnus*, *Uruguay*, *Corimbatichnus*, *Celliforma*), sphinx moths (*Teisseirei*), termites (*Krausichnus*), beetles (*Rebuffoichnus*), crayfish (*Loloichnus*), and cleptoparasites and detritivores (*Tombownichnus*, *Lazaichnus*) (Genise and Bown 1996; Genise and Hazeldine 1998a, b; Genise and Laza 1998; Genise 2000; Genise et al. 2002b, 2013c; Genise and Verde 2000; Mikúlaš and Genise 2003; Sánchez and Genise 2009; Verde and Genise 2010). The extraordinary diversity of this trace-fossil assemblage reveals in turn a higher diversity of insects inhabiting lateritic soils that may be the direct consequence of the high temperatures and precipitation related to the EECO in this grass-dominated habitat. This and the contemporaneous assemblage from the Gran Salitral Formation of La Pampa (Melchor et al. 2002) record the first appearance of *Teisseirei barattinia*, the only paleosol trace fossil attributed to sphinx moths Genise et al (2013c). The oldest records of Sphingidae recognized by Sohn et al. (2012) are an adult from the middle Eocene Baltic Amber (Kusnezov 1941), and a caterpillar from the early Miocene of Baden-Wüttemberg, Esslinger, Germany (Zeuner 1927). Other early body fossil Sphingidae is *Mioclanis shanwangiana* from the middle Miocene (~15–17 My) of Shanwang, Shandong, China (Zhang et al. 1994). Other species named *Sphinx snelleni* was described by Weyenbergh (1869) as a sphingid from the Upper Jurassic Solenhofen Limestone deposits in Bavaria, Germany. However, it has later proved to be a wood wasp of the hymenopteran family Siricidae (Kitching and Sadler 2011). Skalski (1990) recorded also a Sphingidae from the Baltic amber, but Ross (1996) considered this claim to be unsubstantiated.

Other outstanding assemblages belonging to the *Coprinisphaera* Ichnofacies are those from different stratigraphic levels of the middle Eocene–lower Miocene Sarmiento Formation of Argentina (Genise 2016; Genise et al. 2004; Bellosi et al. 2010; Sánchez et al. 2010b). Previous and current research demonstrates that the Sarmiento ichnofauna is composed of trace fossils of cicadas (*Feoichnus*), dung beetles (*Coprinisphaera*, *Chubutolithes*, *Eatonichnus*, *Pallichnus*), sphinx moths (*Teisseirei*), bees (*Celliforma*), earthworms (*Lazaichnus*, *Castrichnus*, diffuse boxworks), and cleptoparasites (*Tombownichnus*) (Krause and Genise 2004; Krause et al. 2008; Bellosi et al. 2010; Sánchez and Genise 2009; Sánchez et al. 2010b). In this case, several paleolatitudinal degrees southwards and about 10 million years later, the extraordinary diversity of dung beetle trace fossils (Sánchez et al. 2010b) cannot be attributed directly to the EECO, but to the establishment of extended grass-dominated habitats, bearing abundant large mammals, which provided the dung for beetle brood masses. The high-resolution ichnostratigraphy of *Coprinisphaera* at the locality of Gran Barranca records important paleoenvironmental changes in those former grass-dominated habitats, including an increase in mammal size by the late Oligocene (Sánchez et al. 2010b).

The major evolutionary event during the Eocene, which represents the appearance and establishment of grass-dominated habitats, produced the appearance of larger mammals and abundant dung, which in turn promoted the evolution of coprophagy in dung beetles. Ichnology can reconstruct partially this history (Genise 2016). The first ichnologic evidence of dung-beetle coprophagy is probably recorded by trace fossils found in dinosaur coprolites from the Upper Cretaceous Two Medicine Formation of Montana (Chin and Gill 1996) (but see Arillo and Ortuño 2008). Theoretically, in the early stages of coprophage evolution, dung beetles produced meniscate burrows inside the dung pads and underneath in the soil substrate. In more derived behavioral stages, dung beetles construct, and bury in the soil, brood balls for rearing their larvae, which are preserved as trace fossils and recognized as specimens of *Coprinisphaera*. Which is the oldest record of *Coprinisphaera* and accordingly of brood ball construction? Halffter and Edmonds (1982) and Krell (2006) hypothesized about ball-making dung beetles utilizing the abundant dung of dinosaurs, whereas Arillo and Ortuño (2008) disregarded dinosaurs as dung providers. Arillo and Ortuño (2008) based their conclusions first, on the mixture of reptilian feces with excretory products; and second, on the poor attraction of extant dung beetles to those feces. With the only exception of a single putative specimen of *Coprinisphaera* found in the Cretaceous of Brazil (Souza Carvalho et al. 2009), there are no reliable records older than Eocene. Which is the ichnologic record of the evolution of coprophagy between the Cretaceous burrows of the Two Medicine Formation and the Eocene brood balls of South America? Sánchez et al. (2010a) described a pupation chamber of extant dung beetles, which matches the morphology of *Eatonichnus* (and partially *Chubutolithes*), trace fossils that are found in Paleocene–early Eocene deposits of Argentina and the USA (Bown et al. 1997; Genise et al. 2001a; Krause and Genise 2004; Krause et al. 2007), predating the appearance of *Coprinisphaera*. These Paleocene trace fossils probably reflect the life habit of Paleocene dung beetles that exhibit similar behaviors to extant species of Eucranini (Scarabaeinae), which provision their nests with fecal pellets of small mammals, as those recorded for the Paleocene. Mature larvae construct a helical pupation chamber composed of pellets similar to *Eatonichnus* (Sánchez et al. 2010a).

Can the body-fossil record of dung beetles corroborate this evolutionary history proposed by ichnology? Regrettably, the body-fossil record of American dung beetles is young. The oldest body fossils identified as Scarabaeinae are *Prionocephale deplanate* Lin (1980) from the Upper Cretaceous of China and *Cretonitis copripes*

Nikolajev (2007) from the Lower Cretaceous of Russia (Krell 2007). However, among those genera whose species are recognized ball makers, the oldest is *Gymnopleurus eocaenicus* Meunier (1921) (Gymnopleurini) from the Eocene of Germany (Krell 2007). The fossil record of other ball makers is still younger. The oldest Dichotomiini are *Heliocopris antiquus* Fujiyama (1968) from the Miocene of Noto, Japan, and *Anachalcos mfwangani* Paulian (1976) from the Miocene of Lake Victoria, Kenya. The oldest Phanaeini are *Phanaeus antiquus* Horn (1876) from the Pleistocene of the Port Kennedy caves, in the USA, and *Palaeocopris labreae* Pierce (1946) from the Pleistocene of Rancho La Brea, USA. Finally, the oldest Canthonini are *Copris leakeyorum* Paulian (1976) and *Metacatharsius rusingae* Paulian (1976) from the Miocene of Lake Victoria, Kenya.

By the Eocene, there are also diverse assemblages belonging to the *Celliforma* Ichnofacies from palustrine carbonates. The Gran Salitral Formation of Argentina (early Eocene) probably was influenced by the elevated temperatures of the EECO, but in drier conditions than those recorded for the Asencio Formation. The assemblage is represented by *Celliforma* ispp., *Teisseirei*, *Rosellichnus*, *Skolithos*, *Taenidium*, and *Fictovichnus* (Melchor et al. 2002). Another assemblage of possible late Eocene age occurs in the Queguay Formation of Uruguay, and is represented by *Celliforma spirifer*, *C. germanica*, *C. rosellii*, *Fictovichnus gobiensis*, *Fictovichnus sciuttoi*, and rhizoliths (Alonso-Zarza et al. 2011).

After the Eocene, few diverse ichnoassemblages in paleosols can be recognized. The youngest paleosol ichnofacies appeared by the Oligocene in the Jebel Qatrani Formation of Egypt. Paleosols of closed-forest paleoenvironments (Fig. 13.4f) preserved in this unit include the first assemblage dominated by termite and ant trace fossils (*Termitichnus*, *Fleaglellius*, *Vondrichnus*, *Krausichnus*) (Genise and Bown 1994b), composing the *Termitichnus* Ichnofacies (Tables 13.1 and 13.2; Figs. 13.2 and 13.3). This incipient ichnofacies has another potential example in some paleosols of the Chui Formation in Brazil (Netto et al. 2007). Even when diverse ichnoassemblages may be expected in closed-forest soils, the geologic record of these associations is very scarce. The lateritization process involves the destruction and incorporation of old termite nests to the soils (e.g., Eschenbrenner 1986; Schaefer 2001), probably reducing the probability of tropical termite nests to cross the taphonomic barrier.

Other diverse trace-fossil assemblages in paleosols are recorded in the lower Oligocene White River Formation of the USA (Hembree and Hasiotis 2007); the upper Oligocene–lower Miocene John Day Formation of the USA (Retallack 2004); the lower Miocene Pinturas Formation of Argentina (Genise and Bown 1994a; Bedatou 2010); Miocene gypsum and gray shales of Spain (Uchman and Alvaro 2000); the Miocene Pawnee Creek Formation of the USA (Hembree and Hasiotis 2008); the upper Miocene Collon Cura Formation of Argentina (Bedatou 2010); and the upper Miocene of the northern African Chad Basin (Duringer et al. 2007). The remaining Miocene, Pleistocene, and Holocene record is composed mostly of descriptions or citations of single or a few trace fossils of the above mentioned groups of insects from different formations, which can be included in the *Coprinisphaera* and *Celliforma* Ichnofacies. The peaks shown by Fig. 13.3 for the

Neogene, even when comparable with older ones, correspond to no particular evolutionary events, but rather to more extensive research mostly carried out in Pliocene and Pleistocene deposits of Argentina and Africa.

13.6 Conclusions

Our analysis of a database composed of 166 cases of invertebrate and plant trace fossils in paleosols resulted in the recognition of four major evolutionary steps from the first paleosols-bearing rhizoliths preserved in Early Devonian rocks to those of the Holocene. Each step constitutes a revolution for paleosol ichnofaunas, which triggered the appearance of a new ichnofacies. These events reflect some of the major changes in the history of life. Other historical events, such as the Cretaceous–Paleocene event, have no reflection in paleosol ichnofaunas or alternatively the data is too scarce for detection.

The first revolution is associated with the appearance and expansion of vascular plants, and took place in the Early Devonian with the first paleosols showing only ichnoassemblages composed of rhizoliths, which constitute half the cases of the Paleozoic and are recorded up to the Holocene. The appearance of vascular plants by the late Silurian resulted in the Early Devonian appearance of several types of paleosols (i.e., Histosols, Spodosols, Alfisols, and Ultisols) linked to the development of new ecosystems. These rhizolith assemblages compose an archetypal ichnofacies, the Rhizolith Ichnofacies, which would be indicative of subaerial exposure and the presence of different types of vegetation. Depending on needed and pending studies on rooting patterns, in the future this ichnofacies can yield more precise and significative paleoenvironmental data. Also, the absence of invertebrate trace fossils may be a clue to interpret better the paleoenvironment. Other Paleozoic ichnofaunas, composed of scarce invertebrate trace fossils, some of them meniscate, are considered herein as representative of the *Scoyenia* Ichnofacies, reflecting the periodical subaerial exposure of the deposits.

These ichnoassemblages are the only recorded for the rest of the Paleozoic until the second revolution, after the end-Permian mass extinction occured, with the appearance of trace-fossil assemblages dominated by earthworm (*Edaphichnium*, *Castrichnus*, diffuse boxworks) and crayfish (*Camborygma*, *Loloichnus*, *Dagnichnus*, *Cellicalichnus*, *Katbergia*) trace fossils. These ichnoassemblages, indicative of paleosols with high fluctuating water tables and representative of local marshes, bogs, swamps, and wetlands, may be grouped into a new archetypal ichnofacies: the *Camborygma* Ichnofacies, which should be defined more completely in the future, when better-documented cases are available.

The third revolution occurred in the Late Cretaceous. By that time, the diversification of flowering plants triggered the diversification of certain soil-inhabiting insects, such as ants, termites, bees, wasps, and some beetles, which were capable of constructing linings and free-standing walls for their chambers and nests that consequently acquired a high preservation potential. By the Late Cretaceous, the first recognizable insect trace fossils in paleosols occurred, either as isolated examples, as part of the *Camborygma* Ichnofacies, or in a new one: the *Celliforma* Ichnofacies. The end Cretaceous mass extinction shows no global changes in paleosol ichnofaunas, although the Paleocene record is scarce for a thorough evaluation. In southern South America, the *Camborygma* Ichnofacies, which was dominant since the Late Jurassic, dissapeared. In North America the *Camborygma* Ichnofacies remains dominant in Paleocene–Early Eocene deposits, bearing recognizable insect trace fossils, resembling those assemblages of the South American Late Cretaceous.

The fourth and most important revolution for ichnodiversity took place in the middle Eocene, influenced by the advent and expansion of grass-dominated habitats. Other favorable conditions that promoted this ichnofacies were the early Eocene Climatic Optimum, and the establishment of modern insect groups. These conditions also lead to the appearance of a new soil type, the Mollisols, displaying granular or crumb peds. Trace fossils of cicadas (*Feoichnus*, *Monesichnus*, *Naktodemasis*), dung beetles (*Coprinisphaera*, *Eatonichnus*, *Chubutolithes*), bees (*Palmiraichnus*, *Elipsoideichnus*, *Uruguay*, *Corimbatichnus*, *Rosellichnus*), sphinx moths (*Teisseirei*), ants (*Attaichnus*), termites (*Krausichnus*), and cleptoparasites and detritivores (*Tombownichnus*, *Lazaichnus*) appeared or diversified during this revolution that led to the establishment of the *Coprinisphaera* Ichnofacies. By the Oligocene, in closed-forest environments, also appears the first assemblage dominated by termite and ant trace fossils (*Termitichnus*, *Fleaglellius*, *Vondrichnus*, *Krausichnus*), comprising the *Termitichnus* Ichnofacies. The *Coprinisphaera* revolution is followed during the Neogene by stasis that was interrupted by the occasional appearance of new trace fossils of the same, previously mentioned groups of insects. In contrast with older ichnofacies (*Scoyenia* and *Camborygma*), which are recorded in flooded or high water table paleosols, the younger ichnofacies (*Celliforma*, *Coprinisphaera*, and *Termitichnus*) reflect paleosols with lower water tables. It is as if the terrestrial ichnofaunas would have shift to drier environments, favored by morphological and behavioral adaptations of their producers.

The ichnofacies model for paleosols is an ongoing approach that still has weak points, all of which arise in the present incompleteness of the trace-fossil record. For developing a stronger foundation, additional documentation will be required, and surely it will be a future task of ichnologists to complete and strengthen the models. There are about 166 case studies (25 for the Paleozoic, 39 for the Mesozoic, and 102 for the Cenozoic), many of which are understudied or involve few trace fossils that presently are insufficient to resolve the entire scenario. Despite this, the model is a very promising one, and currently allows us to recognize within the fog of incompleteness, the silhouettes of five paleosol ichnofacies, each one including a number of ichnoassemblages that show sharply or broadly defined paleoenvironmental significance. After the novel approach presented in this chapter, the paleosol ichnofacies model also provides an evolutionary scenario to track the major changes in the history of terrestrial life.

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Chapter 14
The Cenozoic Radiation of Mammals

Verónica Krapovickas and Sergio Vizcaíno

14.1 Introduction

Mammals are at present among the most successful vertebrates on Earth. On land they inhabit almost all the habitats from the desert to the poles and have diverse locomotor and dietary niches and size ranges. The Mesozoic record of mammals spans about 155 Ma (the earliest mammals are known from the Late Triassic), more than twice the duration of the entire Cenozoic Era (Luo 2007). Even though their fossil record is relatively scarce, Mesozoic mammals were diverse and had assorted biologic roles (Luo 2007). The end-Cretaceous mass extinction event that eliminated non-avian dinosaurs and many other mostly marine taxa has been proposed to having triggered the evolutionary radiation of Cenozoic mammals (Archibald and Deutschman 2001). Following e.g. Alroy (1999), Benton (1995), and Foote et al. (1999), among others, most mammalian orders originated and diversified in a short period of time (10 Mya) soon after the Cretaceous/Tertiary (K/T) boundary. Studies based on molecular data introduced two other models for the diversification on mammals: the long-fuse and the short-fuse models. The first model postulated an extended lag for the radiation of mammals as orders originated in the Cretaceous but diversified after the K/T transition (e.g. Springer et al. 2003). The second model proposed that the origin of orders and their diversification occurred

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well back into the Cretaceous (e.g. Springer 1997; Kumar and Hedges 1998). Recent studies integrating morphologic and molecular data proposed that the origin of extant orders of mammals occurred during the Late Cretaceous and major diversification occurred during and after the early Eocene, remaining the diversification rates unchanged after the K/T transition (Bininda-Emonds et al. 2007). Up to now, fossil evidence supporting the previous models was restricted to body fossils. However, although even more sparse, the Mesozoic footprint record of early mammals may provide further evidence.

In this contribution we briefly summarize the Mesozoic and Cenozoic record of footprints attributed to mammals worldwide. Also, we address in more detail the evolutionary implications of the Cenozoic ichnologic record of South American mammals. Regarding the latter, we will first analyze chronologic and geographic changes in the composition of the mammalian ichnofaunas and compare them with those of body fossils. Second, we will consider the paleoenvironmental distribution of mammalian footprints and their paleoecological significance.

14.1.1 Mammalian Ichnology Before the K/T Transition

The Mesozoic record of mammals is mostly composed of isolated teeth; postcranial skeletons and skulls are rare (Kielan–Jaworowska et al. 2004). This fact complicates in-depth evaluation of morphologic variations of footprints produced by distinct early mammalian lineages, making the assignment to putative producers of footprints vague. Distinguishing footprints assignable to mammals from other taxa of the mammalian evolutionary line as nonmammalian cynodonts and even basal synapsids is problematic (e.g. Schultz-Pittman et al. 1996; Lockley et al. 2004).

One of the most remarkable footprints known from the Mesozoic is *Ameghinichnus patagonicus*, from the Middle Jurassic La Matilde Formation of Santa Cruz Province, Argentina. They are one of the unquestioned examples of footprints attributed to early mammals. Casamiquela (1964) proposed a mammalian trackmaker due to the morphology of the *manus* and *pes* prints and the galloping and hopping gaits evidenced on the trackways. This author inferred that the trackmaker was a quadrupedal animal with similarly-shaped, pentadactyl *manus* and *pes*, with the *manus* being slightly smaller than the *pes*. The impressions of manual and pedal digits II–IV are of similar length, and those of digits I and V are slightly shorter. The metacarpal/tarsal and phalangeal pads are well preserved, and there are no claw marks (Casamiquela 1964). The trackways record a walking gait, with the manus-pes sets in an alternate position in relation to the midline. In contrast, hopping trackways have manus-pes sets grouped at relatively the same position in relation to the midline (Casamiquela 1964). Most authors supported Casamiquela's (1964) identification of the *Ameghinichnus* trackmaker as an early mammal (e.g. Leonardi and de Oliveira 1990; Leonardi 1994; Rainforth and Lockley 1996; Martin and Rauhut 2005; Rougier et al. 2007a, b). Casamiquela (1964) proposed "pantotheres" as the mammalian producer, whereas Kielan-Jaworowska and Gambaryan (1994) attributed *Ameghinichnus* to multituberculates.

Similar tracks from other ichnofossiliferous localities worldwide have been referred to *Ameghinichnus*, as it is the best defined ichnotaxa assigned to an early mammal. Olsen (1980) described a series of ichnofossils from the Lower Jurassic Newark Supergroup, later recognized as representing several species of *Ameghinichnus*, which he ascribed to nonmammalian cynodonts, possibly tritheledontids (Olsen et al. 2002). Footprints with hair impressions have been recorded in the Triassic Stomberg group in Lesotho and inferred to have been produced by nonmammalian cynodonts or early mammals (Ellenberger 1972, 1974, 1975). De Valais (2009) recognized the ichnotaxa *Eopentapodiscus* to be the only synonymous with *Ameghinichnus*, after reviewing numerous icnotaxa (*Acropentapodiscus*, *Amphibiopodiscus*, *Aristopentapodiscus*, *Dinopentapodiscus*, *Eoameghinichnus*, *Grypopentapodiscus*, and *Pseudameghinichnus*) once attributed to the ichnogenus from the Upper Triassic-Lower Jurassic Elliot Formation of Lesotho (Ellenberger 1970), and accepted the assignment to *Ameghinichnus* given by other authors to materials from the Towaco Formation (Lower Jurassic) of the Newark basin, USA (Olsen and Rainforth 2001), and the Lower Jurassic of Sołtyków, Poland (Gierliński et al. 2004).

Another ichnotaxon, *Brasilichnium elusivum*, attributed to Mesozoic early mammals is recorded in numerous localities. This ichnotaxon was originally described from the Botucatu Formation (Upper Jurassic-Lower Cretaceous) of Brazil and interpreted as corresponding to small-sized mammals (Leonardi 1980, 1981; Fernandes and Carvalho 2008). Later, it was recorded in classical Lower Jurassic outcrops of USA, including the Navajo Sandstone and the Moenave Formation, and reinterpreted as possibly produced by advanced therapsids or early mammals (Lockley and Hunt 1995; Lockley et al. 1998; Rainforth and Lockley 1996; Loope 2006). Other Cretaceous footprints of mammals have been reposted from the Gate Formation (Late Cretaceous) of Alberta, Canada, and ascribed to several mammalian trackmakers (Sarjeant 2000; McCrea and Sarjeant 2001).

At present, there is just one example of footprints attributed to marsupial mammals, *Duquettichnus kooli*, described by Sarjeant and Thulborn (1986) from the Lower Cretaceous of the Peace River Canyon, British Columbia. The footprints record syndactyly of pedal digits II and III, supporting a marsupial origin.

Some of the most significant and better preserved ichnologic records of Mesozoic mammals are from Gondwana, despite their relatively scarce body-fossil record (e.g., Kota Formation, India; Yadagiri 1984). This differs from the body-fossil record in boreal landmasses, where Mesozoic mammalian diversity and abundance is much higher (Bonaparte 1986, 1990, 1995; Bonaparte and Kielan-Jaworowska 1987; Luo et al. 2002; Kielan–Jaworowska et al. 2004).

14.1.2 Mammalian Ichnology After the K/T Transition

The global ichnologic record of mammals is poor for the Paleogene, most likely representing less than 17 % of the record for the entire Cenozoic (McDonald et al. 2007). Paleocene footprints are extremely rare, with just a few tracksites reported worldwide (Hunt and Lucas 2007), all of them in North America (e.g. Peabody 1954; Johnson 1986; Lockley and Meyer 2000).

The only confirmed tracksite that contain Paleocene mammal footprints is from Alberta, Canada. It corresponds to a trackway preserved on a fallen block from strata belonging to the Porcupine Hills Formation at Calgary (McCrea et al. 2004). The footprints were ascribed to *Sarjeantipes whitea* and interpreted as produced by creodont mammals. In 1928, Rutherford and Russell unveiled Paleocene footprints found near Red Deer, Alberta, attributed to a mammalian track maker (Rutherford and Russell 1928; Russell 1930). McCrea et al. (2004) re-studied the material suggesting a crocodilian track maker. It is notable that, even apparently depauperate, the Paleocene tetrapod footprints have scarce mammals represented and is mostly composed by amphibian, reptiles, and birds, in contrast with mammal footprints represented during the rest of the Cenozoic (Hunt and Lucas 2008) that became more frequent through the Eocene and Oligocene.

The most diverse and well-studied Eocene mammalian ichnofauna is from the late Eocene of Texas (Sarjeant and Langston 1994). It records footprints attributed to insectivoran, creodont, carnivore, mesonychian, rodent, perissodactyl, and artiodactyl trackmakers. The trans-Peco ichnofauna is one of the best recorded examples of a Paleogene ichnofauna globally, even though it could be enlightening to reevaluate this ichnassemblage in the light of new discoveries. Another remarkable ichnofauna is from the Chuckanut Formation of Northern Washington, USA (Mustoe 2002). This ichnofauna is mainly composed of multiple bird tracks and also record remarkable mammal footprints attributed to extinct lineages, such as Pantodonta or Dinocerata and early equids or tapiroids. Other records are from Europe (e.g. Desnoyers 1859; Ellenberger 1980), Asia (West et al. 1983; Abbassi and Lockley 2004; Ataabadi and Khazaee 2004), North America (e.g. Greben and Lockley 1992; Lockley and Hunt 1995; Moussa 1968), and South America (e.g. Noblet et al. 1995).

One of the best preserved and abundant mammalian footprints corresponds to the lower Oligocene of southeastern France (Demathieu et al. 1984; Costeur et al. 2009). It records abundant perissodactyl (early Rhinocerotids) and artiodactyl (Lophiomerycids and/or Entelodonts) track and trackways and a footprint attributed to a mustelid-like carnivore. Some other examples are recorded from additional localities of Europe (e.g. Tobein 1952; Casanovas-Cladellas and Santafé-Llopis 1982; Astibia et al. 1994; Prats and López 1995; Murelaga et al. 2000; Uchman et al. 2004), North America (e.g. Nixon 1991; Lockley and Hunt 1995; Terry and Wells 1995), and South America (e.g. Noblet et al. 1995).

For the Neogene the number of recorded tracksites grows exponentially (for more detail, see McDonald et al. 2007). Herein, we briefly highlight some of the classic outcrops documenting relevant mammal footprints. The research performed in these localities has documented a wide variety of mammal footprints and established the most used ichnotaxonomy of Cenozoic tracks and trackways. This is the case of the work of Vyalov (1965, 1966) who reported numerous bird and mammal footprints from the Miocene of Ukraine. The mammalian footprints were ascribed to numerous ichnotaxa assigned to canids (*Bestiopeda gracilis*), felids

(*Bestiopeda bestia*, *Bestiopeda sanguinolenta*), artiodactyls (*Pecoripeda amalphaea*, *Pecoripeda dicrocervoides*, *Pecoripeda djali*, *Pecoripeda gazelle*, *Pecoripeda satyri*), and perissodactyls (*Hippipeda aurelianis*). The Miocene of the Romanian Carpathians records also a diverse and excellent preserved avian and mammalian ichnofauna (Panin and Avram 1962; Panin 1965). Mammals are represented by canids (*Canipeda longigriffa*), felids (*Felipeda felis*, *Felipeda lynxi*), artiodactyl (*Pecoripeda gazelle*), and proboscidean (*Proboscipeda enigmatica*) footprints. Other significant records are known from Europe (e.g. Pérez-Lorente et al. 1999; Astibia et al. 2007; Fornós et al. 2002), North America (e.g. Robertson and Sternberg 1942; Scrivner and Bottjer 1986; Lockley and Hunt 1995; McNeil et al. 1999; Lucas 2007), Oceania (e.g Carey et al. 2011), Africa (e.g. Leakey and Harris 1987; Robert et al. 2008; Scott et al. 2009), and South America (e.g. Aramayo and Manera de Bianco 1987a, b). Globally, the Neogene mammalian record is dominated by ungulate footprints as perissodactyls, artiodactyls, and proboscideans, followed by carnivores as felids and canids.

Reviews of Cenozoic vertebrate ichnology are scarce. The contributions of Leonardi (1994), McDonald et al. (2007), Hunt and Lucas (2007), and Lucas (2007) are the starting point to deeper ichnologic analyses, not only compiling bibliography, but also evaluating the biologic, ethologic, and ecologic information provided by footprints in the framework of the evolutionary history of their producers. Hopefully, identifying the problems and promises of the mammalian paleoichnologic record of each continent will help to develop a research program that will permit global comparisons.

14.2 The South American Case Study

The geologic history of the main continental land masses has influenced the evolution and dispersal of their mammal faunas, resulting in radical differences among them. Thus, from many aspects, direct comparisons of mammalian communities between continents are a difficult task. For instance, the magnitude of the disparity achieved is so that the faunas are not used for global age correlations and particular land-mammal-age systems are used for different continental land masses (see Woodburne 2006 for North America; Lindsay 1997 for Eurasia; Megirian et al. 2010 for Australia; and Flynn and Swisher 1995 for South America).

The long-term isolation of the South American continent for the greater part of the Cenozoic produced a highly peculiar terrestrial biota, of which one of the best-known components is its endemic mammalian fauna; probably the best fossil record of mammals among southern hemisphere continents (Croft 2012). Several of the main groups discussed below became partially or fully extinct and/or developed morphologies many times outlying the shape ranges of their living closest relatives (e.g., carnivorous marsupials, glyptodonts, and sloths among xenarthrans, native ungulate groups). As a consequence, inferences about their paleobiology cannot rely on simplistic actualistic reference to the biology of their living closest relatives.

In the last two decades, some effort has been made to overcome this situation through the application of morphofunctional, biomechanical, and ecomorphologic approaches. Overviews on this issue with respect to carnivorous marsupials are available in Prevosti et al. (2012), on xenarthrans in Vizcaíno et al. (2008), Bargo et al. (2012) and Vizcaíno et al. (2012b), and on ungulates in Cassini et al. (2012).

In a strict sense, the inferences resulting from those approaches are in many instances difficult to verify. However, occasionally direct evidence comes to our aid. This is the case when trace fossils, such as footprints attributable to these groups, offer a tool to test functionally based hypotheses about locomotion and/or use of the substrate, and to generate new hypotheses providing valuable paleobiologic information on gait style and particular behavior (e.g., digging, scratching), which may serve as proxies for the size of the putative trackmaker.

In most cases, footprints and bones are not associated in the same stratigraphic units or facies, so then tracks become the primary source for recording the presence of the producer at those levels. As they are normally preserved in situ in the facies where they were produced, fossil footprints involve small temporal and spatial error spans for the analysis of faunal taxonomic composition and distribution and imply a close relationship between the footprints and the environments inhabited by the producers. Thus, fossil footprints emerge as useful tools for paleocommunity analysis and paleoenvironmental interpretations.

Fossil footprints in South America have been reported from different localities and ages, including ichnologic associations preserved on a single surface or several stratigraphically closely related surfaces. Leonardi (1994) summarized the ichnologic fossil record in South America known two decades ago, including that of Cenozoic mammals. In the present state of knowledge, the already mentioned peculiarities of the South American mammalian fauna preclude general comparisons of its paleoichnologic record with that from other continents.

In the second part of this chapter we endeavor to identify the problems and promises of the mammalian paleoichnology record of South America. In doing so, we update the information provided by Leonardi (1994) with new findings, reconsidering the ages according to new chronologic information and reviewing the potential producers. We also analyze chronologic and geographic changes in the composition of the mammalian faunas expressed by the ichnologic record in comparison with that of body fossils. Finally, we evaluate the paleoenvironmental distribution of mammalian footprints and their paleoecologic significance.

14.3 Faunistic Content Through the Cenozoic

Based mostly on the fossil record from Argentine lowland, high-latitude sites, different authors, such as Ameghino, Simpson, Reig, Ortiz-Jaureguizar, and Pascual, among others (for a complete account, see Goin et al. 2012), have stressed the episodic nature of the Cenozoic evolution of South American mammals, probably as a consequence of several important temporal gaps in the knowledge of these successions. The increasing amount of information collected in the last decades from new high-latitude sites and in many other areas of South America, especially the notable faunas uncovered from the Andes, produced at least two different and complementary effects. At a broader regional scale, as the biochronologic sequence of Neogene mammalian associations of southern South America became better known, cycles or phases characterized by faunal turnovers and a distinctive taxonomic composition were recognized, and paleoclimate and tectonics were identified as major driving forces in addition to the intrinsic evolutionary patterns of each mammalian lineage (Goin et al. 2012). At a continental scale, the actual patterns are far more complex, with Cenozoic mammal faunas responding also to biogeographic, sea level, ecologic, and environmental changes (Flynn et al. 2012).

Three of the five successive phases in South American mammalian evolution recognized by Goin et al. (2012) involved the Cenozoic: the Early South American (?latest Cretaceous-latest Eocene), characterized by major radiations within Metatheria and Eutheria; the Late South American (early Oligocene-middle Pliocene), with standardization of relatively few lineages among metatherians and marked radiation of hypsodont types among South American native ungulates; and the Inter-American (late Pliocene-Recent), produced by the mixture of North and South American therian lineages, with progressive decline of native faunas. According to these authors, the events that triggered these phases include global cooling, full development of the Circumpolar Antarctic Current, and arrival of platyrrhine primates and caviomorph rodents between the Early and Late South American phases. The transition from the Late South American and the Inter-American phases is marked by the Panamanian connection between the Americas and the beginning of the Great American Biotic Interchange (GABI).

During the Cenozoic part of the Early South American phase, marsupials, xenarthrans, and native ungulates underwent their first Cenozoic main radiation. Marsupials exploited a variety of adaptive zones and diets, including several small to medium granivorous, insectivorous, and insectivorous–frugivorous groups (polydolopimorphian; didelphimorphian and paucituberculates; Abello et al. 2012) and medium to large carnivorous and carnivorous–omnivorous (i.e., sparassodonts).

Xenarthrans include the Cingulata and the Pilosa. The Cingulata are exemplified by armadillos and glyptodonts, noted for the armor covering the head, body, and tail. The Pilosa are composed of the Vermilingua—the anteaters—and the Tardigrada or Folivora—living tree sloths and a much larger diversity of fossil sloths, including the gigantic ground sloths. The scarce early record of xenarthrans suggests that most of them inhabited regions not yet yielding fossils, an explanation widely accepted by paleontologists, and consistent with the high diversity of xenarthrans in the modern tropics and the correspondingly poor early Cenozoic record of that region (Flynn et al. 2012).

According to Cifelli (1985, 1993), the ungulate groups endemic to South America and the modern Ungulata (Perissodactyla and Cetartiodactyla) share a most recent common ancestor or even form a single clade themselves (Cifelli 1985, 1993). However, a recent phenomic approach split endemic South American ungulates between Pan-Euungulata and Afrotheria (O'Leary et al. 2013). Endemic South

American ungulates fall into five groups: the astrapotheres, pyrotheres, notoungulates, litopterns, and xenungulates (Simpson 1980; Marshall and Muizon 1988). Astrapotheres (including trigonostylopids) were rhinoceros-like mammals (Cifelli 1985) found in deposits of Paleocene to Miocene age. Pyrotheres were elephant-like, with tusks and bilophodont cheek teeth, and were never as diverse nor did they cover as great a span of time as the astrapotheres. They are known only from the middle Eocene through the late Oligocene. Notoungulates are by far the most diverse and abundant lineage of South American ungulates (nearly 140 species in 13 families; Croft 1999), and include animals similar to rhinoceroses, hippopotamuses, rabbits, and rodents; others do not closely resemble any living mammal. Litopterns were the second most successful group of South American ungulates in terms of diversity and longevity, spanning from the late Paleocene to the late Pleistocene (Marshall and Cifelli 1990). They include forms similar to antelopes, horses, and camels. Xenungulates are primitive, poorly known, tapir-like mammals, restricted to the Paleocene deposits of Brazil and Argentina (Gelfo et al. 2008).

The taxonomic and ecologic shift that marked the passage to the Late South American phase (Goin et al. 2012) included the arrival of caviomorph rodents and platyrrhine primates in South America, the last records of marsupials sensitive to low temperatures, the beginning of a rapid diversification of the “shrew opossums” (Paucituberculata), the radiation of large modern borhyaenoids (Sparassodonta), and the origins of the Argyrolagoidea. Among native ungulates, the diversity of hypsodont notoungulates increased after the early Oligocene, and low-crowned, bunodont ungulate types became restricted to the lower latitudes; Astrapotheria and Pyrotheria developed their larger forms during the Oligocene-Miocene (Vizcaíno et al. 2012a), disappeared by the middle late Miocene, and, by the Miocene, some lineages developed limb specialization convergent on that of equids (e.g., in proterotheriid Litopterna).

According to the most recent findings (Antoine et al. 2012), the oldest records of caviomorph rodent come from the late middle Eocene of Perú. Caviomorphs are among the most abundant taxa in every post-Oligocene fauna and soon after their arrival they radiated in a series of lineages that persist up to the present day, evolving some fossil forms that weigh in excess of a hundred kilograms (Vizcaíno et al. 2012a). The oldest record of a platyrrhine primate in South America is *Branisella* from the late Oligocene of Salla, Bolivia (Kay et al. 1998). Fossil South American primates are rare arboreal forms, mostly no larger than 10 kg, but at least one taxon reached 20 kg (Halenar 2011).

Goin et al. (2012) described the Inter-American phase as a series of pulses of the so called Great American Biotic Interchange (Stehli and Webb 1985), possibly reflecting glacial versus interglacial conditions in the Northern Hemisphere. The first North American forms to arrive in South America included cricetid rodents, procyonid, and mustelid carnivorans, and tayassuid artiodactyls. During the early Pleistocene gomphotheriids (proboscideans), camelids and cervids (artiodactyls), equids and tapirids (perissodactyls) are recorded in South America for the first time, in addition to several carnivoran lineages (felids, canids, and ursids).

As mentioned above, there is a significant biogeographic differentiation at a continental scale that was considered recently by Goin et al. (2012) and Flynn et al. (2012). Both contributions stressed the significance of the evidence provided by sites of different ages along the Andes, especially during Goin's et al. earlier phases of the Cenozoic. For instance, the latest Eocene-early Oligocene faunas of central Chile and Patagonia differ in taxonomic representation: the Chilean Tinguiririca fauna lacks hegetotheres but possesses rodents, and a number of species are distinct between the two areas (Croft et al. 2008; Flynn et al. 2003; Flynn et al. 2012). Also, the middle Miocene fauna of Quebrada Honda in southernmost Bolivia is more similar to the slightly older high-latitude fauna of Collón-Curá in Patagonia than to the contemporaneous low-latitude fauna of La Venta of Colombia (Croft 2007; Goin et al. 2012). However, there is also evidence of some late biogeographic differences during the Inter-American phase, such as the differential distributions within ground sloths (e.g. *Eremotherium* and *Megatherium*; Cartelle and De Iuliis 1995) and proboscideans (*Cuvieronius* and *Notiomastodon*; Mothé et al. 2012 and references therein), among others.

14.4 Methods

To analyze the composition of the Cenozoic South American mammal paleocommunities, we compiled incidence (=presence/absence) data for ichnologic assemblages containing diverse footprints and dismissed those represented only by one ichnologic morphotype. We conducted a cluster analysis to explore trace-fossil assemblage groupings (Q.mode) and used the Jaccard similarity index for binary data. The analysis was performed in the statistical package PAST (Hammer et al. 2001).

In the second analysis we compiled a dataset of environments of footprint preservation by age, for all assemblages with information available in the literature. The environmental data were classified in seven categories: (1) floodplain, (2) exposed sandbar, (3) marginal lacustrine, (4) wet interdune, (5) dune, (6) salt flat, and (7) marginal marine. The number of occurrences of each category per age was plotted in histograms.

14.5 The Cenozoic Track Record of South American Mammals

14.5.1 The Footprints of the San Jeronimo Group, Peru

The San Jerónimo Group (early Eocene-early Oligocene) of Peru (Carlotto 2006) holds relevant ichnologic assemblages misinterpreted for nearly a century as dinosaurian in origin, and consequently their stratigraphic levels were taken as Cretaceous in age.

Fig. 14.1 Map indicating mammal-bearing fossil footprint localities in South America

Originally, Gregory (1916) described fossil footprints from the Cuzco valley, Peru, preserved near the base of the "Couches Rouges" (San Jerónimo Group). Later, Noblet et al. (1987, 1995) described other footprint assemblages from three localities, two near Cuzco city (Kayra and Paruro) and the third at Langui near the city of Sicuani (Fig. 14.1). During the past decade, the age of the San Jerónimo Group was established as early Eocene to early Oligocene by stratigraphic studies and analysis of volcanic tuff and fission tracks (Carlotto 1998, 2002, 2006; Carlotto et al. 1995, 2005; Fornari et al. 2002). Subsequently, the producers of the footprints described by Noblet et al. (1987, 1995) were reinterpreted by Lockley et al. (1999) as notoungulates or litopterns and by Carlotto (2011) as birds, although the material was never examined in detail. The material first studied by Noblet was illustrated by Leonardi (1994) and is that discussed herein.

The San Jerónimo Group is divided in two units, both preserving fossil footprints. The footprints from Paruro occur in the lower-middle Eocene Kayra Formation (lower unit). The upper Eocene-lower Oligocene Soncco Formation (upper unit) records two different assemblages, one at Kayra and the other at Langui, near Sicuani (Fig. 14.1).

14.5.1.1 Paruro Footprints

The footprint assemblage comprises three morphotypes preserved on a single surface. The best preserved morphotype consists on homopod tridactyl footprints of a rodent-like mammal of small size (approximately 6 cm long and 3 cm wide), with long pointed digits and a plantar pad of at least one third of the total length of the footprint (Fig. 14.2c) (see plate XXXIV, Fig. 4 in Leonardi 1994). The second footprint morphotype has a poorly defined morphology and is not well illustrated. It consists of at least a tetradactyl footprint of an apparently homopod quadruped (see plate XXXIV, Fig. 2 in Leonardi 1994). The footprints are approximately 7 cm long and 7 cm wide. The material corresponds to three trackways and an isolated footprint. Leonardi (1994) described it as footprints of the size of a cat or a small dog. One poorly defined trackway of a bipedal and at least tridactyl animal represents the third morphotype preserved at Paruro (Fig. 14.2a and b) (see plate XXXIV, Figs. 1 and 3 in Leonardi 1994). It has marked toe drags that gave the impression to Noblet and Leonardi that it was produced by a sick or very old individual.

14.5.1.2 Kayra Footprints

The ichnologic record of Kayra involves an isolated tridactyl footprint, 13 cm long. It represents the impression of a mesaxonic foot with three digits directed forward. The central digit is wider and longer than the lateral digits, though it is incomplete, and lateral digits are pointed (Fig. 14.2e). The plantar pad is wide and is as long as the central digit. The footprints are interpreted here as produced by a toxodontid notoungulate.

14.5.1.3 Langui Footprints

The footprints of Langui are preserved on a single sub-vertical surface with at least three different morphologic types. An unclassifiable fourth morphotype was mentioned by Leonardi (1994). Unfortunately, there is no illustration of the footprint and for this reason we won't consider it here. The largest morphotype is represented by one trackway with two tridactyl footprints, approximately 20 cm long with a central digit longer than the lateral digits, possibly attributable to phorusrhacids (see plate XXXV, Figs. 4 and 1 in Leonardi 1994). The second morphotype consists of one trackway with seven tridactyl footprints, 10–13 cm long, of a quadruped homopod mammal with hoof-like toes (Fig. 14.2d) (see plate XXXV, Figs. 1, 2 and 6 in Leonardi 1994). The footprints are assigned to *Macrauchenichnus* isp. and

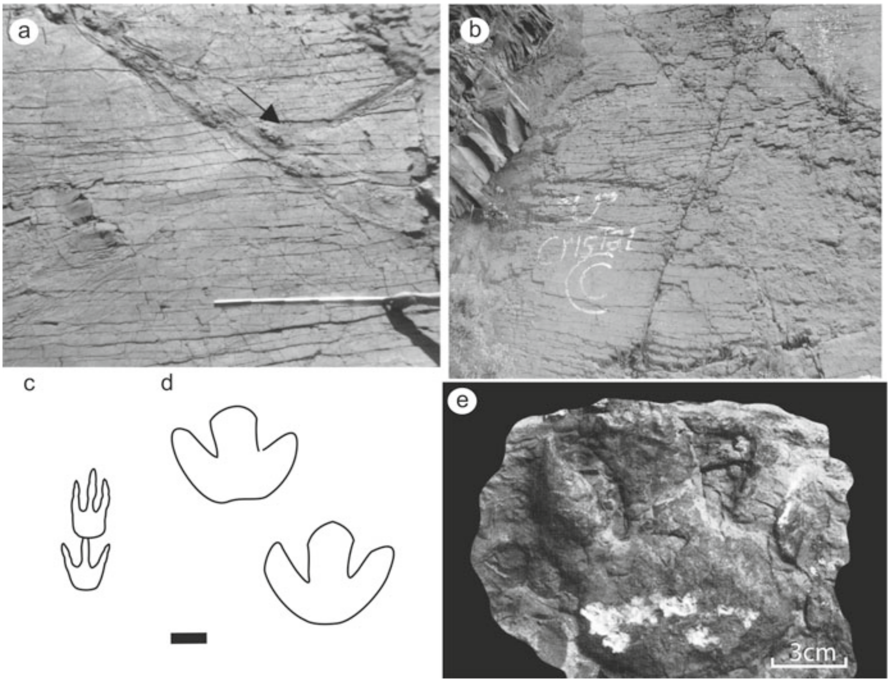

Fig. 14.2 Footprints of the San Jeronimo Group, Peru. Paruro tracksite photographed by Noblet (**a**) and the tracksite today (**b**); (**c**) homopod tridactyl footprints, Paruro. Scale bar = 3 cm; (**d**) Tridactyl quadruped homopod footprint, Langui; (**e**) isolated tridactyl footprint, Kayra

interpreted as possibly produced by toxodontid notoungulates or macraucheniid litopterns. The morphotype III consists of a trackway of a quadrupedal, rodent-like mammal. The manus footprints are overprinted by the well-defined pes footprints. Pes footprints are tridactyl with elongated digits and a plantar pad (see plate XXXV, Figs. 1 and 3 in Leonardi 1994). The footprints are approximately 7 cm long, and the morphology of the pes footprint and the trackway pattern are highly comparable with those of the small heteropod footprints described by Krapovickas et al. (2009a, b, c; see below), suggesting that they were produced by a rodent-like typothere notoungulate or a caviid rodent.

14.5.2 The Footprints of the Vinchina Basin, Argentina

The Vinchina Basin of La Rioja Province, northwestern Argentina (Fig. 14.1), is a thick continental succession deposited under a wide variety of depositional systems (i.e., fluvial, lacustrine, and eolian) that bears diverse and exceptionally well-preserved trace-fossil assemblages. Recent interpretations of the stratigraphy of the basin (Ciccioli et al. 2010, 2014; Limarino et al. 2010) divided the sedimentary succession into five formations, from bottom to top, Puesto La Flecha (Eocene), Vallecito (Oligocene-early Miocene), Vinchina (early Miocene), Toro Negro (late Miocene-Pliocene), and El Corral formations (Pliocene). The body-fossil record for these units (e.g., Turner 1964; Ramos 1970; De Iuliis et al. 2004; Rodríguez Brizuela and Tauber 2006) is fragmentary and scarce. Conversely, fluvial and lacustrine facies of the basin host a rich invertebrate and vertebrate ichnofauna (Frenguelli 1950; Bonaparte 1965; Tripaldi et al. 2001; Krapovickas et al. 2009a; Melchor et al. 2010, 2012; Krapovickas and Nasif 2011). The most remarkable assemblages of mammal footprints are recorded in the Vinchina Formation, at Quebrada de la Troya (lower portion) and Quebrada del Yeso, and Toro Negro Formation at Quebrada de la Troya (upper portion) (Fig. 14.1).

14.5.2.1 Lower Quebrada de la Troya Footprints

The footprints of Quebrada de la Troya, nearby the town of San José de Vinchina, are preserved in floodplain deposits of meandering fluvial systems of the Vinchina Formation. One of the most peculiar footprints is *Tacheria troyana*, approximately 10 cm long, produced by tetradactyl homopod quadrupeds with long digits and well developed plantar pads (Fig. 14.3f). The trackmaker was interpreted by Krapovickas and Nasif (2011) as a dinomyid caviomorph rodent or a close relative. There are also preserved small tridactyl footprints of a homopod rodent-like mammal, possibly a caviomorph rodent or typothere notoungulate (Fig. 14.3h); tridactyl homopod footprints with short broad digits and blunt tips assigned to *Macrauchenichnus* isp. and interpreted as toxodontid notoungulates or macraucheniid litopterns (Fig. 14.3b and d); large tridactyl footprints of rheiformes; footprints of shorebirds assigned to *Gruipeda* isp.; and a small tridactyl to tetradactyl footprint with pronounced scratch marks (Krapovickas et al. 2009b, c)

14.5.2.2 Quebrada del Yeso Footprints

In 1950 Frenguelli mentioned a fossil footprint assemblage preserved in a continental succession at Quebrada del Yeso, between the towns Villa Castelli and Jagüe, La Rioja Province, Argentina. He described *Venatoripes riojanus*, a trackway of large manus-pes sets interpreted originally as produced by a large-size reptile, since the bearing levels were considered early Permian in age (see Fig. 2 in Frenguelli 1950). Later, the succession was interpreted as deposited during the Miocene–Pliocene and the tracks were reinterpreted as produced by xenarthran megatheroids (Turner 1960; Bonaparte 1965). Recently, the outcrops were relocated as close to the top of the Vinchina Formation, suggesting an early-middle Miocene age for the footprint assemblage (Limarino, C.O. pers. comm.). Other elements of the assemblage were documented by Bonaparte (1965), interpreting them as produced by several avian and mammalian taxa, such as rheiformes, charadriiformes, ralliformes, and macraucheniid litopterns (see Fig. 1 in Bonaparte 1965).

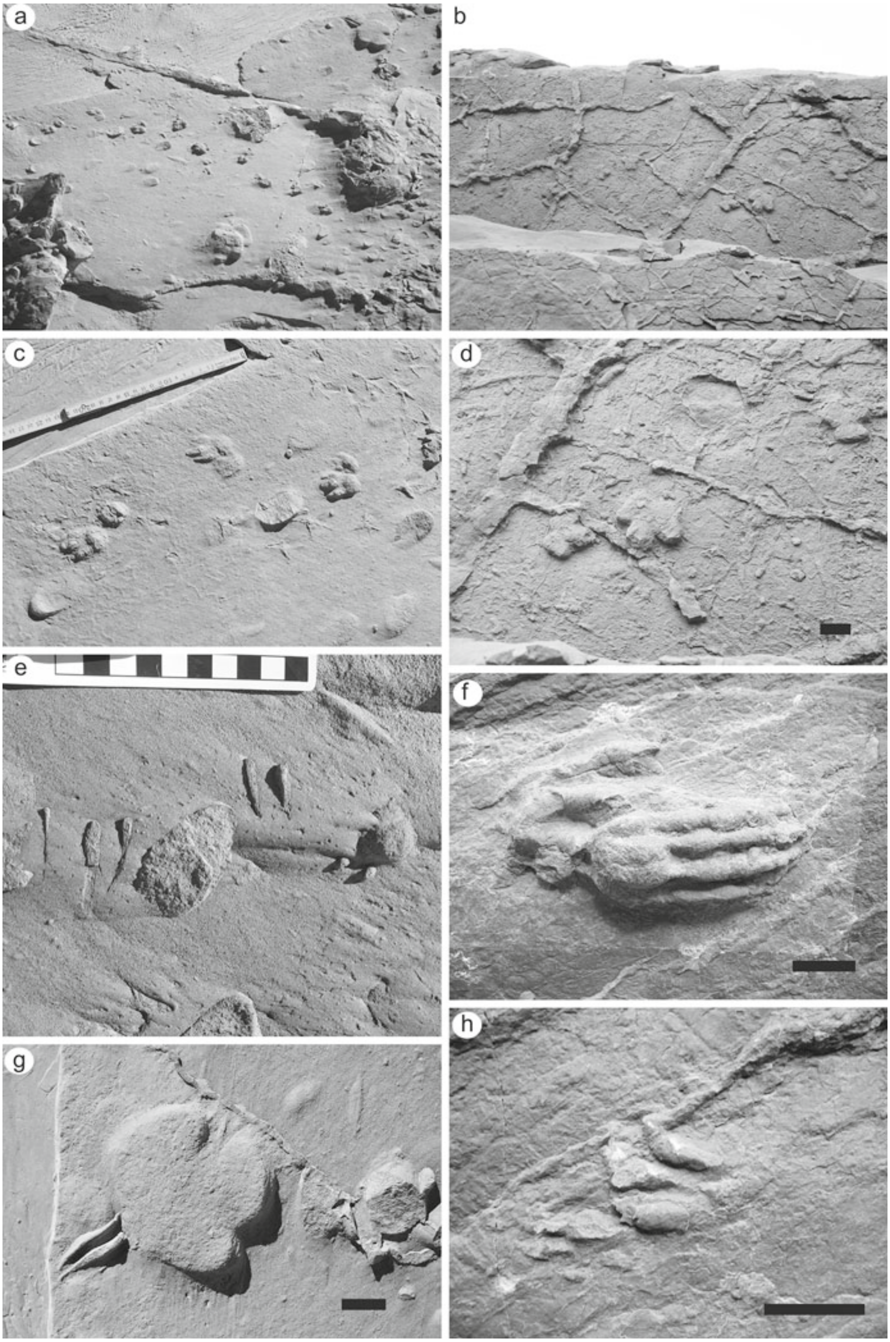

Fig. 14.3 Footprints of the Vinchina Basin, Argentina. (**a**) General view of the main tracking surface of Toro Negro; (**b**) General view of the main tracking surface of Lower Vinchina; (**c**) Small heteropod footprints, Toro Negro; (**d**) *Macrauchenichnus* isp. Scale bar = 3 cm, Lower Vinchina; (**e**) Oval impressions, Toro Negro; (**f**) *Tacheria troyana*, Lower Vinchina. Scale bar = 3 cm; (**g**) *Macrauchenichnus rector*, Toro Negro; (**h**) Small tridactyl footprints, Lower Vinchina. Scale bar = 3 cm

14.5.2.3 Upper Quebrada de la Troya Footprints

The Miocene deposits of the Toro Negro Formation at Quebrada de la Troya, La Rioja Province, Argentina, host a rich vertebrate and invertebrate ichnofauna documented by Krapovickas et al. (2009a, b, c). The trace fossils are recorded from the lower part of the Lower Member of the Toro Negro Formation. The vertebrate ichnofauna is the most diverse of the three ichnologic assemblages preserved in the Vinchina basin and includes avian and mammalian footprints (Fig. 14.3a). The mammalian footprints ascribed to *Macrauchenichnus rector* are interpreted as produced by medium sized macraucheniid litopterns (Fig. 14.3a and g), cf. *Venatoripes riojanus* as large tardigrade mammals (Fig. 14.3a), kidney-like footprints as medium to small tardigrades, oval impressions as proterotheriid litopterns (Fig. 14.3e), and small heteropod footprint originally interpreted as hegetotheriid typotheres or caviomorph rodents and herein as caviid caviomorph rodents (Fig. 14.3c). The avian footprints (e.g., *Fuscinapeda sirin*) are interpreted as produced by shorebirds, incumbent footprint as a large cursorial bird like rheiformes or phororhacids, and slender anisodactyl footprints as perching birds. The tetrapod footprints and rare *Palaeophycus* and *Helminthopsis* are preserved on the top of exposed sandbars of anastomosing fluvial systems developed under a semi-arid climate. Crevasse-splay deposits preserve abundant meniscate trace fossils and dwelling tubes as *Taenidium*, *Scoyenia,* and *Palaeophycus* ascribed to the *Scoyenia* Ichnofacies.

14.5.3 The Footprints of the Santa Cruz Formation, Argentina

The Santa Cruz Formation (late early Miocene) is a continental succession exposed from the Andean Precordillera to the Atlantic coast of southern Patagonia (Matheos and Raigemborn 2012). Along the Atlantic coast, between the Río Coyle and Río Gallegos, Tauber (1997) defined two members, from base to top, the Estancia La Costa and the Estancia La Angelina members. The basal portion of the Estancia la Angelina Member records undetermined mammalian fossils footprints in the present-day intertidal zone (Figs. 14.1 and 14.4d) (Raigemborn et al. 2012). These beds represent distal-floodplain environments with the development of moderately well-drained paleosols due to seasonal shifts between subhumid and semiarid climatic conditions (Krapovickas 2012).

14.5.4 The Footprints of the Mariño Formation, Argentina

The Mariño Formation (Miocene) records a trackway exposed on the margins of the Provincial Road 17 at Cacheuta, Mendoza Province, western Argentina (Fig. 14.1). The footprints consist of a single trackway with oval footprints, approximately 3 cm long, preserved in eolian strata deposited under arid to semi-arid climatic conditions

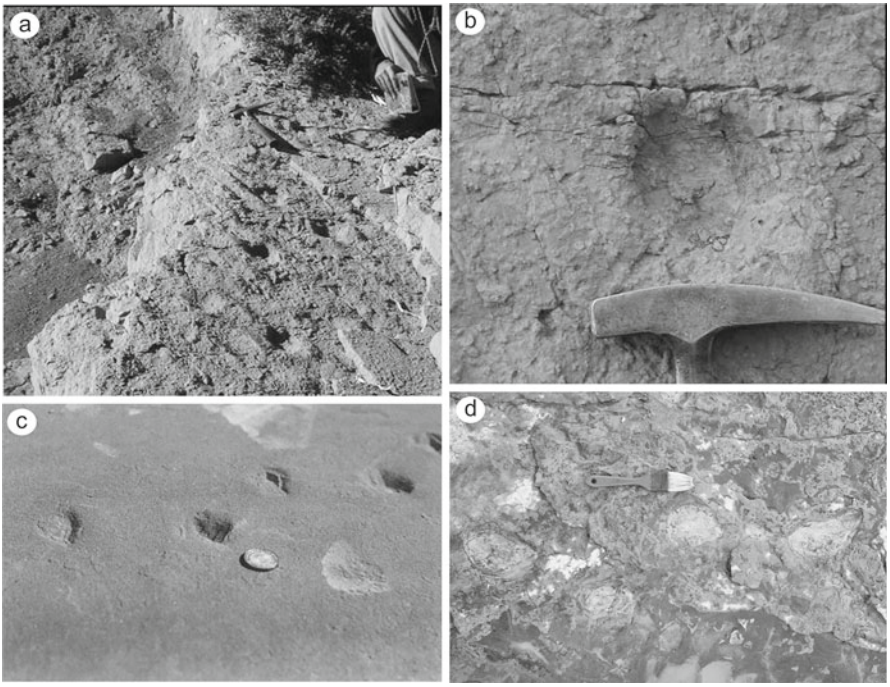

Fig. 14.4 Footprints of the Mariño and Santa Cruz formations, Argentina. (**a**) Tridactyl footprints on fluvial wave-rippled fine-grained sandstone strata, Salagasta; (**b**) detail of the tridactyl footprints; (**c**) Oval footprints, Cacheuta; (**d**) undetermined mammalian footprints, Santa Cruz

(Zavattieri et al. 2001). The footprints correspond to a quadruped monodactyl homopod trackmaker, most-likely a proteroteriid litoptern (Fig. 14.4c). Other exposures of the Mariño Formation at Salagasta, Mendoza Province (Fig. 14.1), record tridactyl footprints on fluvial wave-rippled fine-grained sandstone strata (Ahumada 2004). The footprints were most-likely produced by toxodontiid notoungulates or macraucheniid litopterns (Fig. 14.4a and b).

14.5.5 The Footprints of Las Flores Formation, Argentina

At Puchuzun at the Calingasta valley, San Juan Province, western Argentina (Fig. 14.1), the Las Flores Formation of late Miocene age holds a diverse ichnologic assemblage representing mostly footprints of aquatic and terrestrial birds and a few morphotypes of medium and large size mammals. They consist on bird footprints of Anseriformes, Charadriformes, and Phoenicopteriformes, in addition to footprints of hegetotheriid notoungulates and a large ground sloth preserved in marginal lacustrine facies (Contreras 1996, 2006; Contreras and Peralta 2011).

14.5.6 The Footprint of Quebrada del Jarillal Formation, Argentina

The Cenozoic succession exposed at Sierra de Mogna, San Juan Province, Argentina (Fig. 14.1) records a set of manus-pes footprints preserved on levels of the Quebrada del Jarillal Formation (middle-upper Miocene). The footprints were originally described and illustrated by Casamiquela in Cuerda et al. (1984) (see Plate XV, Fig. 2 and Plate XVI, Figs. 1 and 2 in Cuerda et al. 1984) and later also documented by Leonardi (1994, plate XIX, Fig. 11). Krapovickas and Nasif (2011) assigned the material to *Tacheria troyana* and interpreted it as produced by a dinomyid caviomorph rodent or a close relative.

14.5.7 The Footprints of the Tertiary of the Puna, Argentina

Near the border between the provinces of Salta and Jujuy, Argentina, at Catua (Fig. 14.1), in 1980 R.N. Alonso found mammalian footprints, possibly rodents, on eolian dune cross-beds of possible Miocene age (Leonardi 1994). In addition, R.N. Alonso also discovered a small isolated footprint cast of a mammalian trackmaker, probably a rodent, preserved on salt flats deposits at Salar del Rincón, Salta Province, Argentina (Fig. 14.1). The bearing levels possibly correspond to the Pliocene Trinchera Formation (Leonardi 1994).

14.5.8 The Footprints from the Río Negro Formation

Extensive sea cliffs of northeast Patagonia, Río Negro Province, expose an upper Miocene-lower Pliocene succession corresponding to the Río Negro Formation (Fig. 14.1). The succession corresponds to a complete suite of eolian and eolian-related sub-environments (Zavala and Freije 2001). The Río Negro ichnologic record from the margins of the Río Negro River at Carmen de Patagones was originally described by Casamiquela (1974), who identified novel ground sloth bipedal footprints assigned to *Megatherichnum oportoi* and interpreted as produced by a megatheriid close to *Megatherium*. Later, Angulo and Casamiquela (1982) studied the footprint record of the strata cropping out at the cliffts of the San Matías Gulf at several localities. The most diverse ichnologic assemblage is the one recorded at Balneario El Cóndor, including footprints of megatheriid ground sloths of large and medium size assigned to *Megatherichnum oportoi* and *Falsatorichnum calceocannabius*, respectively (see Plate II in Angulo and Casamiquela 1982); *Porcellusignum consulcator*, corresponding to heteropod footprints with a tetradactyl manus and tridactyl pes most-likely produced by capybaras (see Plate II in Angulo and Casamiquela 1982); *Macrauchenichnus rector* that consist of tridactyl blunt

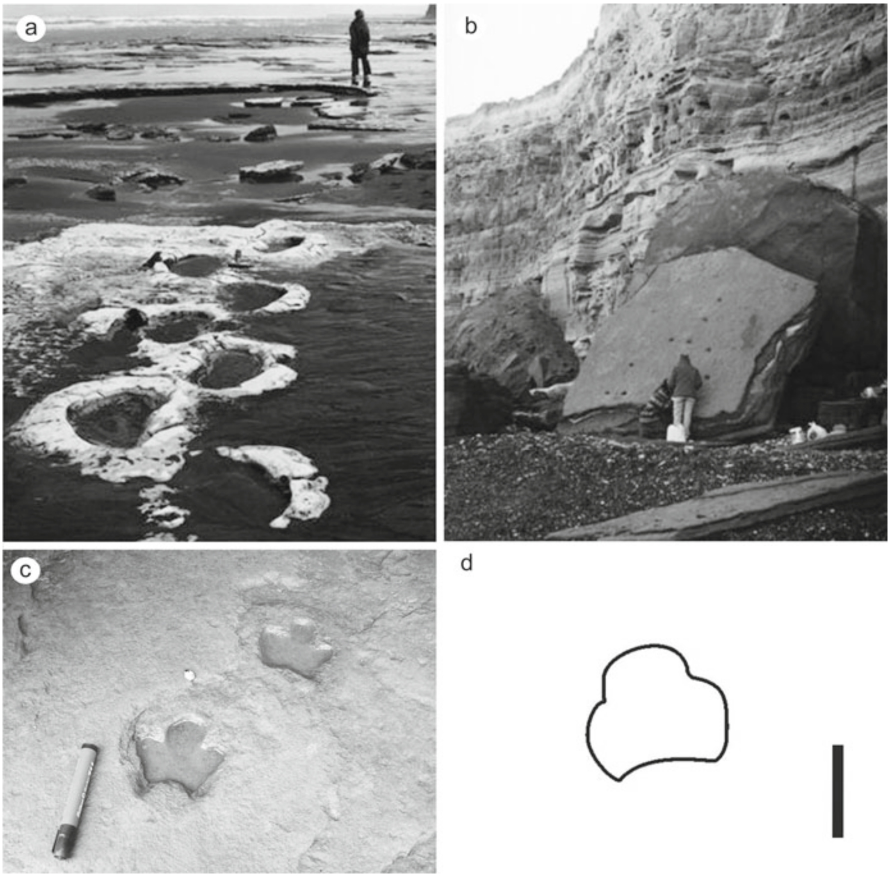

Fig. 14.5 Footprints of the Río Negro Formation. (**a**) *Megatherichnum oportoi*; (**b**) Large slab containing footprints of marsupial saber-toothed tiger; (**c**) *Macrauchenichnus* isp.; (**d**) Schematic drawing of *Macrauchenichnus rector*, scale bar = 10 cm

footprints produced by macraucheniid litopterns (Fig. 14.5d) (see Plate VIII, IX, and X in Angulo and Casamiquela 1982); and *Caballichnus impersonalis*, subcircular footpritns of monodactyl trackmakers interpreted as equids (see Plate V, VI, VII in Angulo and Casamiquela 1982). These authors also mentioned the presence of *Macrauchenichnus rector* in other localities in the studied area (Balneario La Lobería, Balneario La Boca, and Pozo Salado). Because of the poor quality of preservation of the material used to erect *Falsatorichnum calceocannabius* and *Caballichnus impersonalis*, the validity of both ichnotaxa has been questioned (e.g., Melchor 2009). Moreover, the extremely simple morphology (subcircular outline) together with the lack of preservational details expressed on *C.*

impersonalis make its assignation to equids questionable. This would imply extending the record of equids in South America to the late Miocene prior to the GABI. Aramayo et al. (2004, 2007) recorded additional material from the area. These authors reported footprints of ground sloths of large size assigned to *Megatherichnum oportoi* (Fig. 14.5a) and of medium size assigned to cf. *Milodontidichnum* isp., similar in size and shape to *Falsatorichnum calceocannabius*, but interpreted as a mylodonthid . Other material corresponds to capybara footprints (cf. *Porcellusignum* isp.), two ungulate footprints of proteroteriid litopterns and undetermined ungulates, pentadactyl footprints with claw marks most-likely produced by the marsupial saber-toothed tiger (Fig. 14.5b), tridactyl footprints of large size produced by phorusrhacids, and two types of tridactyl bird footprints, ones of shorebirds and the others are webbed footprints of flamingos. Aditional material has been recently documented by Carmona (pers. com., 2012; Fig. 5c). The tridactyl footprints highly resemble *Macrauchenichnus* isp. from the Vinchina Formation (Fig. 14.3d).

14.5.9 The Footprints of Antofagasta, Chile

Plio-Pleistocene marine strata that bear fossil footprints preserved in coastal dunes facies are exposed near Antofagasta, Chile, 3 km from the recent marine coast (Fig. 14.1) (Casamiquela and Chong Diaz 1975). The footprints correspond to a quadruped monodactyl mammal of medium size. The impression of forefoot and hind foot are sub-equal and oval and are more deeply impressed on the anterior margin. Casamiquela and Chong Diaz (1975) interpreted that the footprints were made by equids, although the morphology of the footprints does not correspond exactly with recent equids.

14.5.10 The Footprints of Claromecó, Argentina

In the present-day intertidal zone of the Caracolero beach at Claromecó, Buenos Aires, Argentina (Fig. 14.1), deposits of late Pleistocene age record fossil footprints most likely produced by a large sized mylodontid ground sloth (Azcuy et al. 2011). The footprints have a very different outline and differ from other footprints interpreted as produced by large ground sloth (e.g. *Venatoripes riojanus*, *Megatherichnum oportoi*, *Neomegatherichnum pehuencoensis*). They consist of a plantigrade *pes* track with a general oval outline, with four digits and a prominent sole print. The tracks are approximately 60 cm long and 40 cm wide. The digit III impression is the longest and has a prominent claw mark, the lateral digits (II and IV) are subequal in length and show a sharp ending, and laterally to digit IV is the small impression of digit V.

14.5.11 The Footprints of Monte Hermoso, Argentina

Casamiquela (1983) described ground sloth footprints from fluvial plain deposits of late Pleistocene age on the Atlantic coast at Monte Hermoso, Buenos Aires. Argentina (Fig. 14.1). The footprints correspond to *Iribarnichnum megamericanum* and *Acunaichnus dorregoensis*, interpreted as megatheriids and mylodontid ground sloths, respectively.

14.5.12 The Footprints of Pehuen-Có, Argentina

The continental succession exposed on the Atlantic coast of southern Buenos Aires Province, Pehuen-Có (Fig. 14.1), records the most diverse association of Cenozoic mammalian footprints from South America (Aramayo and Manera de Bianco 1987a; b; 1996; 2009). The footprints are preserved in the present-day intertidal zone in strata of late Pleistocene age and represent a wide variety of mammals, such as large ground sloths (Fig. 14.6a, b and e) (the megatheriid *Neomegatherichnum pehuencoensis* interpreted as produced by *Megatherium* and the mylodontid *Milodontichnum rosalensis*), macraucheniid litopterns (Fig. 14.6c) (*Eumacrauchenichnus patachonicus*), gomphotheres (*Stegomastodonichnum australis*), carnivorans (*Pumaeichnum biancoi*, *Pehuencoichnus gracilis*, *Mustelidichnum enigmaticum*), camelids (Fig. 14.6d) (*Lamaichnum guanicoe* and *Megalamaichnum tulipensis*), cervids (*Odocoileinichnum commune*), equids (*Hippipeda* isp.), glyptodonts (Fig. 14.6f), bears, and caviomorph rodents, along with birds, such as phoenicopteriforms (*Phoenicopterichnum rector*), tinamiforms, anseriforms, rheiforms, and shorebirds. The trackway-bearing levels correspond to floodplain deposits where most of the footprints are preserved on mudstone intervals with desiccation cracks and ripple marks (Manera de Bianco and Aramayo 2004).

14.6 Faunistic and Biogeographic Similarity of Footprints Assemblages

The cluster analysis of the mammalian taxa represented by the fossil footprint record in South America shows a clearly identifiable change in diversity since the Eocene to the Pleistocene. The main dichotomy separates the Eocene to Miocene ichnologic assemblages from the Pliocene-Pleistocene ones. These branches separate the assemblages in which the producers belong to lineages that underwent diversification and ecologic specialization in isolation from other continents, from other assemblages including also representatives of North American lineages (Fig. 14.7a).

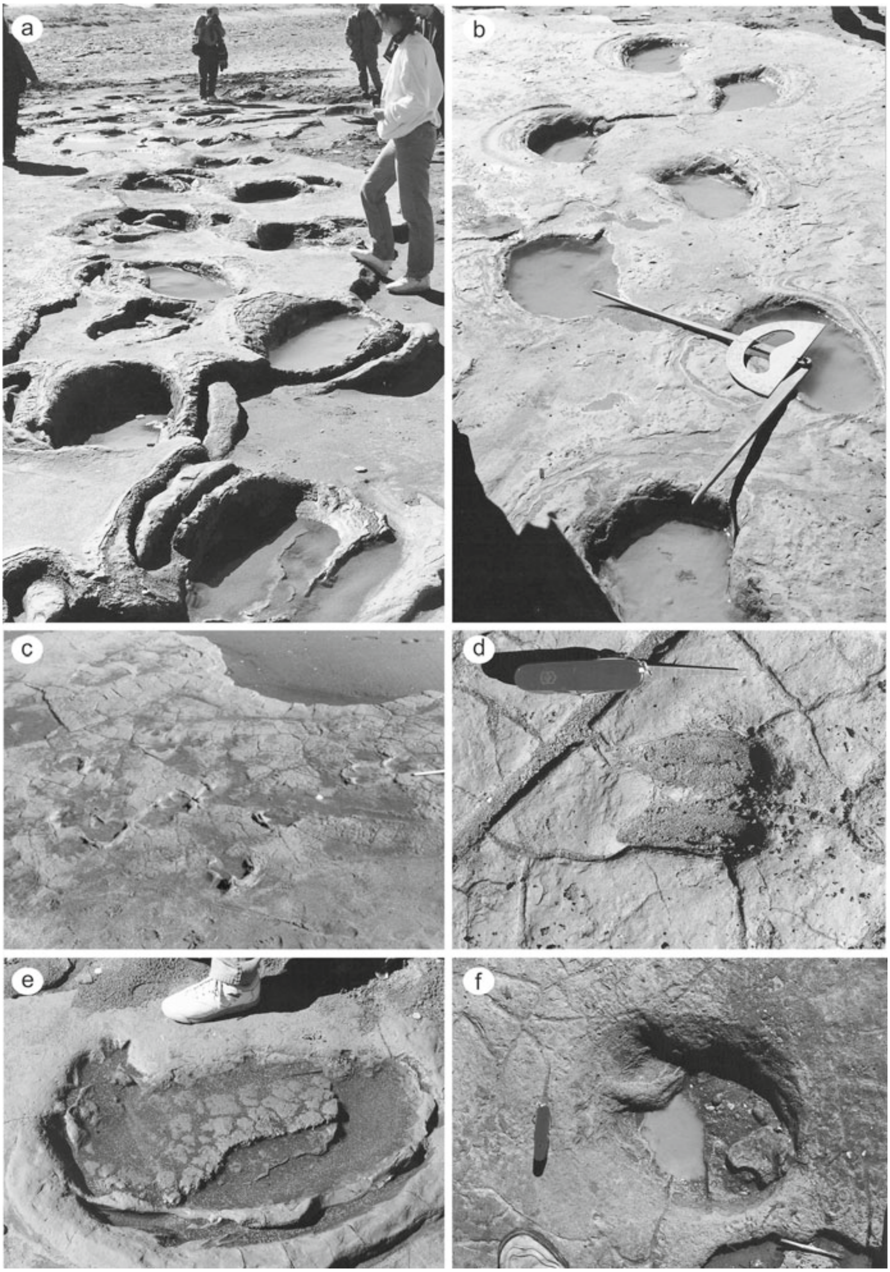

Fig. 14.6 The footprints of Pehuen-Có, Argentina. (**a**) *Neomegatherichnum pehuencoensis* trackways; (**b**) *Milodontichnum rosalensis* trackways; (**c**) Tracking surface with numerous impressions of *Eumacrauchenichnus patachonicus;* (**d**) *Lamaichnum guanicoe*; (**e**) Detail of the pes of *Neomegatherichnum pehuencoensis;* (**f**) Isolated footprint of glyptodont

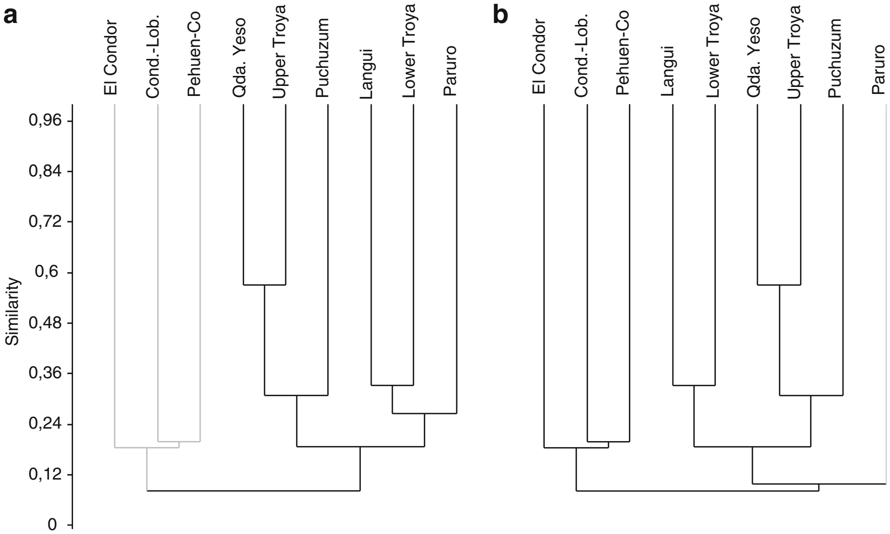

Fig. 14.7 Dendogram with the results of the cluster analysis, including the principal Cenozoic mammalian ichnofaunas

The Eocene-early Miocene ichnologic assemblages mostly represent forms of uncertain affinity. This is the case of rodent-like footprints identified as produced by small caviomorph rodents or typothere notoungulates and footprints assigned to small toxodontid notoungulates or macraucheniid litopterns. Also represented are footprints of large dinomyids caviomorph rodents, large undetermined notoungulates, and medium-size footprints of undetermined tetradactyl mammals (Fig. 14.8).

The rodent-like footprints of the Paruro assemblage may be highly significant. This assemblage comes from the Kayra Formation. The base of this formation is placed near the Paleocene-Eocene boundary and its limit with the unconformably overlying Soncco Formation is at about 43 Ma (Carlotto 2006), constraining the chronologic span of the formation to the early-middle Eocene. The recent discovery of rodents in the middle Eocene of the Peruvian Amazonia (Antoine et al. 2012) renders plausible a caviomorph affinity of the Paruro rodent-like footprints and could reinforce the recent hypothesis of Antoine et al. (2012) about the southward expansion of the earliest caviomorphs during the late middle Eocene–early Oligocene period, from low (Peruvian Amazonia) to middle (central Chile) and then to high latitudes (Patagonian Argentina). However, the stratigraphic information provided in the report of the footprints (Noblet et al. 1995) indicates that they come from the lower levels of the section, suggesting an early Eocene age. If this were true, and further careful analysis confirms its caviomorph affinity, these footprints would expand the early record of rodents in South America to the early Eocene.

There is a marked resemblance between the early Oligocene Langui ichnoassemblage of Peru and the early Miocene Lower Vinchina ichnoassemblage of northwestern Argentina (Fig. 14.7). The fact that the Lower Vinchina record is more

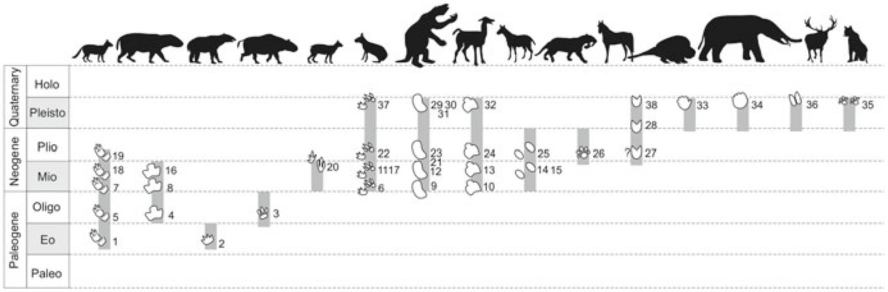

Fig. 14.8 Paruro footprints: (*1*) caviomorph rodents or typothere notoungulates, (*2*) undetermined tetradactyl mammals. Kayra footprints, (*3*) toxodontid notoungulates. Langui footprints: (*4*) toxodontid notoungulates or macraucheniid litopterns, (*5*) caviomorph rodents or typothere notoungulates. Lower Quebrada de la Troya footprints, (*6*) *Tacheria troyana*, (*7*) caviomorph rodents or typothere notoungulates, (*8*) *Macrauchenichnus* isp. Quebrada del Yeso footprints, (*9*) *Venatoripes riojanus*, (*10*) macraucheniid litopterns. Upper Quebrada de la Troya footprints, (*11*) caviomorph rodents, (*12*) cf. *Venatoripes riojanus*, (*13*) *Macrauchenichnus rector*, (*14*) proterotheriid litopterns. Cacheuta footprints, (*15*) proterotheriid litopterns. Salagasta footprints, (*16*) toxodontiid notoungulates or macraucheniid litopterns. Sierra de Mogna, (*17*) *Tacheria troyana*. Catua footprints, (*18*) caviomorph rodents or typothere notoungulates. Salar del Rincón footprints, (*19*) caviomorph rodents or typothere notoungulates. Puchuzun footprints (*20*) hegetotheriid notoungulates, (*21*) ground sloth. Río Negro footprints, (*22*) *Porcellusignum consulcator*, cf. *Porcellusignum* isp., (*23*) *Megatherichnum oportoi*, *Falsatorichnum calceocannabius*, cf. *Milodontidichnum* isp., (*24*) *Macrauchenichnus rector*, (*25*) proteroteriid litopterns, (*26*) marsupial saber-toothed tiger, (*27*) *Caballichnus impersonalis*. Antofagasta footprints, (*28*) equids. Claromecó footprints, (*29*) ground sloth. Monte Hermoso footprints: (*30*) *Iribarnichnum megamericanum* and *Acunaichnus dorregoensis*. Pehuen-Có footprints, (*31*) *Neomegatherichnum pehuencoensis*, *Milodontichnum rosalensis*, (*32*) *Eumacrauchenichnus patachonicus*, (*33*) glyptodonts, (*34*) *Stegomastodonichnum australis*, (*35*) *Pumaeichnum biancoi*, *Pehuencoichnus gracilis*, *Mustelidichnum enigmaticum*, Bear footprints, (*36*) *Lamaichnum guanicoe*, *Megalamaichnum tulipensis*, *Odocoileinichnum commune*, (*37*) caviomorph rodents, (*38*) *Hippipeda* isp.

similar to an older assemblage located to the north (Langui), rather than younger assemblages (middle-late Miocene) located in the same geographic area (Upper Vinchina and Toro Negro), suggests that at least during the earliest Miocene these areas were biogeographically connected and an isolation mechanism potentially operated from the early Miocene onwards. These could be the result of similar climatic conditions and the prevalence of similar faunas. However, it is not possible yet to contrast the similarities of the Lower Vinchina ichnoassemblage with any other ichnologic assemblage of the same age elsewhere.

Among the Miocene assemblages footprints assigned to ground sloth, macraucheniiid and proterotheriid litopterns, caviomorph rodents and rodent-like caviomorph rodents or typothere notoungulates are well represented; footprints assigned to toxodontid notoungulates or macraucheniid litopterns were also present (Fig. 14.8).

Not surprisingly, the major similitudes between ichnoassemblages are among those from the same age (middle-late Miocene) and geographic area (northwestern Argentina), as is the case of the Upper Vinchina and Toro Negro ichnoassemblages (Fig. 14.7).

During this period, footprints of large mammals, such as ground sloths and macraucheniids, are present for the first time, though they did not achieve the major sizes reached during the Plio-Pleistocene. Proteroteriid footprints are also present for the first time (Fig. 14.8). The middle Miocene ichnofaunas, as well as the osteodentary faunas, mark the peak of known diversification achieved by mammals after the arrival of primates and rodents but before the arrival of North American immigrants (Marshall and Cifelli 1990).

The late Miocene-Pliocene and late Pleistocene assemblages include footprints of both native South American mammals and North American taxa arrived during the GABI, recording a variety of ground sloths (Megatheriidae and Milodontidae), macraucheniid and proteroteriid litopterns, hydrochoerid caviomorph rodents and North American equids in both assemblages (Fig. 14.8). Footprints of other taxa are recorded in a single assemblage; a carnivorous marsupial (Thylacosmilidae) is recorded in outcrops of late Miocene-early Pliocene age of Río Negro, Argentina, and glyptodonts, gomphotheriids (proboscideans), camelids, and cervids (artiodactyls), and several carnivoran lineages (felids, ursids, mustelids, and bears) are represented in the late Pleistocene ichnoassemblages of Pehuen-có, Buenos Aires, Argentina (Fig. 14.8).

Comparing our results with the faunal evolutionary phases proposed by Goin et al. (2012) described above, the two major clusters roughly separate the faunas corresponding to the Early and Late South American phases from the Interamerican phase (Fig. 14.7). The dichotomy recorded within the first cluster described does not fit with the separations between the Early and Late South American phases, but there are several factors that may be affecting the results. First, only one lower Eocene locality may represent the Early South American phase; however, this Eocene locality clusters with the Oligocene and Miocene localities of the Late South American phase. The main problem is the ambiguous affinity of the rodent-like footprints (typothere/caviomorph), because the incorporation of caviomorph rodents to the South American record was taken as one of the events that triggered the Late South American Phase. When this footprint is removed from the analysis (Fig. 14.7b), the Eocene locality remains separated from a cluster constituted by the Oligocene and Miocene localities (Late South American phase). However, if the potential affinity of the Paruro footprints is established by a powerful method of trackmaker identification to caviomorphs, it would bring the beginning of the Late South American phase backward to the early Eocene, even earlier than the earliest record of body fossils (Antoine et al. 2012).

14.7 The Paleoenvironmental Distribution of Mammalian Ichnofossils

South American fossil footprints are mostly recorded in fully continental sedimentary systems, with just one example to date, recorded from marginal marine systems corresponding to Plio-Pleistocene outcrops of Antofagasta, Chile (Fig. 14.9).

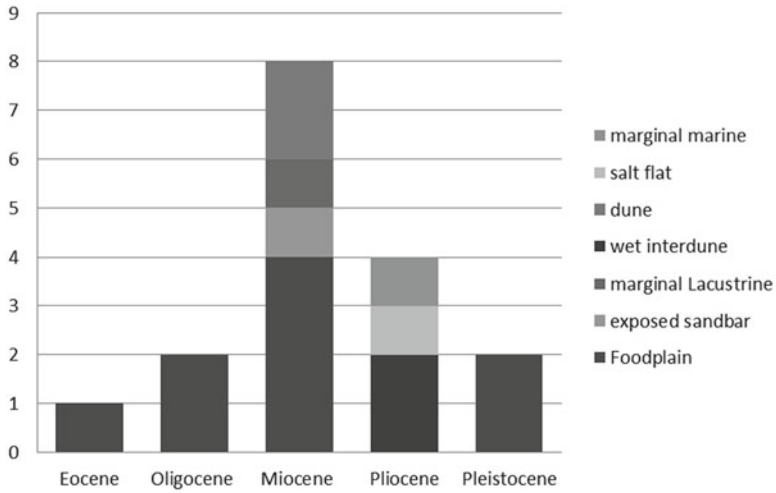

Fig. 14.9 Environmental distribution of Cenozoic mammalian footprints

Among the continental sedimentary systems preserving fossil footprints there are fluvial, lacustrine, and eolian deposits. Fossil footprints are mostly preserved in fluvial deposits, particularly on floodplains with just one example preserved on exposed fluvial sandbars (Fig. 14.9). There are scarce data about fluvial styles preserving fossil footprints in meandering fluvial systems from the lower Miocene Vinchina Formation (Lower Vinchina ichnoassemblage) and anastomosing fluvial systems from the upper Miocene Toro Negro Formation (Toro Negro ichnoassemblage). Lacustrine deposits preserving fossils footprints involve uniquely marginal-lacustrine facies and are only mentioned for the upper Miocene Puchuzun ichnoassemblages (Fig. 14.9). Fossil footprints in eolian deposits are common in Miocene and Pliocene outcrops, preserved mostly on dune and wet interdune facies (footprints of Cacheuta, Catua, and Río Negro). Footprints are also recorded on Pliocene salt flats of the Argentinean Puna (Fig. 14.9).

There is a broad relationship between the facies bearing footprints and biotic and abiotic conditions prevailing at different moments during the Cenozoic in South America. During the Eocene-Oligocene, relatively homogenous conditions were present across the entire continent. Forested areas were widespread together with tropical climate conditions that reached the summit during the early Eocene Climatic Optimun (Zachos et al. 2001; Flynn et al 2012). During this time, mammal footprints are recorded only in floodplain facies (Fig. 14.9).

Large-scale faunal provinciality reflecting latitudinal and altitudinal environmental gradients appear to be present by the early middle Miocene or late Oligocene of South America (Flynn et al. 2012). There are also environmental mosaics at specific areas within these gradients, as reflected by the lower Miocene of Santa Cruz in Patagonia (Kay et al. 2012), the upper Miocene of Toro Negro in northwestern Argentina (Krapovickas et al. 2009a, b, c) and the middle Miocene of La Venta in Colombia (Kay and Madden 1997).

Miocene deposits involving mammalian footprints are recorded in subhumid, semiarid, and arid climates (Fig. 14.9). Examples are distal overbank areas of high-latitude settings (Santa Cruz) with moderately well-drained paleosols due to seasonal shifts between subhumid and semiarid climatic; exposed sandbars of anastomosing fluvial systems under semi-arid climates of mid-latitude areas at northwestern Argentina (Toro Negro) and in arid climates from mid-latitude areas of central western Argentina (Mariño) and northwestern Argentina (Puna). Among these, Toro Negro is the richest assemblage. In this unit, inter-channel areas of anastomosed fluvial systems, under a semi-arid climatic regime, have a high preservation potential for tracks due to seasonal flooding events, which rapidly bury and protect the footprints, preventing rapid degradation of exposed tracks (Krapovickas et al. 2009a, b, c). In comparison, the distal overbank areas of low-sinuosity rivers (Raigemborn et al. 2012) with low rates of deposition and high subaerial exposure result in lower preservation potential for footprints.

Glacial and interglacial oscillations occurred during the Pliocene and Pleistocene, involving increased aridity. Late Miocene-Pliocene deposits bearing mammalian footprints are mostly developed in arid climates of high- (Rio Negro; late Miocene-Pliocene) and mid-latitude (Puna; Pliocene) settings. For most of the middle and late Pleistocene, dry and cold climate caused open areas to predominate in South America (Cione et al. 2009). Pleistocene floodplain facies of the Pampean region bear one of the most impressive footprint assemblages worldwide.

14.8 South American Mammal Tracks and Implications for Paleoecology

In ichnology, as well as in other paleontologic disciplines, paleoecology may be seen from two different complementary perspectives (Kay et al. 2012). The most frequent approach is to reconstruct environmental parameters, such as substrate consistency, climate, food supply, topography (e.g., coastlines, exposed fluvial bars), water saturation, water energy, salinity, oxygenation, rate of sedimentation, light, and temperature, among others. The other approach is to understand aspects of the paleoecology of individual species based upon their adaptive characteristics such as body size, diet, locomotion, and substrate preference (paleoautecology), and to build from this the overall niche characteristics of the fauna as a whole (paleosynecology) (e.g., Gastaldo et al. 1996; Falcon-Lang et al. 2007; Krapovickas et al. 2009a, b, c; Minter and Braddy 2009; Wilson et al. 2009; Kubo 2011). Both approaches have been scarcely applied to the study of South American mammalian ichnoassemblages.

Krapovickas et al. (2009a, b, c) used fossil footprints to infer characteristics of ancient environments. The tetrapod fauna of the lower interval of the Toro Negro Formation revealed by footprints suggested an open environment, possibly related with a seasonal arid or semiarid climate, associated with nearby forested areas (Fig. 14.10).

Fig. 14.10 Reconstruction of the Miocene Vinchina anastomosed fluvial system with exposed sandbars and the putative vertebrate and invertebrate producers

Manera de Bianco and Aramayo (2004) studied the taphonomy of the Pehuen- Có tracksite, considering footprint association, preservation quality, producers, and substrate. They found that mudstones without desiccation cracks or ripple marks display the best preservation quality, reflecting a differential preservation potential related to the proximity to the floodplain water body.

Most of the paloeautoecologic studies are qualitative or biomechanical analysis of the locomotion style or use of the substrate by the producers. Casamiquela (1974) analyzed *Megatherichnum oportoi*, concluding that the absence of hand prints reflects a bipedal locomotion, in accordance to many features of the skeleton of the megatheres. This claim resulted controversial and has been reevaluated in detail by numerous authors. Casinos (1996) studied the biomechanics of locomotion of Pleistocene *Megatherium americanum* by means of the estimation of body mass and using measurements of several trackways originally assigned to megatheres (Frenguelli 1950; Bonaparte 1965; Casamiquela 1974, 1983; Aramayo and Manera de Bianco 1987a, b). Casinos (1996) calculated different mechanical parameters such as speed, Froude number, indicators of athletic abilities, and bending and resistance movements of the vertebrate column calculated in both bipedal and quadrupedal conditions. He concluded that it was not possible to determine whether *Megatherium* was better adapted to bipedal or quadrupedal locomotion. Either bipedal or quadrupedal, in all cases the results indicated a walking mode of locomotion. Studying *Neomegatherichnum pehuencoensis*, Blanco and Czerwonogora (2003) reassessed the locomotory abilities of the Pleistocene *Megatherium americanum*. In doing so, they developed a geometric model to calculate the percentage of body weight supported by each pair of limbs to estimate the pressure they should have exerted on the ground and calculated the speed of locomotion after Alexander (1976). Their conclusion was that *Megatherium* walked roughly as a strategy to minimize the costs of transport and to better withstand big lateral bending moments that appear in bipedal walk. McDonald (2007) inferred the locomotion of *Paramylodon harlani* integrating morphologic and ichnologic data of ground sloth tracks of the Nevada state Prison, Carson City, USA, assigned to *Paramylodon*. He concluded that the known studies of the anatomy of ground sloth and their tracks have not been conclusive about their capacity of bipedal locomotion. He also concluded that the evidence suggests a quadrupedal primary mode of locomotion and that the support for bipedal locomotion has been based on the general absence of manus impressions.

In terms of paleosinecology, Krapovickas et al. (2009a, b, c) analyzed the preservation potential of mammal tracks to estimate the magnitude of time passed on the formation of the Toro Negro tracking surface in order to analyze the footprint assemblage as a partial sample of the original tetrapod community that inhabited western Argentina during the early Miocene. To characterize the paleocommunity structure, these authors identified the number of trackmakers and the relative abundance of footprints. The latter was interpreted as a measure of the activity of the producers and not necessarily as an indicator of the number of individuals involved. Krapovickas et al. (2009a, b, c) measured the relative abundance of footprints by counting the number of footprints and developed an index that records the percentage of the tracking surface which is bioturbated by each ichnotaxa, the Relative Bioturbated Area index.

The study of ichnofossils of the Toro Negro Formation expanded the knowledge of its tetrapod paleocommunity in three main ways: by reinforcing the presence of certain taxa as indicated by body fossils (large and medium-size ground sloths, proterotheriid litopterns, caviid rodents, and birds), by refining the level of identification of certain taxa (shorebirds, perching birds, and large cursorial birds), and by adding taxa that would otherwise be unknown by body fossils (macraucheniid litopterns) (Fig. 14.11).

14.9 Future Directions

Despite the fact that first studies began almost a hundred years ago, the ichnologic knowledge of South American mammals is still in its infancy. As mentioned above, in this chapter we attempt to to identify problems and promises of the South American record hoping to contribute to develop a major research program in mammalian paleoichnology that will permit global comparisons.

To begin with, there are extensive areas of South America where the Cenozoic ichnologic content is still unknown, revealing the necessity of intensive field work: there are no specific reports for Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guiana, Paraguay, Surinam, Uruguay, and Venezuela.

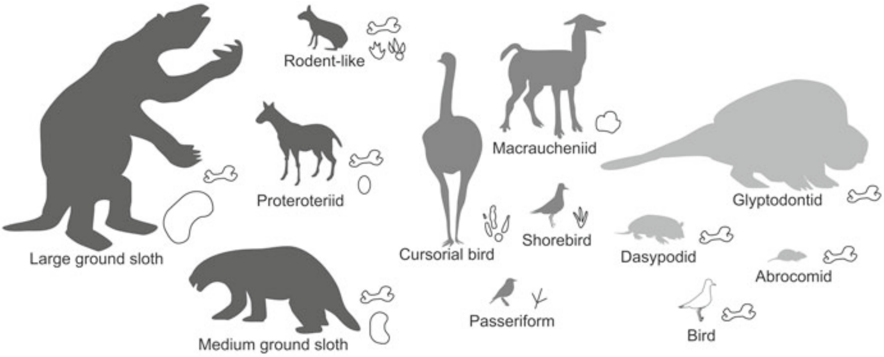

Fig. 14.11 Comparison of the tetrapod ichnological and osteological evidence from the Toro Negro Formation at Quebrada de La Troya, Argentina. *Black outline silhouette*: indeterminate bones. *Black silhouette*: material represented by both evidences. *Light gray silhouette*: material represented by osteological evidence. *Blue silhouette* (medium gray): material represented by the ichnological evidence. Modified from Krapovickas et al. (2009a, b, c)

Most ichnologic studies on Cenozoic South American mammals do not include detailed analyses of the paleoenvironmental context and the bearing facies, and only general aspects are mentioned. Much more analyses on ancient environments and its prevalent climates need to be done to understand under which conditions inhabited the mammalian trackmakers.

From a systematic point of view, at present, there are numerous ichnotaxa erected to name very similar forms produced most likely by related trackmakers. There is a strong need of a comprehensive and updated ichnotaxonomic revision of the existing ichnotaxa in accordance with morphologic and paleobiologic characteristics of the trackmakers. Moreover, in order to provide novel evolutionary, locomotory, and distributional information, the attribution of footprints to body fossils groups needs to be independent from the known body fossil spatial and temporal distribution. Currently, ichnologists analyze putative trackmakers based on anatomic features of the postcranial skeleton that are transcribed to the footprint morphology and trackway pattern. In order to use footprints as an independent source of evidence, when analyzing footprint producers, it is preferable to establish osteologic synapomorphies that could be identified in the fossil footprints (Carrano and Wilson 2001). Unfortunately, until now, phylogenetic studies of South American mammals do not include characters of the distal autopodium in their analyses. The study of trackmakers on the light of the cladistic method of trackmaker identification is still a pending task on the ichnologic agenda.

In terms of trackmaker function, there is scarce information about the range of functional capabilities revealed in South American mammal trackways; it is necessary to conduct deep analysis of the locomotory modes expressed in trackways and analyze how this range compares to that of living mammals. The estimation of the body mass of the footprint producers is another pending issue.

Finally, mammalian fossil footprints are barely used for habitat reconstruction analysis. Both taxon dependent and taxon-free analysis based on the footprint record could result in useful tools for habitat reconstruction.

These are the major problems and promises we were able to identify for South America so far. We understand that reviewing all the available evidence from other continents would identify particular and common problems and promises, contributing to develop a global paleoichnologic mammalian research program.

14.10 Conclusions

Globally, some of the most significant and better preserved ichnologic records of Mesozoic mammals are from Gondwana, including *Ameghinichnus*, *Brasilichnium*, and *Duquettichnus*, in contrast to its meager body-fossil record. In boreal landmasses, the diversity and abundance of the Mesozoic mammalian body-fossil record are much higher, and their footprint record is not as well known.

The Paleocene tetrapod footprint record, albeit apparently depauperate, has scarce mammals represented and is mostly composed by amphibian, reptiles, and birds. In contrast, mammal footprints become more common during the Eocene and Oligocene. The Neogene mammalian record is dominated by ungulate footprints, such as perissodactyls, artiodactyls, and proboscideans, followed in abundance by carnivores as felids and canids.

Presently there are more than 20 known localities that record footprints of South American mammals. Two main ichnologic assemblages are distinguished: (1) those in which the producers belong to lineages that underwent diversification and ecologic specialization in isolation from other continents, and (2) those including also representatives of North American lineages.

The Eocene and Oligocene ichnologic assemblages mostly represent forms of uncertain affinity up to now, including small caviomorph rodents or typothere notoungulates, large undetermined notoungulates, medium-size undetermined tetradactyl mammals, *Macrauchenichnus* isp. assigned to small toxodontid notoungulates or macraucheniid litopterns. Among the Miocene assemblages there are footprints assigned to ground sloths (e.g. *Venatoripes riojanus*, cf. *Venatoripes riojanus*, kidney-like footprints), macrauchenids (e.g. *Macrauchenichnus rector*) and proterotheriid litopterns, rodent-like caviomorph rodents or typothere notoungulates, hegetotheriid notoungulates, and toxodontid notoungulates or macraucheniid litopterns (e.g. *Macrauchenichnus* isp.), and *Tacheria troyana* assigned to a large dinomyid caviomorph rodent.

The late Miocene-Pliocene and late Pleistocene assemblages include footprints of both native South American mammals and North American taxa that arrived during the GABI. The native South American lineages consist of a variety of ground sloths (e.g., *Megatherichnum oportoi*, *Falsatorichnum calceocannabius*) including megatheriids (e.g., *Iribarnichnum megamericanum*, *Neomegatherichnum pehuencoensis*) and mylodontids (e.g., *Acunaichnus dorregoensis*, *Milodontichnum* *rosalensis*), glyptodonts, macraucheniid (e.g., *Macrauchenichnus rector*, *Eumacrauchenichnus patachonicus*) and proterotheriid litopterns, hydrochoerid caviomorph rodents (e.g., *Porcellusignum consulcator*), undetermined ungulates, and carnivorous marsupials. The North American examples are equids (e.g., *Caballichnus impersonalis*, *Ichnhippus cotaposi*, *Hippipeda* isp.), gomphotheriids (e.g., *Stegomastodonichnum australis*), camelids (e.g., *Lamaichnum guanicoe*, *Megalamaichnum tulipensis*), cervids (e.g., *Odocoileinichnum commune*), and several carnivoran lineages as felids and mustelids (e.g., *Pumaeichnum biancoi*, *Pehuencoichnus gracilis*, *Mustelidichnum enigmaticum*).

The cluster analysis of the mammalian taxa represented by the fossil footprint record of South America, compared with the faunal evolutionary phases proposed by Goin et al. (2012), shows two major clusters that roughly separate the faunas corresponding to the Early and Late South American phases from the Interamerican phase.

The early Eocene rodent-like footprints of Paruro are of great importance for the understanding of the early evolution of caviomorph rodents. If future careful analysis confirms the caviomorph affinity of the Paruro footprints, they could reinforce the recent hypothesis of Antoine et al. (2012) about the southward expansion of the earliest caviomorphs during the late middle Eocene–early Oligocene period. Moreover, the footprints would expand the early record of rodents in South America to the early Eocene.

Footprints were uniquely preserved on floodplain facies during the Eocene, Oligocene, and Pleistocene. The record of mammalian fossil footprints in deserts of South America occur in a variety of sub-environments (dunes, wet interdunes, and salt flats), involving semi-arid and arid climates, during the Miocene and Pliocene.

Both approaches, the reconstruction of environmental parameters and the study of the paleoecology of individual species and communities, have been scarcely applied to South American mammalian ichnoassemblages.

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Chapter 15
Major Events in Hominin Evolution

Martin Lockley, Jeff Meldrum, and Jeong Yul Kim

15.1 Introduction

Until recently (reviewed in Kim et al. 2008a, b; Lockley et al. 2007a, b, 2008a, b; Lockley and Roberts 2004), the study of fossil hominin tracks had been largely neglected by ichnologists, paleontologists, and anthropologists, with the exception of the famous Laetoli hominin trackways in east Africa. While it may be speculative to consider why this has been so, the study of hominin footprints, like the study of hominins in general, is of potential mutual interest to several disciplines (paleontology, ichnology, anthropology, archeology), and so has not been claimed as the exclusive province of any one of these. The distinction between hominids and hominins is sometimes confusing to nonspecialists. Here we use the term hominin, in reference to the tribe Hominini, to include representatives of the "australopiths" and the "hominans", as outlined by Wood (2005), and Wood and Richmond (2000).

With a few notable exceptions (Hay and Leakey 1982; Leakey and Harris 1987; Pales 1976) there were almost no hominin footprint-bearing sites that had been subjected to any sort of comprehensive analysis, prior to 2000. Even though a spate of publications in 2004 through 2009 (Meldrum 2004a, b; Lockley et al. 2007a, b, 2008a, b; Meldrum et al. 2010, 2011) marked a re-awakening of interest, most of the few dozen publications to emerge at this time could best be classified as preliminary

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site reports, some dealing with sites that had been known for decades but never studied. Nevertheless, since the publication of two special volumes in *Ichnos* (vol. 15 (3–4) for 2008, and vol. 16 (1–2) for 2009), under the title *Hominid Ichnology*, interest in the subject has been sustained, and a number of papers have emerged dealing both with the oldest African sites, and with other younger more widely distributed sites (e.g., Bennet and Morse 2014). In accordance with the theme of this volume, we herein review the hominin track record from the perspective of the role of trace fossils (primarily fossil footprints) in highlighting major events in hominin evolution, including emphasis on new studies and perspectives not discussed in previous summaries (Lockley et al. 2007a, b, 2008a, b).

While the focus of this contribution is on fossil footprints and their interpretation, the renaissance in "Hominid Ichnology", represented in part by the *Ichnos* volumes, has been accompanied by independent, but simultaneous, interest in redefining the scope of hominid ichnology (Hasiotis et al. 2007; Baucon et al. 2008; Kim et al. 2008a, b). In short, the authors of these articles, as well as those of the present article (Kim et al. 2004, 2008a, b), simultaneously proposed that hominid ichnology should include the study of a wide variety of traces, in addition to footprints. These traces include, but are not limited to, tool marks and artifacts made by modifying (flaking, engraving, sculpting, excavating), of wood, bone, rock, and earth (soil) substrates, as well as various forms of painting and writing, also on a wide range of substrates. While recently made popular in Crime Scene Investigation (CSI) dramas, involving detection of all manner of traces on diverse substrates (Lockley 1999), such facets of hominid ichnology were already evident during the so called Late Paleolithic Cultural Revolution (discussed below) and raise fundamental questions about the importance of ichnology in understanding and reflecting complex cultural behavior during one of the most debated "major events in evolution"—the emergence of modern humans. Hominid ichnology bridges the gap between tetrapod ichnology and what Baucon et al. (2008) appropriately identified as the important subdiscipline of ichnoarcheology. The etymology of words like *ichnos* and *trace*, discussed below, underscore the deep relationships between trace fossils and writing. Without such 'ichnologic' representations of the behavior of modern humans and their ancestors, this volume and all its predecessors would not be possible.

15.2 Early Hominin Bipedalism: Laetoli Revisited

Even the non-paleontologist and non-anthropologist is likely aware of the famous footprints from Laetoli in Tanzania discovered by the Mary Leakey team in 1976 (Leakey and Hay 1979; Hay and Leakey 1982; Leakey and Harris 1987). They ostensibly indicate a group, possibly a family unit, of three individuals, one of which was slightly smaller (creating trackway G-1) walking to the left-hand side of the other two (creating trackways G2/3), which appeared to be two individuals stepping in each other's footprints (Fig. 15.1). Trackmaker height estimates are about 1.10–1.15 m for G-1 and 1.32–1.52 m for G-2/3 (White and Suwa 1987). As noted below, despite this group-of-three scenario, and the many analyses of the trackways that

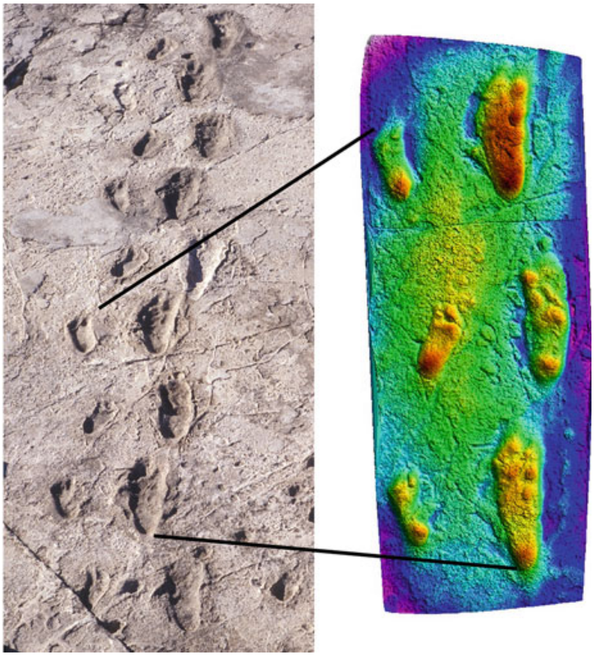

Fig. 15.1 Pliocene hominin trackway from Laetoli (*left*) include the G-1 trackway (*left*) and the overprinted, "double" G-2/3 trackways, possibly open to interpretation as a twice-overprinted, "treble" G-2/3/4 trackway. Photogrammetric image (*right*) after Kim et al. (2008b) shows three consecutive tracks (a stride) and highlights the multiple hallux (big toe) traces in the G-2/3 trackways

have been published since 1976 (e.g., Charteris et al. 1981; Tuttle 1990; Tuttle et al. 1990; White and Suwa 1987; Meldrum 2004a, b; 2007a; Meldrum et al. 2011), this interpretation has recently been challenged, and it has been claimed that there are in fact three trackmakers represented by the overlapping series not two (Musiba et al. 2011; Matthews et al. 2011). This observation implies a G-1 + G-2/3/4 scenario.

Clearly, the most significant implication of the Laetoli trackways and the one on which most researchers agree, is that they provide direct evidence of a ~3.6 Ma old hominin that was capable of walking upright. As almost every anthropologic text proclaims, the transition to a fully upright gait was a major event in hominin evolution, perhaps the seminal adaptation of this radiation. Moreover, given the fragmentary state of many body fossils of this age, trackways arguably provide the best evidence that hominin bipedalism was established by 3.6 Ma. Mary Leakey proclaimed this "the most remarkable find I have made in my whole career" (Lewin 1982, p. 220).

A few other facts may be inferred from the Laetoli tracks and their broader geologic and paleontologic context. First, they form part of a huge trackway assemblage dominated by the tracks of non-hominin mammals and birds, including some that evidently represent extinct species (Leakey and Harris 1987). We may also assert that the body fossil record shows that representatives of genus *Australopithecus* were extant at the time when the tracks were made. Lastly, we may note that the tracks were recently given the name *Praehominipes laetoliensis* (Meldrum et al. 2011). The formal name and diagnosis distinguish them from the previously erected ichnotaxon *Hominipes modernus* (Kim et al. 2009), the latter being the formal name applied to fossil footprints unequivocally attributed to *Homo sapiens* (and possibly *H. neanderthalensis*).

Beyond these *facts* there is far less agreement about the interpretation of the trackway evidence, though Kim et al. (2007) discussed their paleontologic, stratigraphic, and sedimentologic significance. As we have seen, even the number of individuals producing a trackway has recently been disputed (Musiba et al. 2011). In addition, there is disagreement as to whether the tracks were made by a trackmaker with a foot architecture manifestly distinct, in its mosaic and/or intermediate nature (Stern and Susman 1983; Susman et al. 1984; Deloison 1991, 1992; Clarke 1999; Meldrum 2000, 2002; 2004; Berge et al. 2006; Meldrum and Chapman 2007; Bennett et al. 2009; Hatala 2014) or an as yet unrecognized relatively derived hominin (e.g., Day and Wickens 1980; Charteris et al. 1981; Alexander 1984; Suwa 1984; Lovejoy 1988; Tuttle 1985, 1996; Tuttle et al. 1990, 1991; Schmid 2004; Sellers et al. 2005; Harcourt-Smith and Hilton 2005; Kimbel and Delezene 2009; Raichlen et al. 2010; Tuttle 2014). Closely intertwined with this debate is the question of whether the footprints are essentially indistinguishable from arched modern hominin tracks (Tuttle 1990; Tuttle et al. 1990; Crompton et al. 2012) or whether they show evidence of primitive features, including a midtarsal break (*sensu* Meldrum et al. 2011), which would imply that the trackmaker's foot morphology, and dynamic footprint registration differed from that known for modern humans.

It is perhaps surprising that such basic evidence as the number of individual trackways is in dispute. However, it should be remembered that after the initial excavation, molding, and analysis, which included some 3D imaging using 1980s technology, the tracks were reburied and most researchers had to rely on studying planimetric figures or fiberglass replicas representing only a short segment of the G1 and G2/3 trackways (Lockley and Matthews 2007; Meldrum 2007a). Even after the tracks were exhumed by the Getty Conservation Institute (Demas and Agnew 1996) in order to assess disturbances resulting from the reburial, they were again reburied in order to conserve them. It was only in 2011 that they were exhumed for a second time and subjected to high resolution photogrammetric analysis (Musiba et al. 2011; Matthews et al. 2011). These results suggest an assemblage of four, rather than three trackways, in which a group of three rather than two have overlapping footsteps. While popular inference has been tempted to interpret the "group-of-three" scenario as possible evidence for a "family" unit consisting of two larger adults and a smaller juvenile offspring, the new interpretation casts doubt on such a "nuclear family" scenario. Meldrum (2007a), after a careful analysis of two sets of stereophotographs of the G2/3 trackway, determined that the lengths of the G2/3 footprints were approximately 25 cm (G2-25) and 20 cm (G3-9), respectively. The more recent evidence (Musiba et al. 2011; Matthews et al. 2011) calls for a careful reanalysis of the size of the overlapping footprints, which may revise these size estimates. What might the number and size composition imply about the trackmaker demographics and behavior? What induced three trackmakers to follow closely in line, with the two followers stepping repeatedly in the footprints of the leading individual? An unfamiliar substrate? Given the uncertainty surrounding the overstepped footprints (G2/3 or G2/3/4), we can only note that the G1 trail has footprints ~18 cm long and ~8 cm wide with a step of 41–44 cm, indicating a trackmaker with a stature of ~1.32 m (cf. White and Suwa 1987).

As noted by Lockley et al. (2008a, p. 107), the non-hominin Laetoli track assemblages allows a census that ostensibly attributes most trackmakers to "extant species, or species that are indistinguishable from modern species (or generic, and higher categories) on the basis of tracks. The only exceptions are the identification of extinct chalicothere and *Hipparion* tracks, the latter studied by Renders (1984). The census clearly shows that rabbits (or other lagomorphs) were abundant in the area, numerically constituting 88.8 % of the non-hominin vertebrate tracks." Thus, based on rabbit abundance, Laetoli was "the Watership Down" of the ichnologic world (Lockley 1999, p. 241)! However, as this census is based on individual prints—not trackways—it is not a reliable measure of biomass, although potentially useful as a general indicator of ecology and the activity of faunal components.

Lastly, we may note that the Laetoli tracks are preserved in reworked volcaniclastic sediments, which allow for inferences about runoff and seasonal climatic regimes (Hay and Leakey 1982; Houck et al. 2009). In conclusion, therefore, the Laetoli tracks offer us valuable evidence of a major evolutionary event; the emergence and nature of early hominin bipedalism. They also form part of a rich assemblage that has attracted wide scientific interest. However, disparate interpretations of the trackmakers and their behavior continue to be debated, and access to the entire trackways, rather than partial replicas, remains restricted by the need to keep them covered in order to preserve them.

15.3 Walking Erect Phase II: In and Out of Africa

15.3.1 On the Shores of Lake Turkana

There is a huge temporal gap in the hominin track record between the ~3.6 Ma Laetoli occurrence and two ~1.5 Ma track sites recorded in the Koobi Fora Formation on the eastern shore of Lake Turkana. As noted by Behrensmeyer and Laporte (1981, p. 3), the first discovery of Koobi Fora footprints (from a site known as GaJi10) contributed "a reference point on hominin foot morphology, locomotion behavior, and ecology 2 Myr younger than the Laetoli occurrences and ~1 Myr older than the Late Pleistocene human footprints in Europe." Unlike the Laetoli tracks, which are unequivocally Pliocene in age, the Koobi Fora tracks can be assigned to the Lower Pleistocene, which spans the interval between ~1.8 and ~0.8 Ma.

At the time of the first discovery, Behrensmeyer and Laporte (1981) inferred that the Koobi Fora tracks may have been produced by a *Homo erectus* (*H. ergaster*) individual ~1.5–1.6 Ma. This date is more or less confirmed by Bennett et al. (2009), who stated that the track layer is just below a tuff dated at 1.435 Ma. The decided lack of details of morphology in the tracks provides no evidence of significant changes in the hominin foot since the Laetoli trackway.

Behrensmeyer and Laporte (1981) reported tracks visible in a single trackway at site GaJi120, but Bennett et al. (2009) reported that two more tracks were excavated at the site. According to Behrensmeyer and Laporte (1981), the tracks range in length from 25 to 32 cm and the mean foot size dimensions are estimated at 26 cm long and 10 cm wide, suggesting an individual 1.6–1.8 m in height. In addition to some isolated tracks at the Ileret site, Bennett et al. (2009) reported at least four trackway segments, one from the lower level, and three from the upper level, and they estimated the height of the track makers as between 1.75 and 1.78 m (±0.26 m), with a possible subadult print from the lower level representing an individual only 0.92 m (±0.13 m).

Bennett et al. (2009) reported another site at Ileret, Kenya, about 45 km north of the GaJi10 site that reveals two hominin track-bearing layers, ~5 m apart stratigraphically, dated at ~1.53 Ma. The Ileret site reveals tracks which have better preservation than the GaJi10 site footprints as they reveal individual digital pad impressions. Dingwall et al. (2013) concluded that some or all of the footprints found on three levels could be either *Homo erectus* (*H. ergaster*) or *Paranthropus boisei*. Bennett et al. (2009) concluded that the footprints provide "the oldest evidence of an essentially modern human-like foot anatomy, with a relatively adducted hallux, medial longitudinal arch, and medial weight transfer before push-off." We find support for only one of these three points (i.e. a relatively adducted hallux). We find no evidence to support the consistent presence of a longitudinal arch or for a medial weight transfer. The suggestions of a medial longitudinal arch in the clearest examples (such as depicted on the cover of *Science*; Bennett et al. 2009) are the result of distortions caused by secondary impressions with extrusion left by passing ungulates, which obscure the medial margin of the hominin footprints (Fig. 15.2). In other instances, the preservation is so poor that the actual topography of the medial contact surface is indiscernible. A number of the published examples show a clear lack of medial weight transfer. Although differences of substrate properties may influence the general appearance of individual footprints as demonstrated by Morse et al. (2013), we observe consistent distinctions to the specific appearance of modern human footprints, regardless of substrate. Therefore, we maintain that *Homo erectus* (*H. ergaster*) had neither a fixed longitudinal arch (*sensu* Mauch et al. 2008) nor a modern toe-off mechanism, in concordance with analysis of the hallucal metatarsal KNM BK-63 (Meldrum et al. 2010), or that of the Dmanisi hominin post crania (*contra* Lordkipanidze et al. 2007; Pontzer et al. 2010).

15.3.2 Out of Africa

The phrase "Out of Africa" has become synonymous with the now entrenched view that our hominin ancestors originated in Africa, an opinion that can be traced back at least to Darwin's *Descent of Man* (Darwin 1872). Certainly there is little or no evidence to refute the idea that australopithecines and early *Homo* had their origins in Africa and may never have left that continent (although interpretations of *Homo floresiensis* from Indonesia, as potentially a relict late australopith/early *Homo* sp. raises the possibility of earlier dispersal out of Africa). Likewise, it has traditionally

Fig. 15.2 Tracks attributed to *Homo erectus* (*H. ergaster*) at Ileret, Kenya (after Bennett et al. 2009)

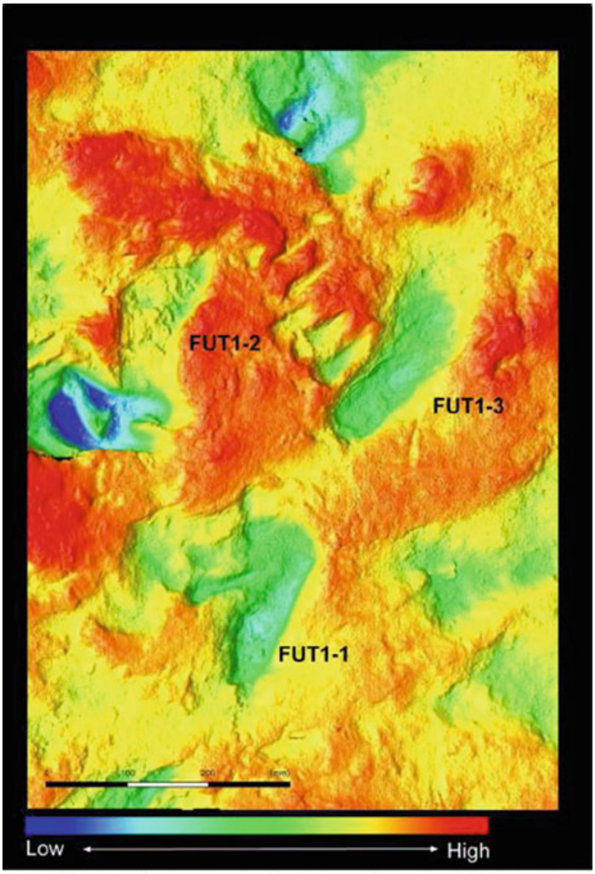

Figure S7. Mosaic of scans viewed vertically showing potential hominin prints FUT1-1 to FUT1-3. The surface has been color rendered in to 5 mm vertical isopleths.

been assumed that *Homo erectus* (*H. ergaster*), a species that existed from ~2.0 to 0.2 Ma, with little pronounced morphologic change, originated in Africa, even though primitive representatives of this species dispersed across the old world at an early date. For example, remains are reported from Dmanisi, Georgia as early as ~1.8 Ma, raising the possibility of an Asian origin for *H. erectus* (Ferring et al. 2011).

Following the hominin footprint trail from the early Pleistocene sites east of Lake Turkana, the next youngest reports are from three European sites, one dated to the Early Pleistocene, between 1.0 and 0.78 Ma, and the other two dated to the Middle Pleistocene. The oldest site, recently reported by Ashton et al. (2014), is associated with estuarine sediments of the Cromer Forest-bed Formation at the Happisburgh site in east Anglia, England. The footprints identified at this site occur in parallel-laminated silts, but are not very well preserved. In fact, only one footprint shows toe impressions and none preserve clear evidence of a medial arch. However, although the footprints are susceptible to destruction by marine erosion soon after they are exhumed, about 50 elongate footprints (length 14–25 cm, width

6–11 cm) were nevertheless identified in an area of about 12 m^2. Ashton et al. (2005, p. 7) argued that "the shape of the footprints suggests that they were most likely made by hominins and none of the prints are consistent with those formed by other mammals." Moreover, Parfitt et al. (2005) have established that flint tools made by hominins occur in this same formation.

Prior to the reports from Happisburgh, the oldest, best-dated, and best-studied footprint site was the Middle Pleistocene Roccamonfina Volcano site in Italy, reported by Mietto et al. (2003) and Avanzini et al. (2004, 2008), dated between ~385,000 and ~325,000 yBP. The trackways occur in a volcanic ash deposited on the slopes of the Rocamonfina volcanic complex and, due to the slope, one trackway of 27 footprints has a zig-zag configuration, indicating an individual switch-backing. Another trackway of 19 prints follows a gently curved course, with a few hand- or palm-prints where the trackmaker put his/her hand on the ground. A third trackway of ten prints forms a straight line. The footprint details are quite indistinct and not very well-preserved. Most lack clear toe impressions, even though faint traces of the hallux are recognized in some cases, even indicating a gap between digits I and II typical of habitually unshod individuals. The tracks are generally flat, but show possible inconsistent traces of a transient medial longitudinal arch in some cases. They are described as short and broad (~20–24 cm long and ~10–12 cm wide), suggesting a stature for the trackmaker of ~1.56 m. Based on age, these tracks likely represent a pre-*sapiens* or pre-*neanderthalensis* species such as *H. heidlebergensis*, or possibly late *Homo erectus* (*H. ergaster*) (Scaillet et al. 2008).

A second mid-Pleistocene footprint from Terra Amata, in southern France, has been tentatively dated at ~300,000–400,000 YYBP (De Lumley 1966, 1967; Miskovski 1967; Meldrum 2006, p. 246; De Lumley et al. 2011). The site only reveals one track, but it clearly shows a diagnostic hominin big toe (hallux) trace. However, like the Rocamonfina tracks, there is little evidence of a well-defined medial longitudinal arch (Meldrum 2004a, b). It is interesting that the lack of a well-defined arch is noted in both the Italian and French tracks. This is presumably open to several possible interpretations. For example: (1) the lack of a discernible arch could be due to poor footprint preservation, resulting from suboptimal substrate conditions at the time of registration, or post-track-making or post-exhumation weathering of the footprints, (2) the trackmaker may have been an individual or a member of a species in which arches were not well-defined, or inconspicuous as the result of having robust fleshy feet, or (3) hominins exhibit a mosaic pattern in evolution of features of the foot and stability of the foot's medial column was still lacking at this stage of hominin evolution.

Barnaby (1975) noted that hominin footprints from a volcanic ash near Demirköprü, Turkey were assigned an age of 250,000 yBP, suggesting they represent a pre-*sapiens* species (Ozansoy 1969). However, subsequent thermoluminescence dating of associated tuffs in the area gave much younger dates on the order of 65 ± 7 ka and 49 ± 9 ka (Westaway et al. 2003, 2004, 2006). These dates have been amended, yet again, to suggest dates as young as 12 ka (Tekkaya 1976; see Lockley et al. 2008a, b for summary). Some 50 pairs of footprints have been removed and are stored at the MTA Museum (Ocakoglu, personal communication). They measure ~29 cm in length and 11 cm wide, and show a robust hallux impression and well-developed ball, heel pad, and medial longitudinal arch, suggesting the footprint of a fully modern foot.

15.4 Tracking the Dawn of *H. sapiens* in Africa

The fossil footprint record in Southern Africa is important for understanding Middle-Late Pleistocene transitions, which were more or less temporally coincident with the emergence of modern *Homo sapiens*. Roberts (2008) reported the two important tracksites: one at Nahoon Point, near East London (Deacon 1966; Mountain 1966), now dated at about 127,000 ± 8000, and another in the Langebaan Lagoon area, 130 km south of Cape Town, dated to about 117,000 YYBP (Gore 1997; Roberts and Berger 1997; Roberts 2008). Thus, both track sites represent the last interglacial period that coincides with the sub-Series boundary between Middle and Late Pleistocene (Gibbard 2003). The Nahoon Point tracks are better preserved, showing well-preserved toe impressions and a footprint length of ~19 cm, and are associated with poorly preserved mammal and bird tracks. The Langebaan lagoon tracks are larger (~23 cm long), but less well-defined. They are associated with probable hyena tracks (Roberts 2008). Hatala et al. (2011), Richmond et al. (2011) and Zimmer et al. (2012) reported an assemblage of about 350 tracks comprising 18 trackways from Lake Natron, Tanzania dated at about 120,000 YYBP (Wong 2011). Charles Helm (personal communication 2012) reports a number of other mammal and bird track sites along the South African coast.

15.5 The Late Pleistocene: *H. sapiens* Produces a New Type of Ichnologic Record

The ichnologic record of *Homo sapiens* in the Late Pleistocene contains evidence of an evolutionary event that can only be characterized as “revolutionary.” Simply put, this is because humans changed the fundamental nature of the ichnologic record. Whereas they had previously created footprints, and a few butcher marks on bone, only inadvertently, by as early as 30,000–35,000 years ago they were deliberately producing artifacts and artwork, which most anthropologists acknowledge as an unprecedented “creative revolution.” Before proceeding any further we need to explore the justification for including human creations, such as art work and other traces produced by the growth of civilization, under the broad umbrella of vertebrate ichnology. The word *ichnos* derives from the Greek meaning footprint or trace. In this regard the English word “trace” has deep etymologic roots connecting it with the words, draw, drag, and trace. So, for example, a draw horse, drags or draws a plow leaving a furrow or trace (see Smith and Hall 1914 or Harper 2012, for Latin translation of “to drag” as *traho*).

On the one hand, one might argue that it would be simpler and more consistent with our account of the pre-Late Pleistocene record, to confine our discussion of hominin ichnology to footprints left "inadvertently" by humans, or human ancestors, and therefore to "avoid" discussion of a plethora of traces created deliberately by humans, leaving it to be dealt with in the fields of archeology and anthropology (Kim et al. 2008a; Baucon et al. 2008). On the other hand, it can be persuasively argued that it is entirely arbitrary to draw a line between human traces produced inadvertently and those produced deliberately. A bird builds a nest deliberately, not inadvertently, and the same goes for animals that dig burrows. One might also argue that avoiding the problem is the lazy way out, because it fails to address the question of what is legitimately classified as a hominin trace fossil. The separation or avoidance approach would in effect treat humans as a "special" species, somehow outside the evolutionary continuum, creating a charge of unwarranted bias, contrary to much contemporary scientific philosophy. Moreover it is difficult if not impossible to draw an arbitrary dividing line between the cultural artifacts and traces produced by *H. sapiens* and non-*H. sapiens* species. Pre- or non-*sapiens* species were already producing trace fossils, such as butcher marks on bone and knapping marks on flint long before the first *sapiens* cultural revolution was underway in the Late Paleolithic.

As noted in Sect. 15.1, there is also scientific precedent, for including many diverse *sapiens* artifacts as an integral part of hominin ichnology (Hasiotis et al. 2007; Baucon et al. 2008). Kim et al. (2008a) presented some of the aforementioned rationale in arguing for four categories of hominin trace fossils, including (1) Pliocene through Holocene footprints, (2) Pleistocene through Holocene butcher marks (feeding traces), (3) Early and Mid Pleistocene stone tools, and (4) Late Pleistocene multimedia technology (including art, dwelling traces, etc.). Examples of traces in the latter two categories can be found through to the present time. In a similar, but more detailed evolutionary scheme, Rothschild and Lister (2003), in a standard textbook on evolution, listed ten major events in hominin evolution, occurring in the last 5 million years. Among these, a majority leave a trace fossil record, notably (1) bipedal locomotion, (2) utilization of new food resources, (3) stone tool manufacture, (4) control of fire, (6) symbolic communication, (9), and complex cultural and technologic diversification (10). Hasiotis et al. (2007) proposed a classification of hominid trace fossils that is somewhat different from the fourfold classification of Kim et al. (2008a). Their classification includes "features, biofacts/ecofacts and artifacts" which are further divided into multiple categories, including almost all manufactured items or creations including structural remains, lithic, ceramic, and metal items. However, in general, the two classifications are similar in so far as they recognize almost all human creations that leave physical traces as some category of trace fossil. As noted above, this discussion has been enlarged by Baucon et al. (2008) in their definitions of the broad scope of ichnoarcheology.

For convenience, in the sections that follow, we discriminate between artifacts themselves and the traces left by their creation. For example, stones are not trace fossils, but worked stone tools, and especially flake scars are trace fossils. Likewise, a fire is an artifact in a different category from the charred hearth left behind as the trace of the fire. In the same way a shelter or building is not in the same category as the post holes or foundation ditches created during their construction.

In any event, from a philosophic and methodologic perspective, we arrive at the following conclusions. There is no scientific justification for confining discussion of hominin ichnology only to footprints (produced inadvertently or otherwise). Thus, we may include such diverse traces as flaked stone tools, fire traces, cave painting, ditches, and foundations. While these trace fossil categories are commonly different from those associated with animal activity during most of the Phanerozoic, they are nevertheless unequivocal evidence of behavior and activity. Like other trace fossils, evidence of activity of organisms (Mcllroy 2004) or work of organisms (ICZN 1999), hominin traces are significant in paleontology, stratigraphy, and sedimentology, but unlike other trace fossils, however, hominin traces can uniquely contribute to understanding the work or activities of our ancestors (Kim et al. 2007). Since it is we humans who attempt to evaluate "differences" between traces produced by different species, some subjectivity is perhaps inevitable, and the question arises as to whether these are "differences of kind or differences of degree." These issues are further discussed below. It is also worth noting that while the creation of a diverse suite of new hominin trace fossils in the Late Pleistocene is a considered a revolutionary leap forward in cultural terms (Diamond 1999; Mellars 2006) appearing as a major ichnologic event in the trace fossil record (Hasiotis et al. 2007; Kim et al. 2008a), it is not necessarily an anomalous evolutionary event. Rather it can be viewed as an example of a "punctuated evolution" scenario, or a change in the tempo of cultural evolution following a long Early–Middle Paleolithic period of relative stasis.

15.5.1 Breaking New Ground: Prelude to the Late Pleistocene Cultural Revolution

The geologically defined Late Pleistocene age extends from ~130,000 to 10,000 yBP. However, in comparison with the rapid developments of human cultural development in the later part of the Late Pleistocene, which falls within the range of ^{14}C dating techniques, the early part of this age (before ~50,000) has, until recently, produced comparatively little evidence of any major evolutionary events. There are no Late Pleistocene hominin tracksites dated with confidence in the first half of this interval (between ~130,000 and ~65,000). By contrast the latter part of the Late Pleistocene saw the worldwide spread of *Homo sapiens*. Unequivocal evidence, including footprints, establishes the presence of modern humans (*H. sapiens*) in both Australia and the Americas, as well as in ostensibly remote regions such as the Tibetan Plateau and Jeju island, Korea (Zhang and Li 2002; Kim et al. 2009). Along the way there may have been interactions with, even gene flow between, other late-*Homo* species—Neanderthals, Denisovans, and Red Deer Cave hominins (Meldrum 2012b). Tracks left by any of these species would likely be fully modern in appearance, albeit robust in proportions. In contrast, the persistence of more archaic hominins into this period—*Homo heidlebergensis*, even *Homo erectus* (Swisher et al. 1996) and the enigmatic and as yet very restricted species *H. floresiensis* (Morwood et al. 2005) raises the possibility of additional footprint morphotypes. Given the perennial interest in the relationship of Neanderthals to modern humans, their inferred extinction as recently as ~25–30,000 yBP is generally considered a major event in hominin evolutionary history (Delson and Harvati 2006 and refs. therein). However, despite a footprint record spanning this time interval, it is not sufficient to shed useful light on the timing of this or other similar events.

However, before accepting that the so called Late Paleolithic cultural revolution or "great leap forward" into modernity (Diamond 1999; Mellars 2006) occurred quite abruptly ~50,000 yBP, perhaps coincident with, or in some way related to, the extinction of the Neanderthals it is important to note that this is a rather Eurocentric view that has been challenged by McBrearty and Brooks (2000). These authors show that many technologic advances, considered typical of European cultures existing between ~10,000 and ~50,000 yBP, have been identified significantly earlier in Africa on the order of >100,000 yBP.

Lockley et al. (2009) reported a total sample of 19 Late Pleistocene hominin tracksites from diverse localities around the world. Such geographically widespread occurrences demonstrate that the hominin track record is consistent with that obtained from archeologic evidence. In comparison with the important Pliocene through earliest Late Pleistocene track record in Africa, the record from most of the Late Pleistocene of Africa is sparse. Scott et al. (2008a, b) reported an isolated and poorly preserved track from the Lake Bogoria area of the Kenyan Rift valley. The track is ~20 cm long and 8.5 cm wide, and occurs in association with the footprints of bovids, suids, and birds.

Turning to Europe, we find some of the earliest of the Late Pleistocene track records associated with caves. Based on published dates, the oldest Late Pleistocene human footprints are those reported from Vârtop Cave, Romania (Onac et al. 2005) and assigned an age of ~62,000 yBP. Three footprints, one with a well-defined outline (22 cm long and 10.6 cm wide), are preserved. However, details are obscured by infill of soda straws and moonmilk. Of note was a distinctive gap (1.6 cm) between the first and second digits (Fig. 15.3). According to these authors, the Vârtop Cave tracks may be the only footprint sample unequivocally attributable to Neanderthals.

Human footprints were reported from a "deep Middle Paleolithic layer" at Theopetra Cave in Thessaly, Central Greece (Facorellis et al. 2001). This cave was evidently occupied from the Middle Paleolithic until the post Neolithic, with minimal ^{14}C dates of ~48,000 yBP obtained for the oldest layers with which the footprints are associated.

15.5.2 The Hominin Track Record Goes Underground

Many Late Pleistocene hominin footprint sites are associated with Late Paleolithic cultural evidence found in subterranean cave sites in southern France, Spain, and Italy. The region is perhaps most famous for cave paintings, but though less often reported in detail, many sites contain tracks and other evidence of Late Paleolithic

Fig. 15.3 Purported Neanderthal footprints, Vârtop Cave, Romania. Note growth of cave calcite, obscuring track morphology

activity. Tracks are documented from Lascaux (Berriere and Sahly 1964) and the Niaux cave system (Pales 1976). Tracks from the Niaux caves have been described and illustrated in detail by Pales (1976), and apparently include patterned arrangements of footprints that have been interpreted as deliberate activity of children at play (Lockley and Meyer 2000) (Fig. 15.4). Here the issue of intention is raised, reminding us that by the Late Paleolithic not all human tracks were made as the result of purely unintentional passage of individuals through a particular area. Indeed, it is generally assumed, if not explicitly stated, that humans entered underground caves deliberately, even if the motives, other than creating artwork, are not clear. In a similar vein, human tracks from Grotte de Cabrerets or "Pech Merle" cave famously reveal traces indicating an individual using a walking stick (Begouen 1927; Vallois 1927, 1931).

In other cases, the interpretations put on tracks are more ambiguous. Tracks from Grotte Aldène assigned an age of ~15,000 yBP by Casteret (1948), but assigned and age of ~8000 yBP by Ambert et al. (2000), are associated with charcoal, hyena tracks, and cave bear nests, but the behavior of the track maker, in relation to other animal and human traces is unclear. In Fontanet Cave, footprints suggest a child may have followed a puppy or fox into a cave, but this inference can hardly be confirmed or denied on the basis of available analysis (Bahn and Vertut 1988). As noted

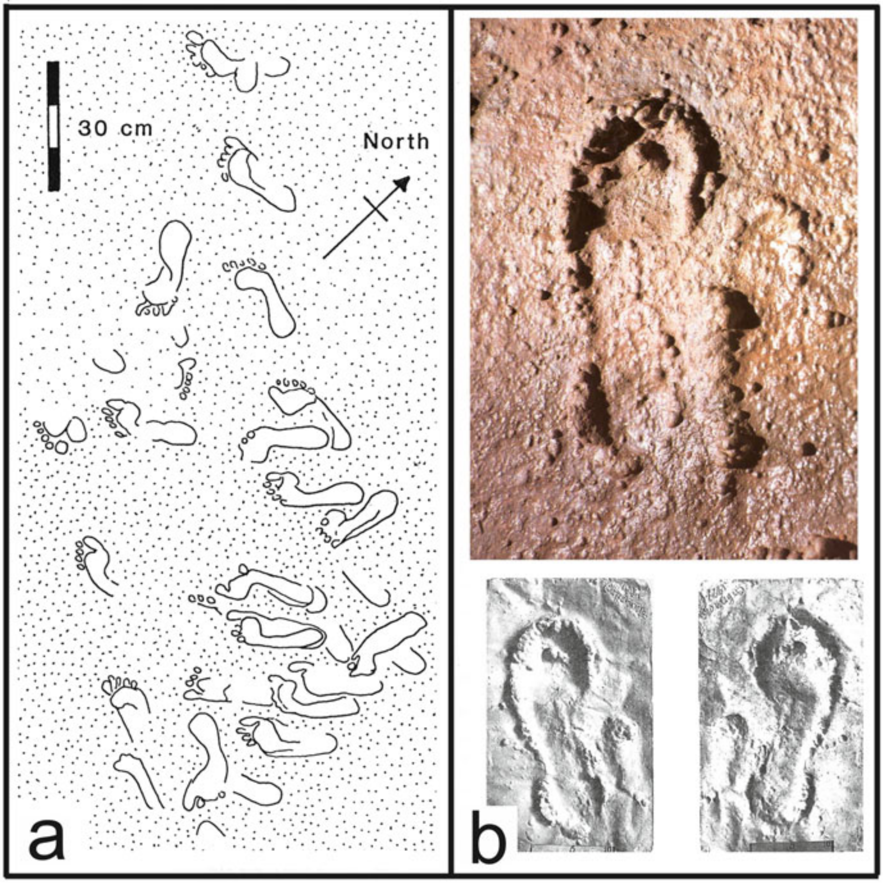

Fig. 15.4 (**a**) Tracks in a patterned arrangement from Niaux cave, suggest children at play (after Pales 1976 and Lockley and Meyer 2000, Fig. 10.12). (**b**) Track from Peche Merle cave

elsewhere (Lockley et al. 2007a; 2009), the footprints of children appear as common components of the track record of Paleolithic caves. For example, in Chauvet Cave near Vallon-Pont-d'Arc in southern France, a trail of footprints claimed to represent those of a young boy, about 8 years old and about 1.5 m tall, are possibly the oldest European footprints of *Homo sapiens*, perhaps as old as 35,000 yBP. At Ariège three trackways of children are recorded (Bahn and Vertut 1988). The footprints extend for about 50 m across the cave floor and may be between 20,000 and 30,000 years old (Harrington 1999; García 1999, 2001). Many other Late Paleolithic caves with hominin tracks have been mentioned or illustrated without detailed descriptions (Kuhn 1955; Marshack 1972; Vialou 1986; Bahn and Vertut 1988). As already implied, in many cases these sites reveal evidence that other animals, evidently all mammalian carnivores, shared these cave habitats, at least on some occasions (Lockley et al. 2007a, b; 2009).

Tana della Basura cave near Toirano, Northern Italy is here mentioned separately due to the intriguing but controversial suggestion that the "human tracks" reported by Chiapella (1952) are attributable to Neanderthals (Pales 1954, 1960). At present, despite the skeletal evidence that may be available from various sites to help distinguish *H. sapiens* from *H. neaderthalensis*, we have no reliable criteria for identifying isolated Neanderthal footprints. As pointed out by Molleson et al. (1972) and by Onac et al. (2005), the date of this site may be as young as 12,000 yBP, in which case the Neanderthal claim is questionable. Its morphology certainly does not distinguish it from a *H. sapiens* (Fig. 15.5).

The abundance of human tracks at cave sites is perhaps surprising, especially given the lack of detailed description of many sites. For example, in Ojo Guareña, a cave near Burgos, Spain, hundreds of footprints are reported, but the site is illustrated by only two photographs (Marcos 2001). Dates of 15,600 yBP, suggesting a Late Pleistocene age, were obtained from carbonized wood. As noted by Lockley et al. (2008a, b), a "light patina of carbonate" gives the tracks "a very ancient appearance" (translation of phrases from Marcos 2001, p. 35).

This type of discrepancy between abundance and documentation is understandable when considering the problems of access, and the dangers of disturbing the footprints by walking on them, or otherwise causing damage. Likewise, dating of the cave site tracks is often difficult due to the lack of suitable materials in the

Fig. 15.5 Footprint from Tana della Basura cave near Toirano, Northern Italy

substrate, the likely differences in age between substrate and tracks, and the preference for dating other materials such as charcoal which may or may not be contemporaneous with the tracks. For example, footprints from Tempranas Cave, near Niembro in the Llanes region of Asturias Spain (Noval Fonseca 2007) remain undated at the present time.

Despite the problems involved in obtaining accurate dates, tracks in caves have good preservation potential and, as noted above, tracks are apparently more abundant, at least at some sites, than the literature might suggest. However, another factor must be considered—that is the attraction of cave paintings. On the positive side, efforts to date cave paintings make it possible to infer the age of footprints, assuming there is no strong evidence to suggest that paintings and footprints represent different phases of activity. On the negative side, paintings distract attention from other features, such as footprints and charcoal. Obviously, paintings indicate that caves were frequented by people on foot, even if footprints are not found. Footprints may occur in caves without paintings or other evidence of human habitation (see below), but it is impossible to speculate on how common tracks are in caves lacking other human-produced evidence.

For all the problems and ambiguities that surround the discovery, documentation, dating, and interpretation of cave site footprints, cave tracks indicate a certain type of behavior and ecology. For whatever reason, modern humans (*H. sapiens*) and perhaps close relatives (e.g. *H. neanderthalensis*) began to frequent caves sometime in the Late Pleistocene. This can be considered a significant event in hominin evolution and, in the most general terms, the evidence seems to suggest a human impulse to colonize new habitats. This was just one example of the geographic spread of humans to colonize new regions, such as Australia and the Americas. In ecologic terms, as explicitly noted by Lockley et al. (2007a, b; 2008a, b), the nonhuman footprints reported from Late Pleistocene caves are almost exclusively those of carnivores (including bear, hyena, and fox), and stand in contrast to open-air hominin track sites, where tracks of ungulates and birds are typically dominant. The aforementioned cave-dwelling carnivores had evidently inhabited caves long before their habitations were invaded by modern humans. Thus, human cave-colonization behavior precipitated new "ecologic" interactions between humans and cave dwelling mammals. While the co-occurrence of footprints of both groups is tangible evidence of such cohabitation, even more evocative evidence of interaction is found in the archeologic record of paintings and supposed shrines indicative of "cave bear cults" (a once-popular notion, especially for the Middle Paleolithic, but long discredited by taphonomic studies [Bahn 2012]).

15.5.3 Vertebrate Ichnology Investigates Cave Paintings

Lockley and Meyer (2000) and Kim et al. (2008a) noted that cave art (or the more neutral term "painting") is itself a type of hominin ichnology, as is any type of engraving. Likewise, as noted by Lockley et al. (2008a, p. 113), "[b] ecause tracks are a type of symbol or signature of the trackmaker, their artistic renderings have sometimes been the subject of debate.” Indeed, as noted above, many human creations can be considered as ichnologic phenomena, including most forms of sculpture and writing. However, in order to constrain the discussion to the realm of prehistory, we confine our discussion to the implications of Late Pleistocene evidence, which sheds light on evolutionary events. For example, just as footprints indicate the co-occurrence of modern humans and Late Pleistocene carnivores in caves, so cave art provides direct evidence of the interaction of humans with the Pleistocene megafauna. The interest for vertebrate ichnology is compounded when Paleolithic hominins also depicted the footprints of the animals they were tracking, observing, or hunting (Mithen 1988). In this regard, it could be inferred that just as tracks are potentially useful as a census of animals in a particular area (Lockley 1991), so cave art is also potentially a census of animals in a given area in the past. For example, at Closquier cave, in southern France, there are depictions of what is interpreted as the now-extinct great auk, “a seabird that could only live in a cold biotope” (Clottes and Courtir 1996, p. 128). Just as these authors at first found it difficult to interpret the depiction of the great auk, so too footprints depicted by Late Paleolithic artists have proved difficult to interpret. As noted by Lockley et al. (2009, p. 113), a particularly “interesting episode in the annals of anthropology was a debate over whether certain symbols represented tracks or were representations of female genitalia (Bahn 1986).”

European Cave art, especially from France and Spain, has been the subject of endless debate. For example, do animal depictions indicate hunting activity, sympathetic magic, or other shamanistic symbolism? Likewise, one can argue endlessly as to whether animal and track depictions are realistic or stylized, the result of superior or inferior artistic ability. Possibly the most significant depictions from an ichnologic view point are these that show the co-occurrence of animals and the tracks they made. One famous example is the bovids depicted at Altimira, Spain, where the animals are seen in profile, but their feet are shown in “plan view” appearing as cloven hoofed tracks stuck on the end of the legs. While it is obvious from such examples that Late Paleolithic humans could correlate between animals and their tracks, this is still a highly significant record from the “dawn of vertebrate ichnology” essentially no different from that produced by contemporary vertebrate ichnologists who correlate between tracks and track makers. Thus, our Paleolithic ancestors deserve full credit for being the authors of the first the vertebrate track field guides (Seilacher 2007). Whether, we can infer that they only interpreted the track-track maker correlation in causal terms, the way we do, remains an open question, and we have to consider the possibility that tracks had other significance in various Paleolithic cultures (Lockley 1999); see Baucon et al. (2008) for discussion of podomorphs (footprint representations) and “ichnohierophanies” (traces of religious or spiritual significance).

15.6 New Intercontinental Travel Frontiers

Archeology and anthropology regard the colonization of Australia and the Americas by *Homo sapiens* (if not earlier *Homo* species), as evidence of the ability of modern humans to permanently expand their ranges into previously “uninhabited” territory, by undertaking what we can describe as intercontinental travel. Exactly when and where the first emigrants broke out of the “old world” to set foot in Australia and America is unknown. However, these expansions of range seem to have been part of a pattern that was first manifest with the spread of human ancestors “out of Africa” into Europe and Asia, including inaccessible regions, such as present day Tibet (Zhang and Li. 2002) and various islands of the Indonesia archipelago (Morwood et al. 2005).

15.6.1 Into Australia

The colonization of Australia is considered (Bowler et al. 2003) a major event in hominin evolution, reflecting an ever-increasing ability of humans to colonize new continents. Humans probably first colonized Australia around 50,000 yBP, showing their ability to cross the famous Wallace line which separates the marsupial-dominated faunas of Australia from the placental-dominated faunas of southeast Asia (Oppenheimer 2009). Webb et al. (2006) and Webb (2007) reported tracks that have been optically dated to between ~19,000 and 23,000 yBP in the Willandra Lakes region of southeastern Australia. This is evidently one of the world’s largest collection of Pleistocene human footprints, with at least 123 footprints, and the site is part of a property nominated for World Heritage status. The largest tracks measure 29 cm in length by 10 cm wide. The tracks for which close-up photos have been published (Fig. 15.6) present an unusual and less than fully modern morphology: quite flat, exceptionally broad heel, deep and long toe impressions (up to 7 cm) and a large robust hallux, but lack any clear medial arch and ball impressions (Webb et al. 2006, Fig. 4).

15.6.2 The Trail to the New World

According to controversial footprint evidence, modern humans may have first set foot in the New World as early as ~40,000 yBP (Gonzalez et al. 2006a; Huddart et al. 2008). According to the initial claims of these authors, footprints from a Late Pleistocene site from Toluquilla Quarry, at Valsequillo, near Puebla Mexico, indicate this reliable 40,000 yBP date for the presence of *Homo sapiens* in the New World. However, while the date may be credible, the features interpreted as footprints are controversial, and several of the original authors now admit that these purported tracks are of questionable origin (Morse et al. 2010). They lack clear

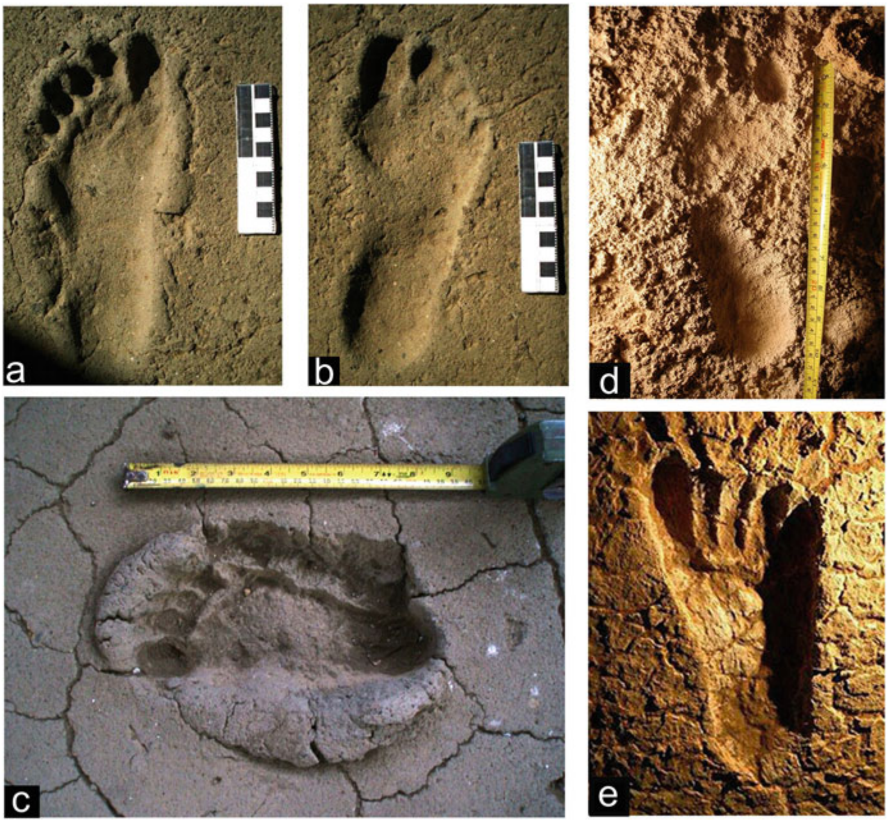

Fig. 15.6 *Homo sapiens* tracks from the New World and Australia. (**a**–**c**) tracks from the Acahualinca site Nicaragua (after Lockley et al. 2009, Fig. 10), (**d**) track from Cuatrocienegas, Mexico (after Gonzalez et al. 2009), (**e**) track from Willandra Lakes site, Australia

evidence of the big toe (hallux) impression, arch, or differentiated ball and heel traces. In short they are elongate depressions or traces that may be artifacts produced by quarry equipment. Renne et al. (2005) referred to these features as “alleged” footprints and also questioned the dates, instead inferring much older dates of 1.3 Ma, corroborated by paleomagnetic studies. However, Gonzalez et al. (2006b) and Huddart et al. (2008) held to their claim arguing that the dating of Renne et al. (2005) is incorrect.

According to evidence other than footprints humans are not proven to have been resident in the Americas prior to ~20,000 yBP (Nemecek 2000). Footprints on the western coast of Canada, dating to 12,500 yBP, may indicate a coastal route for colonization of the Americas (De Pastino 2015). Tracks from Buenos Aires Province Argentina (Aramayo and Manera de Bianco 2009), have produced dates in the range of ~12,000–16,000 yBP. Hominin tracksites reported from Monte Verde, Chile are associated with dates of 11,500–12,500 yBP (Dillehay 1999). The rediscovery of a tracksite associated with tufa deposits at

Cuatrociénegas, Coahuila, Mexico has produced tentative dates of ~10,000 yBP (Gonzalez et al. 2006c, d, 2007, 2009). Two sets of tracks from Cuatrociénegas have recently yielded U-series dates of 10.55 ± 0.03 ka and 7.24 ± 0.13 ka (Morse et al. 2010). Given the doubts about the age of the Valsequillo footprints referred to above, Morse et al. (2014) claimed that the former date represents the oldest known for any footprints from Mexico. Other tracksites reported from Mexico (Ordoñez 1945; Aveleyra Arroyo de Anda 1950; Rodríguez-de la Rosa et al. 2004) are poorly known, but likely include mostly Holocene rather than Pleistocene tracks.

Among the Holocene track sites listed by Lockley et al. (2007a, b; 2008a, b), two sites from La Olla and Monte Hermoso Argentina dated at ~7000 yBP (Bayon and Politis 1996, 1998; Aramayo and Manera de Bianco 2009; Bayón et al. 2011) are significant, and comparable in age to a site from Laguna La María (near Villa Cañás) dated to ~8000 yBP. Abundant well-preserved tracks from the footprint museum at Acahualinca, (Huellas de Acahualinca) Managua, Nicaragua (Flint 1883; Brinton 1887) have been ^{14}C-dated at 5945 ± 145 yBP (Bryan 1973), at 6500 yBP by Bice (1979), and between 2000 and 6000 yBP (Schmincke et al., 2005, 2007, 2008, 2009). The site is now the type locality for *Hominipes modernus* (Kim et al. 2008b) and preserves the trackways of at least 15 individuals, an ungulate, a possum and a bird (Lockley et al. 2007a, b; 2008a, b). Another nearby site, known as El Recreo (Williams 1952), has yielded bison and tapir tracks. Plant remains are also reported (Brown 1947). The Oro Grande Site near Victorville, southern California (Rector 1979, 1983, 1999), has given a ^{14}C date of 5070 ± 120 yBP (Rector 1983) for tracks of at least four individuals, where tracks of raccoon, coyote, and ungulates were also documented.

Haberland and Grebe (1957) reported a tracksite from El Salvador tentatively dated between ~1200 and 1800 yBP. Undated footprints were also reported from a volcanic deposit near Guaimaca, Honduras (Veliz 1978). Similarly sparse information comes from a report (Anon undated) of a cave site from Naj Tunich, Guatemala, with footprints attributed to indigenous Mayan inhabitants tentatively dated on the basis of artifacts, not footprints, between ~1450 and 1950 yBP.

To complete the New World track record, we may refer to Willey et al. (2009), who noted footprints reported from Pocket Cave in Arizona, and dated at ~1450–1500 yBP based on dendrochronology. Finally, footprints from eastern North America are associated with underground caverns, such as Jaguar Cave, Tennessee, Unknown Cave, Kentucky, third Unnamed Cave, Tennessee, Fisher Ridge Cave, Kentucky, Mud Glyph Cave, Tennessee, Sequoyah Caverns, Alabama, Footprint Cave, Virginia, and Lon Odell Memorial Cave, Missouri (Watson et al. 2005; Willey et al. 2005, 2009). Collectively, these cave sites date from between 4695 ± 85 and ~400 yBP.

15.6.3 *Other Exploratory Trails*

As summarized by Lockley et al. (2008a, b), Zhang and Li (2002) and Zhang et al. (2003) reported a series of hand and footprints associated with calcareous tufa deposits at an elevation of 4200 m on the Tibetan Plateau optically dated at about 20,000 yBP. This unusual combination of hand and footprints may be related to the site being a hot springs with a hearth, therefore presumably used as a campsite, rather than an area simply passed through.

Late Pleistocene footprints dated at about 19,000–25,000 yBP from Jeju Island, Korea (Kim and Kim 2004a, b; Kim et al. 2004, 2009, 2010) indicate that humans were exploring remote islands at about the same time that they were exploring the Tibetan Plateau. As a coastal site, Jeju provides evidence of a variety of bird and mammal tracks diverse invertebrate traces and body fossils, at multiple levels, suggesting an ecology obviously different from that found in Tibet. Nevertheless, despite the geographic and ecologic differences between these two Asian sites, they both provide striking evidence of the ability of Late Paleolithic humans to explore habitats that had not previously been frequented by hominins.

15.7 The Prelude to History

15.7.1 *Life on the Sea Shore*

Lockley et al. (2007a, b, 2008a, b) have already listed known hominin track sites that bridge the gap between unequivocally Pleistocene and prehistoric Holocene sites, to those that yield comparatively recent dates that bring us into historic time. It is not necessary to repeat detailed accounts of these sites which are already widely distributed. However, a brief summary allows us to pick out features that highlight the utility of footprints in interpreting "events" in historic time.

Among the earliest Holocene tracks to fit in our post-Pleistocene category, we can cite abundant human footprints from near the Sebkra el Azrag, Mauritania (Mafart 2006). These date from ~9000 yBP and are associated with footprints of elephants, hippopotamus, giant eland, and bovids.

Younger Holocene footprint sites are known from near Clare Bay, in South Australia (Belperio and Fotheringham 1990), estimated to be ~5000 yBP. Undocumented tracks are also reported from near Broome in western Australia (Long 1998; Baldwin personal communication 2011). Both are coastal sites. Other significant coastal hominin tracksites are known in Britain (Aldhouse-Green et al. 1995; Cowell et al. 1993; Roberts et al. 1996; Roberts 2009; Doyle 2007; Bennett et al. 2010a, b). An assemblage of exceptionally preserved footprints of between six and nine children (ranging in length from 114 to 206 mm) has been described from Walvis Bay, Namibia (Bennett and Morse 2014). They date to 1500 yBP and are preceded by the tracks of an apparent flock of domesticated sheep/goats.

Human footprints reported from Rawthey Cave, Cumbria, England (Chamberlain et al. 1997) could be as recent as the 14th century AD. Some coastal sites (Patton 1993) have only the tracks of domestic animals. Human tracks have also been reported from Holocene beach rock in Greece (Bromley et al. 2009).

The coastal situation of many Holocene track sites seems to reflect two factors. (1) Suitable environments for track preservation (e.g., estuarine and beach substrates) and (2) preferred habitats or foraging sites of humans. We know from other lines of evidence, such as shell middens, that foraging was an important activity at such sites.

15.7.2 In the Shadow of Volcanoes

Human tracks are reported from numerous agricultural sites (rice fields) in Japan, (Harada and Noto 1984) that date from ~720 to 1600 yBP. At many of these Japanese sites, volcanic ash played an important role in track preservation. Human tracks also occur at various stratigraphic levels in volcanic ashes dated at 1400 AD on Motutapu Island, New Zealand. Nichol (1982) suggested that track makers were evidently not deterred by the continuing ash falling over the area. Traces of digging sticks suggest that individuals were digging gardens.

Footprints from Hawaii Volcanoes National Park site are from two distinct footprint-bearing horizons, the younger precisely dated to a 1790 Kilauea eruption and ashfall (Meldrum 2004a, b; Moniz Nakamura 2009). The record of modern pedestrian trackways in ash of remarkably similar physical and chemical characteristics as the Laetoli ashfall, provides in the Hawaiian footprints a meaningful comparison and contrast to the Laetoli hominin footprints. This contrast highlights the diagnostic distinctions between *Praehominipes laetoliensis* and *Hominipes modernus* (Meldrum 2004a, b; Meldrum et al. 2011). Because of the drama associated with volcanic eruptions, various scenarios regarding the relationship between ash fall and track-making activity have been proposed, not only for the Hawaiian sites (Jaggar 1921, 1934; Meldrum 2004a, b; Mayor and Sarjeant 2001), but also for the aforementioned Nicaraguan site (Schmincke et al. 2005, 2007, 2008, 2009) and the New Zealand levels (Nichol 1982).

Regarding the Hawaiian sites, Moniz Nakamura (2009) suggested footprints were made in the area both before and after the eruption, thus indicating that individuals were not deterred by the ash fall and not fleeing or about to perish as a direct result of the eruption. Were indigenous populations accustomed to repeat volcanic activity, and undeterred by smaller eruptions? Possibly, but sometimes large eruptions did create truly dramatic, life-threatening scenarios as in the case of the famous 79 AD eruption of Vesuvius. Unlike this eruption, which is not associated with footprints, footprints are found in association with deposits created by the 3780 yBP eruption of Vesuvius, known as the Avellino plinian eruption, that fell on Nola, a Bronze Age village near Naples, Italy (Mastrolorenzo et al. 2006). These devastating ash falls created a remarkable footprint record NNW of Vesuvius where “thousands of footprints [are] directed

NNW away from the volcano." These "testify to an *en masse* exodus from the devastated zone" (Mastrolorenzo et al. 2006, p. 4368). Footprints registered on "all horizons in the ash bed" indicating that "the evacuation occurred during the settling of the surge cloud." "Flood and lahar deposits overlying the surge bed also include footprints and local raindrop imprints as well, thus testifying that the ongoing exodus occurred during both the ash fall and the post-eruption rainstorms and floods" (Mastrolorenzo et al. 2006, p. 4368).

From these accounts of human tracks in volcanic ashes, we can infer that, at the times indicated above, humans lived in volcanic terrains, as they do in some areas today, risking the dangers inherent in such environments. Although we do not know exactly how they reacted to localized or small eruptions, the evidence at some sites (New Zealand, Nicaragua, Hawaii) suggests they were not sufficiently deterred by the threats, to vacate these areas. Thus, on occasion they did not evacuate, or move very far from small eruptions that created small ash falls. However, as the Nola eruption indicates, humans reacted to large eruptions and ash falls by fleeing, although in this case escape was not possible and individuals literally died in their tracks.

15.8 Vertebrate Ichnology Transcends Planet Earth

One of the major events in human history was the landing of humans at six sites on the Moon (Fig. 15.7). Arguably, this is a major evolutionary event akin to the migration of a species onto a new continent on which that species had not previously set foot. Just as the fossil record, including the track record, provides evidence of such migrations, so the artifacts and tracks and traces left by humans on the Moon also provide unequivocal evidence that the range of living humans has extended from one celestial body (planet Earth) to another (its moon). In the case of the machines that humans have landed on Mars, the artifact and trace fossil evidence is slightly different, and it is intriguing to speculate as to how it might be interpreted and compared with the lunar evidence, by someone unfamiliar with human history (Lockley 1999).

While most humans regard the Moon landing as a momentous event in human history, it is perhaps too recent an event to have had its evolutionary significance evaluated in the context of deep time. In any event, the track making activity of humans on the Moon, while creating visually spectacular traces, is so distinctive as to have been treated as a special event, unrelated to the long history of hominin track making on Earth. Nevertheless, while it is legitimate to regard lunar and terrestrial tracks records as two quite separate ichnologic records, in obviously different substrates, environments, and geographic locations, they are still indisputable parts of the continuum of an expanding hominin track record (Fig. 15.6). So, what are the implications?

Humans are the only large vertebrate species to have set foot on the Moon. In this regard, they crossed a new frontier in much the same way as they did when they cross the Wallace line between Asia and Australia, or the Bering Straits between

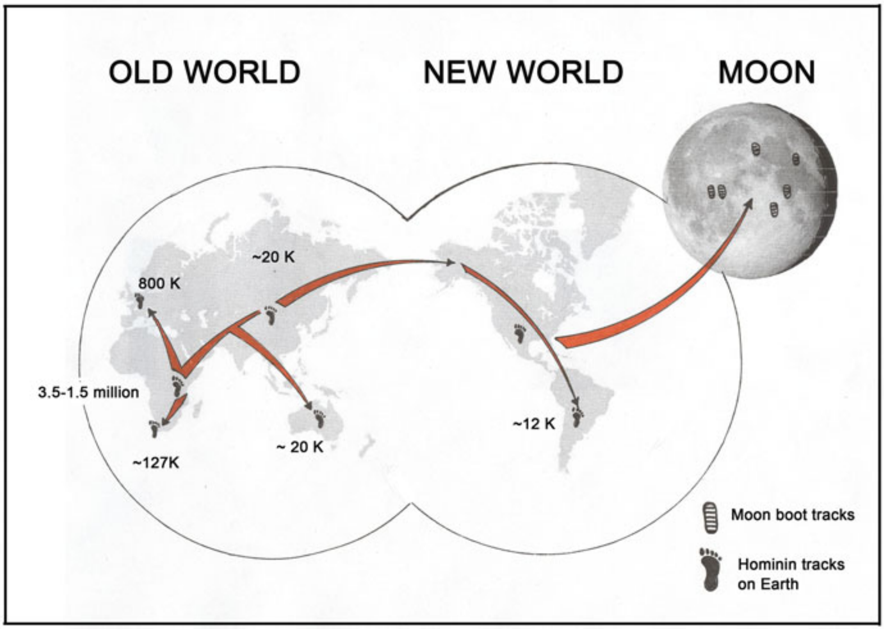

Fig. 15.7 The dispersal of hominins from the old world to the new world and Moon as demonstrated by the footprint record, is in broad agreement with the evidence obtained from the record of body fossils and artifacts

Asia and North America. The principle is succinctly stated by Morwood and Oosterzee (2007, p. 182): "Modern humans were the only large Asian animals that made the west-to-east crossing to Greater Australia on their own account." Here, these authors evidently imply that the migration into Australia was not accidental, as in the oft-cited, but speculative, explanation of dispersal of animals, rafted by accident from one land mass to another. Lockley (1999) described some of the configurations of human traces on the Moon. First, of course they are limited to a very small area, and secondly they loop out from the lunar module and back. Secondly the total census of individual trackways is known to represent only 12 individuals. An intelligent species analyzing the footprint evidence might correctly infer that very few individual track makers, of a distinctive bipedal species, had visited the Moon, but had been unable to explore very far. The track makers were not adapted to colonize extensively.

It is perhaps unduly speculative to consider how another intelligent species might interpret the trails of the lunar rover, the actual rover itself, or the trails and machines on Mars (Lockley 1999). We know that the Martian traces were made without humans being present on the planet, but would this be deduced by an intelligent species unaware of the details of an Earth-based space program? It is perhaps debatable as to whether traces left by robotic machines legitimately fall in the category of biogenic sedimentary structures. Clearly, feet and shod foot traces represent human functional anatomy and behavior, but lunar and Martian rovers represent a different type of function, only indirectly related to human movement. Since these robotic machines are tools, we argue that in principle the traces they leave are similar to those produced by other human-manufactured tools that register traces on a variety of substrates.

In conclusion, as noted below, a broad-based interpretation of hominin ichnology indicates that there have been at least four major threshold events that starkly punctuate the ichnologic record. The first was bipedalism, the second was the spread of hominins to Australia and the New World, the third was painting, sculpture, and tool making, associated with extensive cave exploration, and the fourth was the ability to set foot on other celestial bodies.

15.9 Discussion

At least 65 hominin tracksites are reported in the literature (Lockley et al. 2007a, b, 2008a, b) of which about one third (~24) are Late Pleistocene or older. Only a few (4) sites represent pre-*sapiens* track makers. The advent of erect posture and gait was clearly a major event in hominin evolution. However, the question of whether such features as midfoot morphology (flexibility vs. a fully modern arch) and separation of the big toe (digit I) from traces of digits II–V, and their different inferred lengths, constitute evidence of major evolutionary changes remains open to question, and may not be fully resolved without additions to the body and trace fossil records. Debates about the affinity of the 3.6-million-year-old Laetoli track maker are made partly on the basis of the age of the sites and contemporary body fossils. However, they are also at least partially based on footprint morphology, when correlated pedal skeletal fossils are known. Tuttle et al. (1990) inferred that the Laetoli track maker may have been an as-yet-unknown hominin indistinguishable from modern *H. sapiens*, and therefore not an australopithecine as inferred by Stern and Susman (1983; see also Suwa 1984). In contrast, Meldrum (2006, 2007a) pointed to evidence of mid-tarsal pressure ridges and extrusion fronts, in the GI trail indicating ape-like midfoot flexibility largely if not altogether absent in modern humans (but see DeSilva and Gill 2013). The distinctions in the Laetoli tracks when compared to modern unshod pedestrians are expressed in the introduction of the new ichnotaxon *Praehominipes laetoliensis* (Meldrum et al. 2011) in contrast to footprints of fully modern humans, designated as *Hominipes modernus* (Kim et al. 2008a, b). However, if we exclude the overprinted trackways (G2 and G3), and possibly a fourth (G4) according to Musiba et al. (2011), the *Praehominipes* sample of un-obscured footprints remains small consisting of only the G1 trackway (Fig. 15.1).

The inference of an *H. erectus* (*H. ergaster*) trackmaker, in the case of the poorly preserved Koobi Fora footprints (Behrensmeyer and Laporte 1981), is based on age. The Ileret footprints also exhibit insufficient detail to infer modern footprint morphology with certainty. This inference is contra Bennett et al. (2010a), who concluded that these footprints provide “the oldest evidence of an essentially modern human-like foot anatomy, with a relatively adducted hallux, medial longitudinal arch, and medial weight transfer before push-off." We find support for only one of these three points (i.e. a relatively adducted hallux). We find no evidence to support the consistent presence of a longitudinal arch or for a medial weight transfer. Preservation is poor, and the actual topography of the contact surface is indiscernible. Even in footprints as young as 300,000–400,000 years old, such as the Terra Amata footprint (De Lumley 1966, 1967; De Lumley et al. 2011), evidence of a modern arch is lacking (Meldrum 2004a, b; 2006). Likewise, tracks from the Middle Pleistocene Roccamonfina Volcano site in Italy (Mietto et al. 2003; Avanzini et al. 2004, 2008), which falls in the same age bracket as the Terra Amata footprint, are not sufficiently well-preserved to determine if a fully modern arch is present.

Thus, given the small size and quality of the pre-Late Pleistocene footprint sample, few universally accepted conclusions can be drawn regarding the possibility of diagnostic differences between tracks made by various hominin species of early to middle *Homo*. However, the strong possibility remains that much of the hominin history of bipedalism took place on flat flexible feet in contrast to the modern human foot form of relatively recent vintage, as characterized by the ichnospecies *Hominipes modernus* (Kim et al. 2009). The scarce fossil record of the distal hallucal metatarsal, a key element in the modern longitudinal arch, clearly points to this interpretation.

Distinguishing between the tracks of *Homo sapiens* and the comparatively unknown track record of *H. neanderthalensis* on the basis of footprint morphology is evidently not reliable at present, despite a few claims to the contrary (Onac et al. 2005). It stands to reason that the robusticity of the neanderthal skeleton would produce footprints with relatively larger breadth to length ratios. However, the sample of Neanderthal footprints is too meager to test this prediction.

As noted by Lockley et al. (2008a, b), although the majority of known sites have assigned ages, in many cases the dates are uncertain, and the literature indicates frequent age date revisions, such as in the case of the Turkish and Nicaraguan sites. These authors also discussed the respective proportion of outdoor or open-air sites versus cave sites as about 65 % versus 35 %. Likewise, the proportion of sites in well-documented volcaniclastic/pyroclastic rather than non-volcaniclastic substrates is discussed by Houck et al. (2009).

The study of hominid traces raises philosophic issues that deal with the controversial question of the "exclusivity" of the human species in comparison with other vertebrates. Many scientists and philosophers argue for and against the idea that humans are fundamentally different from other species (see Guldberg 2010 for discussion of both sides of this debate). The traditional argument in favor of human exclusivity is that we have language, self-awareness, and culture, not to mention the power to change the environment in ways that other species cannot. This is not to say that other microbial, plant, and animal species have not changed environments dramatically, but in different ways. We also recognize that the exclusivity argument, with respect to tool use, language, and self-awareness, has been challenged in cases were such attributes have been reported for other species (Galef 2003, 2009; Rendell and Whitehead 2001). However, detailed discussion of these debates is beyond the scope of this paper. As the foregoing discussions emphasize, an objective look at the hominin track record indicates that the ichnologic record of *H. sapiens* is unlike that of any other species, with respect to many features including, geographic distribution, diversity of traces registered, substrates on which traces are registered, and behavioral implications of traces (e.g., Hasiotis et al. 2007; Baucon et al. 2008; Kim et al. 2008a). Again, in the context of this review of footprints and other traces created by *sapiens* and pre-*sapiens* hominins, it is clear that, even though foot and hand prints may be similar among all hominins, the diversity and behavioral implications of most other *sapiens*-produced traces is different from those of pre-*sapiens* hominins and other vertebrates both in absolute and relative terms (i.e. they are both differences of "degree and kind"). Thus, the use and creation of stone, bone and wood tools, and artifacts, while not entirely unknown in pre-*sapiens* hominins or other vertebrate species, reaches a degree of complexity indicating behaviors and cultural shifts that truly represent major evolutionary advances during the *sapiens* phase of hominin prehistory. This shift in turn heralded entirely novel and ultimately historically documented additions to the anthropologic and trace fossil records, such as ceramics, metal-work, and writing which have no pre-*sapiens* precursors (Hasiotis et al. 2007; Baucon et al. 2008; Kim et al. 2008a). In short, as hominins have evolved over the last ~4 million years, their ichnologic record has become increasingly well differentiated from that of their ancestors, a process that shows its most dramatic acceleration or shift after about 30,000 yBP.

While prior to that date multiple hominin species, a half dozen or more, coexisted across the landscape at any given time it is generally inferred that since ~30 kyBP, *H. sapiens* has been the only or "exclusive" extant hominin species However, there is a growing appreciation for the bushiness of the hominin (even hominoid) tree, as well as accumulating examples of quite recent persistence of individual branches of said tree, as evidenced in the fossil record (Meldrum 2012a, b). Is it justified to simply assume we are "the last hominin standing"? Or is there a case to be made for the possible existence of "relict hominoids" today? The discovery of the extraordinarily recent remains of *Homo floresiensis*, combined with the acknowledgement of historical anecdotes of encounters with little hairy "people" in the mountain forests of Flores should have made that point clearly enough (e.g., Forth 2012).

There is considerable ichnologic evidence for the existence of relict hominoids. By far the most extensive footprint evidence is attributed to the so-called "Bigfoot" (or sasquatch) of North America, as well as reports of similar tracks in Asia (Meldrum and Gouxing 2012), where the comparatively recent existence of the giant hominoid *Gigantopithecus* is unequivocally accepted (Meldrum 2004b, 2006, 2007b and references therein). Meldrum (2007b) formally named and diagnosed the alleged sasquatch tracks as *Anthropoidipes ameriborealis*.

While it is outside the scope of the present review to explore this intriguing but controversial issue further, it is fair to say that the possible existence of relict hominoids represents a significant dimension in hominid evolution. While most anthropologists ignore or refute the existence of relict hominoids without detailed analysis of the evidence at hand, there is nevertheless an extensive literature on the subject including a number of books by *bona fide* scientists who have taken the evidence seriously (see Lockley 1999 and Meldrum 2006 for reviews). Did *Gigantopithecus* or some similar large bipedal relict hominoid (such as a form of paranthropine) cross from Asia to North America, along with *Homo sapiens*, during the Pleistocene, along with 75 % of the mammals now considered endemic to this continent? And if so, what sort of ichnologic evidence might we expect to find? Are contemporary reports of the tracks of a giant hominid in North America's remote mountain forests, or those of a diminutive "hobbit" in the jungles of southeast Asia, any more surprising than *H. sapiens* tracks on the Moon, or 25,000 year old tracks alongside pictures of Great Auks in a deep cave in the South of France, or 20,000 year old tracks on the Tibetan plateau at the height of the Ice Age?

Finally, it is relevant to consider the extent to which *Homo sapiens*' intentional behavior is affecting the track record as a whole. While large scale megalopolis construction and landscape alteration will surely leave an ichnologic footprint that dwarfs such relatively local traces as Japanese rice paddies, it will at the same time remove or diminish the track record of many other species, by erasing or modifying substrates. This process could be considered similar, or analogous, to other natural, non-human-induced, processes such as erosion, that lead to the differential preservation or destruction of trace-bearing deposits. While such human-generated traces may vastly modify natural cycles of track registration, preservation, exhumation, and destruction, humans also *intentionally* preserve the ancient track record. This is done not just by preserving fossil footprints in museums, but in the creation of a symbolic, documentary record (a type of ichnologic record: e.g., this book) of extinct species and lost cultures that would not otherwise exist without human intentionality. Thus, *Homo sapiens* has created a wide array of highly distinctive and "exclusively" human traces.

15.10 Conclusions

We conclude that the track record has significant implications for our understanding of major events in hominin evolution and can be summarized in two categories: major and minor events. Major events include the following:

1. The advent of bipedalism, confirmed by the Laetoli site, and dated not later than ~3.6 Myr.
2. The arrival of modern humans in Australia and the New World (the Americas), confirmed by footprints and other archeologic evidence 15,000–20,000 yBP. A date of ~40,000 yBP has been suggested for colonization of Australia, but in the case of the Americas such an early date, although claimed in one case, is controversial and dubious.
3. The ichnology manifest in the creation of art (painting, sculpture, etc.,) and tools in the Late Paleolithic, especially between ~30,000 and 10,000 yBP, indicates that humans underwent a "cultural revolution" at this time. They made extensive

use of underground cave sites, leaving 2D and 3D art and artifacts and, in one case, a set of footprints indicating a game or ritual.

4. The extraordinary Holocene diversification of culturally- and technologically produced large and small scale traces culminated in the arrival of track making *Homo sapiens* on the Moon, and the generation of traces on Mars by human-manipulated machines.

A common theme of events 2–4 is geographical expansion of the *Homo sapiens*, and a steady increase in the diversity and size range (both large and small) of trace fossils produced.

Other minor but significant events recorded in the hominin track record can be listed as follows:

1. Inferred significant modifications in the morphology of the hominin foot and corresponding footprints between 3.6 million and ~50,000 yBP. The extent to which these modifications are evident in the track record is debatable, but there are two distinct polar morphologies (*Praehominipes* and *Hominipes*) now documented in the ichnologic literature.
2. Morphologic distinctions between inferred *H. sapiens* and *H. neanderthalensis* footprints could be of significance, if unequivocally established, but at present, claims of inferred differences are poorly documented.
3. The movements to, or colonization of, remote sites, such as the Tibetan Plateau and remote archipelagos, such as Jeju Island, Korea, or New Zealand, are demonstrated by footprints which are as old as, or older than, other archeologic evidence. As such, these represent significant events in the history of prehistoric human exploration, at least on the regional scale.
4. The colonization and use of caves and rock shelters as art galleries, often depicting animals, represents a significant development in human–animal interactions.
5. An extraordinary diversification and complexification of human-produced trace fossils since the Late Pleistocene and Early Holocene has allowed paleontologists to expand the academic definition of vertebrate ichnology into realms traditionally considered the province of archeology and anthropology.
6. This recent complexification of the trace fossil record by *Homo sapiens* activity has profound implications for how recent, present, and future traces will be registered as dominant components of the deep time ichnological record. In this regard humans are presently creating an ichnological revolution with significant implications for debate about the global impact and exclusivity of our species.

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Chapter 16
Recurrent Patterns and Processes: The Significance of Ichnology in Evolutionary Paleoecology

Luis A. Buatois and M. Gabriela Mángano

16.1 Introduction

Gould (1980) established a distinction between idiographic and nomothetic paleobiology. Whereas the former deals with individual evolutionary events, the latter attempts to find regularities in the history of life. This book is rooted in an idiographic approach because most chapters review a single major evolutionary event. However, after gathering such a wealth of information on specific events, it is worth to close the book with a brief attempt at exploring the nomothetic perspective by trying to find recurrent patterns and processes in evolutionary paleoecology using ichnologic data. In fact, as noted by Gould (1980) himself regarding J. J. Sepkoski's (1978, 1979, 1984) kinetic model of diversification, the approach employed here attempts to reach a balance between nomothetics and idiographics by producing a nomothetic model which is empirically grounded (see D. Sepkoski 2012 for an insightful review). Therefore, this chapter compares several evolutionary events, searching for common themes. In order to do so, we will compare organism-substrate interactions during evolutionary radiations, benthic fauna response to mass extinctions, patterns of ecospace colonization, and environmental shifts through time.

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16.2 Evolutionary Radiations

Evolutionary radiations are dramatic proliferations of taxa within clades (Erwin 1992; Simões et al. 2016). From an ichnologic perspective, three major events in marine settings are compared in this book and are, therefore, addressed in this chapter, the Cambrian Explosion (see Chap. 3), the Great Ordovician Biodiversification Event (see Chap. 4) and the Mesozoic Marine Revolution (see Chap. 9). Figures 16.1 and 16.2 summarize changes in ichnodiversity and ichnodisparity through time, respectively. Only invertebrate trace fossils were considered. Ichnogeneric occurrences were compiled on a case-by-case basis, therefore summarizing actual occurrences. However, the curves were plotted as “range-through” data, and therefore they are based on lower and upper appearances for each ichnogenus/category of architectural design and then extrapolating their presence through any intervening gap in the continuity of its record. This allows eliminating the noise generated by small-scale fluctuations in ichnodiversity and ichnodisparity that may result from the uneven number of studies for each time span. However, a disadvantage of this approach is that it is not particularly useful to detect potential drops in ichnodiversity and ichnodisparity as a result of mass extinctions (see Sect. 16.3).

Compilation of ichnogeneric diversity through geologic time indicates that the Cambrian Explosion, the Great Ordovician Biodiversification Event and the Mesozoic Marine Revolution, all evolutionary radiations established based on body fossils, are associated with increases in ichnodiversity (Fig. 16.1). This pattern shows a remarkable consistency with our knowledge derived from the analysis of diversity based on the body-fossil record. In fact, similarities between the curve of

Fig. 16.1 (continued) were compiled at the ichnogenus level because the taxonomy is more firmly established than for ichnospecies. Total number of ichnogenera is 523 ichnogenera (417 for bioturbation structures and 106 for bioerosion structures). Synonymies have been checked to make ichnotaxonomy consistent. Individual curves were constructed for continental, shallow-marine and deep-marine bioturbation ichnotaxa, and marine and continental bioerosion. In turn, separate ichnodiversity curves were compiled for all marine bioturbation ichnogenera, all marine ichnogenera (bioerosion plus bioturbation), and all continental ichnogenera (bioerosion plus bioturbation). In order to differentiate between shallow marine, deep marine and continental occurrences, original paleoenvironmental interpretations in the literature, as well as personal data, were considered. Curves plotted as “range-through” data, and therefore based on lower and upper appearances for each ichnogenus, extrapolating their presence through any intervening gap in the continuity of its record. Temporal resolution is at Epoch rank. Because there are no formal subdivisions for the Ediacaran Period, this bin has been further divided using the informal subdivision of Vendian (560–550 Ma) and Namibian (550–541 Ma) (*sensu* Jensen et al. 2006). Biogenic structures recorded in modern sediments have been included in the Holocene. Although it occurs in both hardgrounds and firmgrounds, *Gastrochaenolites* was considered under bioerosion. The record of mirobioerosion ichnotaxa extends further into the Precambrian with *Granulohyalichnus* and *Tubulohyalichnus* ranging into 3.5 Ga (Furnes et al. 2004, 2007; Banerjee et al. 2006, 2007; McLoughlin et al. 2009), representing in fact the oldest trace fossils. Because these two ichnogenera are produced by microbial activity and our analysis is centered on invertebrates, they have not been considered in the discussion presented in the text

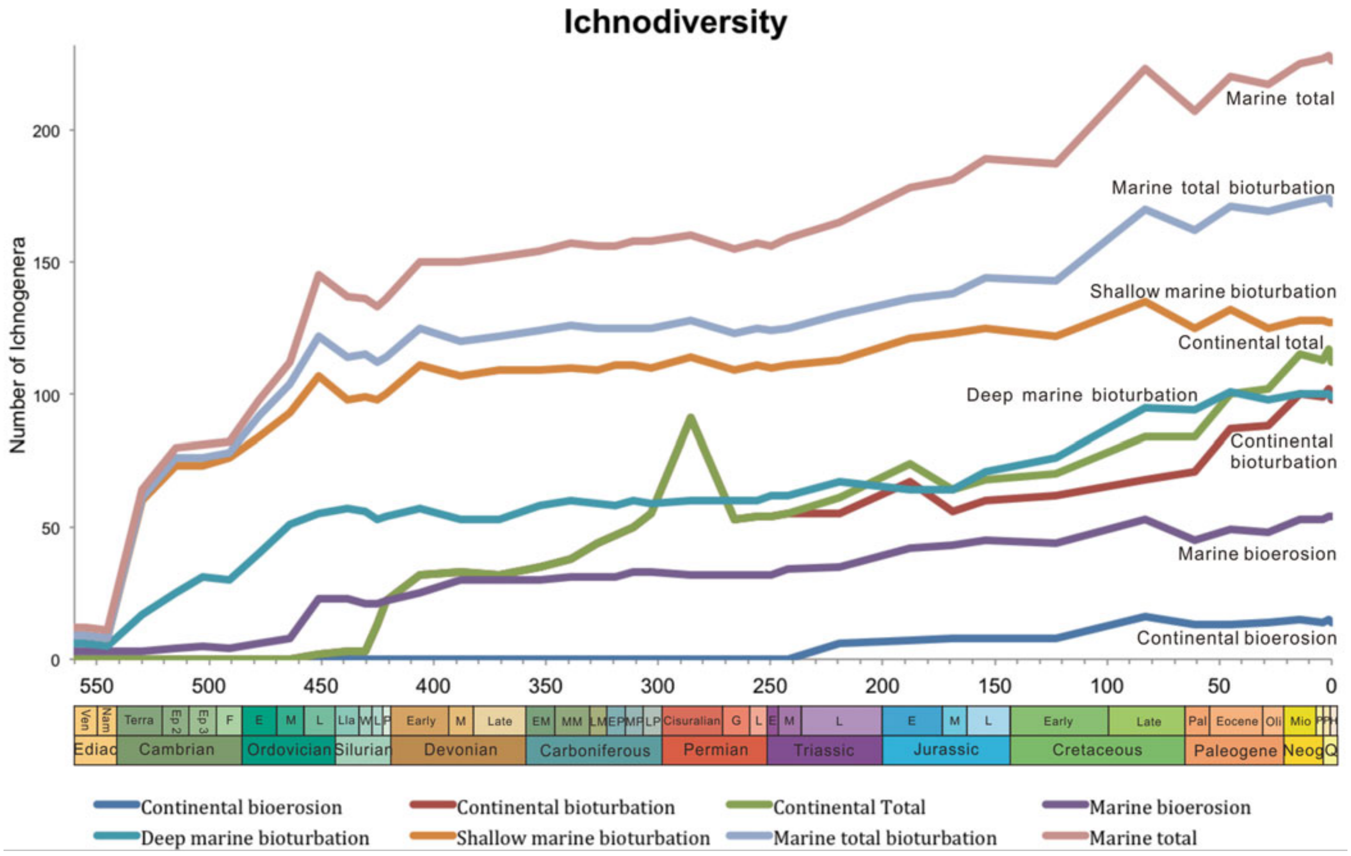
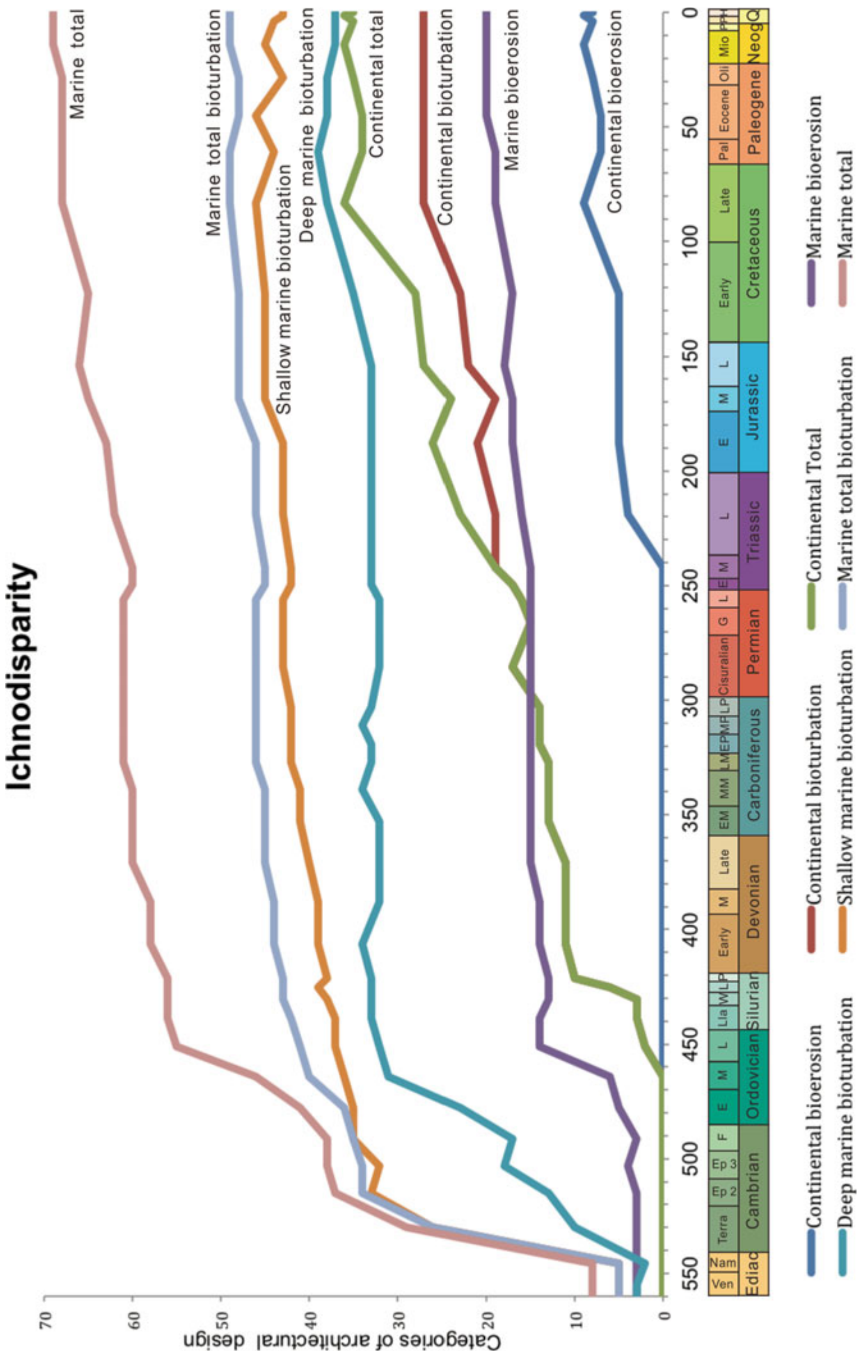


Fig. 16.1 Ichnodiversity changes through geologic time. Compilation based on literature and personal data. The main literature sources used to compile the ichnogeneric list were the Treatise volume on trace fossils (Häntzschel 1975) and the more recent revision by Knaust (2012). In addition, we have checked each ichnogenus by consulting the original ichnologic literature and pertinent reviews in order to revise its validity and potential synonyms. The ichnodiversity curves


Ichnodisparity
Categories of architectural design
0
10
20
30
40
50
60
70
550
500
450
400
350
300
250
200
150
100
50
0
Marine total
Marine total bioturbation
Shallow marine bioturbation
Deep marine bioturbation
Continental total
Continental bioturbation
Marine bioerosion
Continental bioerosion
Ven
Nam
Ediac
Terra
Ep 2
Ep 3
F
Cambrian
E
M
L
Ordovician
Lla
W
L
P
Silurian
Early
M
Late
Devonian
EM
MM
LM
EP
MP
LP
Carboniferous
Cisuralian
G
L
Permian
E
M
L
Triassic
E
M
L
Jurassic
Early
Late
Cretaceous
Pal
Eocene
Oli
Paleogene
Mio
P
P
H
Neog
Q
Continental bioerosion
Deep marine bioturbation
Continental bioturbation
Shallow marine bioturbation
Continental Total
Marine total bioturbation
Marine bioerosion
Marine total

marine ichnodiversity and that of marine animal genera produced by Sepkoski (1997) are striking with regards to the Cambrian Explosion and the Great Ordovician Biodiversification Event (Buatois et al. 2016a). A 433 % increase in ichnodiversity took place in marine environments during the Terraneuvian (12 and 64 ichnogenera in the Ediacaran and Terraneuvian, respectively), whereas a 77 % occurred as a result of the Great Ordovician Biodiversification Event (82 ichnogenera in the Furongian and 145 ichnogenera by the Late Ordovician). Whereas the Cambrian Explosion is essentially restricted to bioturbation structures, the Great Ordovician Biodiversification Event is expressed by bioerosion structures as well, an event that has been referred to as the Ordovician bioerosion revolution (Wilson and Palmer 2006). Ichnogeneric compilations show that the explosion in bioerosion took place approximately 80 my after the Cambrian Explosion in bioturbation (Buatois et al. 2016a). The explosive diversification of the early Cambrian supports an exponential model for the early phases of diversification as advocated originally by Sepkoski (1978) based on shelly fossils. Despite these similarities, two main differences are apparent. First, trace-fossil data indicate that the rapid diversification took place in the early Cambrian, rather than in the late early Cambrian as indicated by shelly fossils, suggesting that the Fortunian may be regarded as part of the phylogenetic fuse (Mángano and Buatois 2014; see Chap. 3). Second, marine animal genera show minor diversity fluctuations during the middle to late Cambrian, but ichnodiversity reached a plateau that spanned from the middle Cambrian to the onset of the Great Ordovician Biodiversification Event (Buatois et al. 2016a).

The ichnodiversity curve for marine trace fossils shows another, but more modest, increase in the Early Jurassic (8 %; 165 and 178 ichnogenera in the Late Triassic and Early Jurassic, respectively) and a more important one in the Late Cretaceous (19 %; 187 and 223 ichnogenera in the Early and Late Cretaceous, respectively) (Fig. 16.1). A more limited, but constant, increase took place between the Early Jurassic and Early Cretaceous. These changes in ichnodiversity are expressed by both bioerosion and bioturbation structures. This increase is undoubtedly a reflection of the Mesozoic Marine Revolution. Comparing ichnodiversity levels between the Late Triassic (164 ichnogenera) and the Late Cretaceous (223 ichnogenera) reveals a total 35 % ichnodiversity increase that is attributed to this evolutionary radiation. Ichnologic data indicate that the Early Jurassic experienced a change in ichnotaxonomic composition and the complexity of infaunal tiering, which is consistent with the timing of the Mesozoic Marine Revolution as revealed by our compilations (see Chap. 9).

Fig. 16.2 Ichnodisparity changes through geologic time. Compilation based on literature and personal data. Total number of categories of architectural designs is 79 (58 for bioturbation structures and 21 for bioerosion structures). Curves were constructed for ichnodisparity following the same environmental subdivision used for ichnodiversity. Curves plotted as "range-through" data, and therefore based on lower and upper appearances for each category of architectural design, extrapolating their presence through any intervening gap in the continuity of its record. Ichnodisparity was compiled following the approach of Buatois and Mángano (2013; see also Chap. 1) and categories of architectural designs summarized by Buatois et al. (2016b). Table 16.1 summarizes the different categories and the ichnogenera included. For further information, see caption of Fig. 16.1

Table 16.1 Categories of architectural designs and their ichnotaxa in alphabetical order (after Buatois et al. 2016b)

Architectural designs	Ichnogenera
1-Simple horizontal trails	*Archaeonassa, Circulichnis, Cochlichnus, Gordia, Helminthoidichnites, Helminthopsis, Herpystezoum, Mermia, Talitrichnus*
2-Trilobate flattened trails	*Curvolithus, Trisulcus*
3-Chevronate trails	*Protovirgularia, Rhadhostium*
4-Trails with undulating transverse bars and furrows	*Climactichnites, Steinsfjordichnus*
5-Bilobate trails and paired grooves	*Carpatichnis, Cruziana, Davichnia, Didymaulichnus, Diplopodichnus, Taphrhelminthoides, Tumblagoodichnus*
6-Trackways and scratch imprints	*Acanthichnus, Acripes, Allocotichnus, Angulichnus, Arachnomorphichnus, Arcichnus, Asaphoidichnus, Biformites, Bifurcatichnus, Bifurculapes, Climacodichnus, Coenobichnus, Conopsoides, Copeza, Danstairia, Dendroidichnites, Dimorphichnus, Diplichnites, Etterwindichnus, Euproopichnus, Foersterichnus, Glasbachichnium, Glaciichnium, Hamipes, Harpepus, Harpichnus, Heftebergichnus, Heteropodichnus, Heterotripodichnus, Hexapodichnus, Homopodichnus, Irichnus, Ixalichnus, Kalnaichnus, Keircalia, Kivanichnus, Konbergichnium, Kouphichnium, Lineatichnus, Lithographus, Lusatichnium, Maculichna, Megapodichnus, Merostomichnites, Mirandaichnium, Mitchellichnus, Monomorphichnus, Multipodichnus, Octopodichnus, Oklahomaichnus, Oniscoidichnus, Orchesteropus, Paleohelcura, Palmichnium, Parahamipes, Pentapodichnus, Petalichnus, Pirandikus, Protichnites, Pterichnus, Punctichnium, Siskemia, Stiallia, Stiaria, Striatichnium, Tambia, Tarichnus, Tarsichnus, Taslerella, Tasmanadia, Telsonichnus, Teratichnus, Terricolichnus, Tortilichnus, Trachomatichnus, Umfolozia, Vadichnites, Warvichnium*
7-Bilaterally symmetrical short, scratched imprints	*Avolatichnium, Arborichnus, Chagrinichnites, Cheliceratichnus, Gluckstadella, Huilmuichnus, Kingella, Orbiculichnus, Pollichianum, Ramosichnus, Rotterodichnium, Solusichnium, Surculichnus, Tonganoxichnus, Tripartichnus*

(continued)

Table 16.1 (continued)

8-Bilaterally symmetrical short, scratched impressions and burrows	*Aglaspidichnus, Alph, Cardioichnus, Cheiichnus, Craticulichnum, Crescentichnus, Faciemichnus, Limulicubichnus, Raaschichnus, Rusophycus, Selenichnites, Svalbardichnus*
9-Fan-shaped to radiating scratched imprints	*Kimberichnus, Radichnus*
10-Passively filled horizontal burrows	*Didymaulyponomos, Palaeophycus*
11-Simple actively filled (massive) horizontal to oblique structures	*Furculosus, Macaronichnus, Nenoxites, Planolites, Sericichnus, Torrowangea,*
12-Simple actively filled (meniscate) horizontal to oblique structures	*Ancorichnus, Beaconites, Compaginatichnus, Entradichnus, Imponoglyphus, Jamesonichnites, Scoyenia, Squamichnus, Taenidium*
13-Simple, actively filled (pelletoidal) horizontal burrows	*Alcyonidiopsis, Castrichnus, Edaphichnium, Quebecichnus, Sphaerapus, Tubotomaculum, Tubularina*
14-Complex actively filled horizontal structures	*Bichordites, Bolonia, Nereites, Paramargaritichnus, Parataenidium, Psammichnites, Rutichnus, Scolecocoprus, Scolicia, Tylichnus*
15-Armored burrows	*Crininicaminus, Diopatrichnus, Ereipichnus, Ichnospongiella, Lepidenteron, Nummipera*
16-Horizontal branching burrow systems	*Agrichnium, Arachnostega, Korymbichnus, Labyrintichnus, Multina, Paracanthorhaphe, Pilichnus, Saportia, Shanwangichnus, Taotieichnus, Vagorichnus, Virgaichnus*
17-Horizontal burrows with horizontal to vertical branches	*Arthrophycus, Caugichnus, Ctenopholeus, Intexalvichnus, Microspherichnus, Phycodes, Phymatoderma, Polykampton, Saerichnites, Streptichnus, Treptichnus, Tuberculichnus, Vitichnus*
18-Surface-coverage branching burrows	*Oldhamia*
19-Radial to rosetted structures	*Arenituba, Asterichnites, Asterichnus, Bifasciculus, Capodistria, Cladichnus, Clematischnia, Cycloichnus, Dactyloidites, Dactylophycus, Guanshanichnus, Gyrophyllites, Haentzschelinia, Hartsellea, Heliochone, Monocraterion, Parahaentzschelinia, Phoebichnus, Radiichnus, Rotamedusa, Scotolithus, Sphaerichnus, Stelloglyphus, Taxichnites, Volkichnium*
20-Sheaf burrow of thickly lined tubes	*Bornichnus, Schaubcylindrichnus*
21-Horizontal burrows with serial chambers	*Halimedides, Omanichnus, Sidichnus, Solanichnium, Strobilorhaphe*
22-Horizontal burrows with simple vertically oriented spreiten	*Halopoa, Teichichnus, Trichophycus*
23-Horizontal spiral burrows	*Multilaqueichnus, Pramollichnus, Spiralites, Spirodesmos, Spirophycus*
24-Horizontal helicoidal burrows	*Augerinoichnus, Avetoichnus, Helicodromites*

(continued)

Table 16.1 (continued)

25-Burrows with complex vertically oriented spreiten	*Caridolites, Daedalus, Dictyodora, Euflabella, Gyrochorte, Heimdallia, Paradictyodora, Stellavelum, Syringomorpha, Tursia*
26-Burrows with horizontal spreiten	*Criophycus, Falcichnites, Fuersichnus, Hydrancylus, Lamellaeichnus, Lobichnus, Lophoctenium, Multilamella, Phycosiphon, Rhizocorallium*
27-Burrows with helicoidal spreiten	*Echinospira, Spirophyton, Zoophycos*
28-Basal axial tubes with feather-like and spreite-like structures	*Hillichnus*
29-Mound-shaped structures	*Amanitichnus, Chomatichnus, Trusheimichnus*
30-Isolated and serial oval to almond-shaped burrows	*Calceoformites, Lockeia, Oravaichnium, Ptychoplasma*
31-Pentameral-shaped imprints and burrows	*Asteriacites, Pentichnus*
32-Oval-shaped imprints	*Astacimorphichnus, Corpusculichnus, Epibaion, Ichnocumulus, Musculopodus*
33-Dumbbell- and arrow-shaped burrows	*Arthraria, Bifungites, Monofungites*
34-Vertical plug-shaped burrows	*Amphorichnus, Astropolichnus, Bergaueria, Conichnus, Conostichus, Lithoplaision, Mammillichnis, Metaichna, Solicyclus*
35-Vertical unbranched burrows	*Altichnus, Bathichnus, Caletichnus, Cylindricum, Digitichnus, Felderichnus, Funalichnus, Guerraichnus, Laevicyclus, Lingulichnus, Lunatubichnus, Oikobesalon, Pustulichnus, Scalichnus, Siphonichnus, Skolithos*
36-Vertical single U- and Y-shaped burrows	*Arenicolites, Balanoglossites, Catenichnus, Diplocraterion, Glyphichnus, Liholites, Loloichnus, Paratisoa, Parmaichnus, Pholeus, Polarichnus, Psilonichnus, Solemyatuba, Tisoa*
37-Vertical multiple U- and Y-shaped burrows	*Kauriichnus, Lanicoidichna, Polykladichnus*
38-Vertical simple J-shaped burrows	*Artichnus, Keilorites, Naviculichnium*
39-Burrows with vertical tubes and stacked discs	*Tasselia*
40-Vertical helicoidal burrows	*Gyrolithes, Lapispira*
41-Burrows with shaft or bunch with downwards radiating probes	*Chondrites, Fascifodina, Lennea, Pragichnus, Saronichnus, Skolichnus, Trichichnus*
42-Vertical concentrically filled burrows	*Cylindrichnus, Rosselia*
43-Horizontal, branched concentrically filled burrows	*Asterosoma, Patagonichnus*
44-Spiral graphoglyptids	*Spirorhaphe*
45-Guided meandering graphoglyptids	*Cosmorhaphe, Helminthorhaphe, Spirocosmorhaphe*
46-Uniramous meandering graphoglyptids	*Belocosmorhaphe, Belorhaphe, Dendrotichnium, Helicolithus, Helicorhaphe, Punctorhaphe, Ubinia, Urohelminthoida*

(continued)

Table 16.1 (continued)

47-Radial graphoglyptids	*Arabesca, Chondrorhaphe, Dendrorhaphe, Estrellichnus, Fascisichnium, Glockerichnus, Lorenzinia, Persichnus, Tuapseichnium, Yakutatia*
48-Biramous meandering graphoglyptids	*Desmograpton, Oscillorhaphe, Paleomeandron*
49-Regular to irregular network graphoglyptids	*Acanthorhaphe, Megagrapton, Paleodictyon, Protopaleodictyon*
50-Maze and boxwork burrows	*Ardelia, Ophiomorpha, Sinusichnus, Spongeliomorpha, Thalassinoides*
51-Vertical to oblique simple ornamented burrows	*Capayanichnus, Liticuniculatus, Lunulichnus, Spirographites*
52-Simple to complex burrows with terminal chambers	*Camborygma, Egbellichnus, Katbergia, Macanopsis, Platicytes*
53-Chambers surrounded by burrows	*Maiakarichnus, Dagnichnus*
54-Isolated, clustered or interconnected cells	*Cellicalichnus, Celliforma, Corimbatichnus, Elipsoideichnus, Palmiraichnus, Rosellichnus, Uruguay*
55-Chambers with discrete thick linings	*Chubutolithes, Coprinisphaera, Eatonichnus, Feoichnus, Monesichnus, Quirogaichnus, Rebuffoichnus, Teisseirei*
56-Excavated chambers with thin linings undetachable from rock matrix	*Fictovichnus, Pallichnus, Scaphichnium*
57-Interconnected chambers and boxworks	*Attaichnus, Barberichnus, Coatonichnus, Daimoniobarax, Fleaglellius, Krausichnus, Masrichnus, Microfavichnus, Parowanichnus, Socialites, Syntermesichnus, Tacuruichnus, Termitichnus, Vondrichnus*
58-Holes, pits and galleries in walls and fillings	*Lazaichnus, Tombownichnus*
59-Cylindrical vertical to oblique borings	*Carporichnus, Flagrichnus, Linkichnus, Pecinolites, Stipitichnus, Trypanites, Tubulohyalichnus*
60-Borings with elliptical to sub-rectangular cross sections	*Osprioneides, Xylonichnus*
61-Winding borings	*Lapispecus, Maeandropolydora*
62-U-shaped borings	*Canaliparva, Caulostrepsis, Diorygma, Pseudopolydorites, Sertaterebrites*
63- Circular holes and pit-shaped borings	*Circolites, Curvichnus, Dipatulichnus, Lamniporichnus, Oichnus, Planavolites, Polydorichnus, Stellatichnus, Tremichnus*
64-Globular to spherical borings	*Granulohyalichnus, Planobola*
65-Pouch borings	*Asthenopodichnium, Aurimorpha, Bascomella, Cuenulites, Cubiculum, Petroxestes, Rogerella, Umbichnus*
66-Clavate-shaped borings	*Cavernula, Cylindricavus, Gastrochaenolites, Palaeosabella, Phrixichnus, Ramosulcichnus, Sanctum, Teredolites, Xylokrypta*

(continued)

Table 16.1 (continued)

67-Fracture-shaped bioerosion traces	*Belichnus, Bicrescomanducator, Caedichnus, Mandibulichnus*
68-Branched tubular borings	*Calciroda, Clionoides, Cunctichnus, Dekosichnus, Ichnoreticulina, Paleobuprestis, Paleoipidus, Paleoscolytus, Runia, Scolecia, Talpina*
69-Non-camerate network borings	*Anobichnium, Filuroda, Orthogonum, Rodocanalis*
70-Camerate network borings	*Feldmannia, Haimeina, Ichnogutta, Iramena, Pennatichnus, Pinaceocladichnus, Rhopalia, Saccomorpha*
71-Non-camerate boxwork borings	*Chaetophorites, Cycalichnus, Eurygonum*
72-Camerate boxwork borings	*Entobia, Unellichnus*
73-Spiral borings	*Helicotaphrichnus, Spirichnus*
74-Radial borings	*Fascichnus, Polyactina*
75-Dendritic and rosetted borings	*Abeliella, Calcideletrix, Clionolithes, Dendrina, Dictyoporus, Megascolytinus, Nododendrina, Pyrodendrina, Scolytolarvariumichnus*
76-Single circular to tear-shaped attachment bioerosion traces	*Anellusichnus, Centrichnus, Kardopomorphos, Lacrimichnus, Ophthalmichnus*
77-Multiple attachment bioerosion traces	*Finichnus, Flosculichnus, Podichnus*
78-Elongate or branched attachment bioerosion traces	*Camarichnus, Canalichnus, Renichnus, Stellichnus, Sulcichnus*
79-Groove bioerosion traces	*Ericichnus, Gnathichnus, Osteocallis, Radulichnus*

Analysis of ichnodiversity changes from the Ediacaran to the Holocene supports the three-phase kinetic model of Sepkoski (1984) based on analysis of marine body fossils. According to this model, the three main evolutionary radiations in the marine biosphere display an early exponential growth followed by subsequent slowing of growth. In the case of the Cambrian and Ordovician radiations there was very rapid growth of diversity in their initial stages until a plateau was reached later, whereas diversity rose slowly during the onset of the Mesozoic Marine Revolution and continues to do so. Controversies regarding this model have essentially revolved around potential geologic and paleontologic biases, such as increased exposure of sedimentary rocks, uneven number of studies per interval, and increased ease of fossil extraction (Raup 1976; Peters and Foote 2001; Alroy et al. 2008; Alroy 2010). For our interest here, the most serious controversy is the one on the diversity levels attained in the post-Paleozoic world. It has been argued that standardized curves show a final diversity only slightly higher than the Paleozoic maximum (e.g., Alroy et al. 2008; Alroy 2010, 2014) in sharp contrast with the much higher diversity levels shown by Sepkoski's curves (see also Bambach et al. 2004). However, new standardized curves show that Cenozoic diversity doubles Paleozoic values, supporting sustained marine diversification during the Mesozoic–Cenozoic (Bush and Bambach 2015), a pattern more consistent with the original Sepkoski's curves.

In particular, one of the potential biases affecting estimation of post-Paleozoic diversity levels is the so-called Pull of the Recent (Raup 1979). This effect operates in two ways. First, there is an increase in the volume of Cenozoic (and to a lesser extent Mesozoic) outcrops. Second, because the modern is much better sampled that the rest of the fossil record, taxa that occur in just one stratigraphic interval and have a modern representative will be plotted as occurring through the whole interval, resulting in an inflation of diversity levels in post-Paleozoic strata. Interestingly, the trace-fossil record is not biased in the same way. Certainly, neoichnologic studies are instrumental in recognizing some biogenic structures in the modern, helping to extend the stratigraphic range of some ichnotaxa. However, at the same time, modern counterparts of some trace fossils are lacking not because these behaviors have gone extinct, but because identification of modern traces is typically much more difficult than with fossil material, particularly in the case of bioturbation structures (Bromley 1996; Buatois and Mángano 2011a). Trace fossils tend to be enhanced by diagenetic processes that assist in their recognition (Magwood 1992) and many biogenic structures are cumulative structures, which consist of both abandoned and active components (Bromley and Frey 1974); casts of modern representatives of cumulative structures would only reflect the morphology of the open components occupied by the producer, resulting in a simpler morphology than the actual overall architecture, making identification of the ichnotaxon virtually impossible (Frey 1975; Frey and Seilacher 1980; Magwood 1992). The practical result of this would be an artificial drop in ichnodiversity in the modern. This more complex pattern exhibited by the trace-fossil record is referred herein as the Push and Pull of the Recent. To avoid this problem, we have plotted in the final curves together the Holocene and the modern.

Similar to Sepkoski's curves, ichnologic data show a phase of exponential growth in ichnodiversity followed by an equilibrium stage during the Cambrian Explosion and the Great Ordovician Biodiversification Event. Identical to body fossils, the Mesozoic Marine Revolution is associated with a slower increase in ichnodiversity. The overall coincidence between Sepkoski's curves and those presented in this chapter indicates similar diversity trajectories for animal diversity and their behaviors. However, in the case of post-Paleozoic faunas, whereas the curve for marine animals does not show any evidence of a plateau, ichnologic information seems to suggest that a plateau may have been reached for both marine bioturbation and bioerosion.

In contrast, trends in ichnodisparity reveal a more complicated picture (Fig. 16.2). Whereas the Cambrian Explosion is associated with an increase in both ichnodisparity and ichnodiversity (Mángano and Buatois 2014; see Chap. 3), the Great Ordovician Biodiversification Event and the Mesozoic Marine Revolution display different trends. A 263 % increase in ichnodisparity took place during the Terraneuvian as a result of the Cambrian Explosion (8 and 29 categories of architectural designs in the Ediacaran and Terraneuvian, respectively), but only a 45 % is associated with the Great Ordovician Biodiversification Event (38 categories of architectural design in the Furongian and 55 by the Late Ordovician). In addition, if bioturbation and bioerosion structures are considered separately, it is clear that bioerosion is responsible for the overall increase (17 % increase in ichnodisparity for bioturbation structures and 367 % for bioerosion structures). Whereas the Cambrian Explosion was the main event in the Phanerozoic for large-scale innovations in animal-sediment interactions, it is the Great Ordovician Biodiversification Event that played this role regarding bioerosion (Buatois et al. 2016a). If bioturbation structures are considered separately for shallow- and deep-marine environments, it is apparent that ichnodisparity in shallow-marine settings remained very close to Cambrian levels, whereas an increase took place in the deep sea (88 %; 17 categories of architectural design in the Furongian and 32 by the Late Ordovician). In the same fashion that broad innovations in bioerosion lagged behind those in bioturbation, the establishment of the main types of animal-sediment interactions in the deep sea took place later than in shallow-marine settings, as originally envisaged in models of deep-sea colonization (e.g., Uchman 2004). Because approximately half of the architectural categories that typify Ordovician deep-sea ichnofaunas first occurred in shallow-marine settings during the Cambrian, the overall impact of Ordovician deep-sea categories in global marine ichnodisparity levels is limited (Buatois et al. 2016a).

In turn, although an increase in ichnodisparity is apparent as a result of the Mesozoic Marine Revolution, distinguishing between bioturbation and bioerosion structures shows that the increase is restricted to the latter (19 % increase between the Late Triassic and the Late Cretaceous). Ichnodisparity of bioturbation structures in both shallow- and deep-marine settings does not display any significant increase in connection to the Mesozoic Marine Revolution.

A main conclusion of our analysis of secular changes in ichnodiversity and ichnodisparity during the Cambrian Explosion, the Great Ordovician Biodiversification Event and the Mesozoic Marine Revolution is that, although increases in ichnodiversity are invariably linked to evolutionary radiations, these are necessary but not sufficient conditions for ichnodisparity increases. In order to further explore the links between ichnodiversity and ichnodisparity and the possible underlying causes for increases in the latter, it is now useful to analyze the results of our compilations regarding continental environments.

Ichnodiversity compilations for continental environments show a more protracted process of colonization through the whole Phanerozoic as revealed by bioturbation structures (Fig. 16.1). Although the process of invasion of the continents seems to have been slow and gradual, an initial rapid increase took place by the Silurian-Devonian transition (see Chap. 6), with an impressive 967 % increase in ichnodiversity between the Wenlock and the Early Devonian (3 and 32 ichnogenera in the Wenlock and Early Devonian, respectively). As in the case of the Cambrian Explosion, this rapid diversification in continental settings is consistent with Sepkoski's (1978) exponential model for early diversification. Subsequent to that increase a plateau until the Early Mississippian is apparent. However, this may be in part simply an artifact due to the scarcity of continental outcrops of Late Devonian age (see Chap. 6). Subsequently, a slow but constant increase in ichnodiversity took place until the early Permian (Cisuralian), which displays an unusual peak (65 %, 91 ichnogenera). This peak has been noted in earlier studies and deemed controversial (Buatois et al. 1998).

It reflects the presence of a wide variety of arthropod trackways in overbank deposits, which at least in part results from a marked tendency towards oversplitting in trackway taxonomy. In particular, many arthropod are only known from the Permian of Germany (e.g., Holub and Kozur 1981; Walter 1983); many of these are considered doubtful (see Chap. 6). After a plateau that lasted the whole Triassic, another more modest peak is apparent in the Early Jurassic. This is, at least in part, a monographic effect (Raup 1976) resulting from the high number of new arthropod trackway genera introduced by Hitchcock (1858, 1865) based on his analysis of continental trace fossils from the Connecticut Valley. Many of these have never been recorded elsewhere and are now regarded as doubtful (Rainforth 2005), so they have been omitted in our compilation. However, even leaving aside these doubtful ichnotaxa and only retaining those regarded as valid, the Early Jurassic ichnodiversity peak still persists (21 %; 61 and 74 ichnogenera in the Late Triassic and Early Jurassic, respectively). Since the Middle Jurassic onwards, ichnodiversity experienced a relatively constant increase.

Bioerosion in continental environments experienced a much later development than bioturbation. Although wood borings were mentioned for the early Permian (von Kušta 1880), the earliest convincing evidence of bioerosion in continental environments is from the Late Triassic, with the recording of six ichnotaxa representing wood bioerosion (Tapanila and Roberts 2012). Notably, this record predates the earliest record of marine bioerosion in wood, which is Early Jurassic (Villegas-Martín et al. 2012). In turn, the earliest record of bioerosion in bone is from the Early Jurassic (undetermined ichnotaxon), with the ichnogenus *Cubiculum* being recorded for the first time in the Late Jurassic (Xing et al. 2015). This was followed by a plateau until the Late Cretaceous with the addition of ten new ichnogenera. Since then, ichnodiversity of bioerosion structures reached a plateau that continues until the Holocene.

After the initial rapid increase in ichnodiversity of bioturbation structures by the Silurian-Devonian transition, colonization of freshwater settings was apparently quite gradual. It has been suggested that this slow pace may have resulted from the need to develop innovative styles of reproduction and dispersal, as well as complex osmoregulatory systems (Miller and Labandeira 2002). The fact that no plateau indicating an equilibrium stage in diversification is apparent for bioturbation structures may suggest that the invasion of terrestrial environments is a still ongoing process. This is consistent with the fact that the utilization of freshwater infaunal ecospace seems to have been less complete than in their marine counterparts (Miller and Labandeira 2002). Continental bioerosion ichnogenera seem to have reached a plateau by the end of the Mesozoic, but their ichnotaxonomy is still in its infancy and it is not unexpected that this trend will change with further studies.

As with ichnodiversity, ichnodisparity in continental environments reflects the process of protracted colonization (Fig. 16.2). Ichnodisparity curves of bioturbation structures reveal a rapid increase with the onset of widespread colonization by the Silurian-Devonian transition (see Chap. 6), with a 267 % increase in ichnodisparity between the Wenlock and the Early Devonian (3 and 11 categories of architectural designs in the Wenlock and Early Devonian, respectively). This was followed by a very slow increase until the Late Cretaceous that records a hike (29 %; 28 categories of architectural design in the Early Cretaceous and 36 in the Late Cretaceous), albeit limited, reaching ichnodisparity levels that persist until the Recent. The Late Cretaceous ichnodisparity peak is also expressed by bioerosion structures. However, it should be noted that all categories of architectural designs in freshwater subaqueous environments and transitional terrestrial to subaqueous settings originated in marine environments and only subsequently occurred in continental settings. In contrast, there are six categories that are exclusive of terrestrial settings (see Chap. 11). In other words, the main innovations required to invade freshwater were already present in the marine realm, but the only true behavioral innovations in continental environments were those required to colonize subaerially exposed settings. These are mostly the architectural designs developed by insects nesting in paleosols (see Chap. 13).

To summarize, our analysis shows that the key factor in building up ichnodisparity is not the existence of an evolutionary radiation *per se*, but the colonization of empty ecospace. The Cambrian Explosion records the colonization of empty ecospace and, therefore, displayed an increase in both ichnodisparity and ichnodiversity. A similar situation is expressed by bioerosion during the Great Ordovician Biodiversification Event in connection with the colonization of hard substrates. A third increase in ichnodisparity is revealed by the colonization of paleosols which experienced dramatic evolutionary innovations by the end of the Mesozoic. Finally, the cradle of evolutionary innovations is in shallow-marine settings (see Sect. 16.5). This is revealed by the appearance in shallow seas of all the architectural designs that subsequently expanded into freshwater and a substantial number of those that later bloomed in the deep sea. In almost all these cases, the ichnodisparity increase is followed by a subsequent further increase in ichnodiversity, as it is illustrated, by the diversification of insect nesting structures during the Cenozoic, following the establishment of the basic architectural designs in the Late Cretaceous. This pattern supports analysis based on body fossils that indicates a "first disparity, then diversity" scenario (Foote 1993, 1997; Erwin 2007; see Chap. 6).

Finally, the limitations of ichnodiversity analysis to unravel evolutionary trends need to be addressed (see Buatois and Mángano 2013 for a detailed analysis). As stated many times, the fact that ichnodiversity cannot be equated with the actual diversity of organisms represents a cautionary note (Ekdale 1985). Behavioral convergence resulting in different organisms being able to produce the same ichnotaxon may mask evolutionary trends. The opposite case, the one of several ichnotaxa resulting from the work of a single producer, also undoubtedly introduced a bias in ichnodiversity analysis through geologic time. Because of this, the different chapters exploring the ichnologic blueprints of evolutionary radiations use a plurality of conceptual and methodological tools rather than being restricted to an analysis of the number of ichnogenera or architectural designs. For example, it is clear that burrows produced by decapod crustaceans represent one of the most, if not the most, archetypal biogenic structures of the Mesozoic Marine Revolution. However, because some of its most characteristic structures, namely burrow systems included in *Thalassinoides*, are produced not only by decapod crustaceans, but by other organisms with a stratigraphic range that extends well before the Mesozoic, the importance of crustacean burrows remains undetected if only ichnodiversity is considered. In other words, the long stratigraphic range of *Thalassinoides* is misleading with respect to its key role during the Mesozoic Marine Revolution. A clearer picture emerges when, for example, abundance is considered as well (Carmona et al. 2004; see Chap. 9).

Also, in part as a result of behavioral convergence, ichnogeneric extinction rates are remarkably low. It has been noted that increases in diversity within clades may be produced from a drop in extinction rate rather that diversification *per se*, resulting in the so-called “pseudoradiations” (Simões et al. 2016). In the case of trace-fossil data, extinction rates can be regarded not only as low but also as constant, the latter at least since the Ordovician. Because of the impossibility of equating biological diversity and ichnodiversity, the trace-fossil expression of evolutionary radiations is not primarily of a phylogenetic nature, but rather reflects behavioral innovations.

Other problems are evident while dealing with ichnodiversity changes in specific environments through the Phanerozoic. Because there is a trend to increased infaunalization through time, the colonization of deeper tiers is conducive to obliteration of the more shallowly emplaced structures, which in many cases represent a substantial contribution to ichnodiversity. As a result, a decrease in ichnodiversity through time rather than an increase, has been noted in the case of tidal flats (Mángano et al. 2002; Mángano and Buatois 2015) and lakes (see Chap. 11). These cases underscore the importance of careful evaluation of taphonomic overprints.

Also, using ichnodiversity at ichnogeneric level may preclude detection of other patterns. Ichnospecies reflect minor behavioral variations and, therefore, they may help to detect more subtle trends in behavioral innovations (see Chap. 3). A large number of ichnogenera that have their first occurrence early in the Paleozoic seem to have displayed an increase in the number of ichnospecies through the Phanerozoic (see Chaps. 3 and 9). Exploring patterns of ichnospecies distribution through time is a promising line of research, although this would imply in-depth critical reevaluation of trace-fossil taxonomy at this rank, something beyond the scope of the present study.

Regardless of potential shortcomings, our review indicates that ichnologic information (including both ichnodiversity and ichnodisparity) is highly useful as an independent line of evidence to understand paleobiologic trends through geologic time.

16.3 Benthic Fauna Response to Mass Extinctions

Ichnologic information typically reveals a set of common responses to the three mass extinctions analyzed in this book, the end-Permian (see Chap. 7), the end-Triassic (see Chap. 8), and the end-Cretaceous (see Chap. 12). Most of these extinction events are characterized by a reduction in ichnodiversity, decrease in degree of bioturbation, reduction of bioturbation depth, size reduction, dominance of simple trace fossils in post-extinction strata, preferential survival of ichnotaxa produced by deposit feeders, and selective extinction in shallow-marine ecosystems. How pronounced were these effects seems to depend on the severity of the mass extinction event, with the end-Permian mass extinction clearly showing the most severe impact from an ichnologic standpoint, showing consistency with body-fossil data. In turn, this is reflected in the pattern of recovery after the extinction, with longer recovery times involved in the end-Permian mass extinction in comparison with the end-Cretaceous event. Ichnologic information on the other two major events, the end-Ordovician and late Devonian extinctions is patchy, with only a few studies available (McCann 1990; Herringshaw and Davies 2008; Buatois et al. 2013) and, therefore, any generalization remains premature.

Although these extinctions are associated to a decrease in ichnodiversity, actual extinction of invertebrate ichnotaxa is quite rare. On the contrary, ichnotaxa that disappeared after the mass extinctions for the most part reappeared during the recovery time, representing Lazarus ichnotaxa (Gibert 2003). As noted previously, trace-fossil extinction rates tend to be very low, a fact that, at least in the case of relatively simple behaviors, results from behavioral convergence. Some ichnotaxa (e.g., the undermat miner *Oldhamia*, the large trail *Climactichnites*), however, seem to reflect behaviors that have apparently disappeared by the end of the Cambrian, together with their producers.

Because the curves illustrated in Figs. 16.1 and 16.2 have been compiled as range through data, they are of limited use to detect changes in ichnodiversity as a result of mass extinctions. For example, whereas a significant drop in ichnodiversity is associated with the end-Permian mass extinction (see Chap. 7), this is not reflected by the ichnodiversity curves. Similarly, the end-Triassic mass extinction resulted in a decrease in ichnodiversity, albeit more modest (see Chap. 8), which is not recorded in our ichnodiversity curves. The absence of an ichnodiversity drop in these curves is simply an artifact resulting from the methodology employed in their construction. It is therefore surprising that a 7 % decrease in total marine ichnodiversity (5 % for bioturbation structures and 15 % for bioerosion structures) is revealed by these curves in connection with the end-Cretaceous mass extinction. The Late Cretaceous peak and subsequent drop in ichnodiversity are also present in the curves that were plotted eliminating the occurrence of singletons.

Decrease in the degree of bioturbation has been noted in connection with many mass extinction events. Although comparative analysis of mass extinctions from a trace-fossil perspective are still in their infancy, available information seems to suggest that the extent of this decrease in intensity of bioturbation tends to reflect how profound was the impact of the event. This is illustrated by the end-Permian mass extinction, which shows a collapse of the mixed layer (see Chap. 7 and Sect. 16.4; Buatois and Mángano 2011b; Hofmann et al. 2015). A similar situation has not been recorded so far associated with any of the other mass extinction events. In fact, intense bioturbation has been noted in Danian post-extinction deposits (see Chap. 12).

Reduction in the size of trace fossils has been detected in connection with many mass extinction events, most notably the end-Permian (see Chap. 7) and end-Triassic (see Chap. 8). In other cases, such as the end-Cretaceous, this trend is not apparent (see Chap. 12, although see Wiest et al. 2015 for documentation of trace-fossil size reduction in the aftermath of the end-Cretaceous mass extinction). The so-called Lilliput effect has been noted in the paleobiologic literature to explain the sharp decrease in body size, based on both the body fossil and trace-fossil records, in the aftermath of mass extinctions (Urbanek 1993; Twitchett 2007). Explanations for this size reduction are still unclear, with both externalist and internalist causes being involved. Limited oxygen and food have been invoked as likely candidates for the former (Twitchett 2007), whereas survival of small taxa; the dwarfing of larger lineages and the evolutionary miniaturization from larger ancestral stocks fall among the later (Harries and Knorr 2009).

Dominance of simple trace fossils is another typical feature in post-extinction strata. For example, simple trace fossils attributed to *Planolites* are the first in reappearing after the end-Permian mass extinction (see Chap. 7). Simple forms, such as *Planolites* and *Palaeophycus*, seem to be common in Lower Jurassic post-extinction deposits as well (see Chap. 8). The prevalence of these simple morphologies overall reflect very simple feeding behaviors, most likely reflecting opportunistic population strategies in the aftermath of mass extinctions (Fraiser and Bottjer 2009).

It has long been noted that organisms are differentially affected during extinctions according to trophic type (Jablonski and Raup 1995; Smith and Jeffrey 1998; Hansen et al. 2004; Twitchett 2006). In particular, suspension feeders tend to have been more affected than deposit feeders during mass extinctions. In this regard, it has been concluded that both selective deposit feeding and omnivory significantly enhance survivability during mass extinction events (Twitchett 2006). This is clearly illustrated by the overwhelming dominance of deposit-feeding traces in Danian post-extinction deposits (see Chap. 12). Also, post-extinction late Devonian ichnofaunas are dominated by structures produced by selective deposit feeders, whereas suspension-feeding burrows are absent (Buatois et al. 2013).

Ichnofaunas from shallow-marine environments tend to be more strongly affected than those in marginal-marine and deep-marine settings. Marginal-marine, brackish-water faunas typically consist of opportunistic animals that flourish under extreme conditions. Therefore, they are able to rapidly colonize environments after a major disturbance, such as mass extinctions. Of the five colonization phases recognized for brackish-water settings by Buatois et al. (2005), only the end of the first (Ediacaran–Ordovician) and the third (Permian–Triassic) coincide with mass extinctions (the Late Ordovician and Late Triassic mass extinctions, respectively). The remaining three of the "Big Five", the late Devonian, end-Permian, and end-Cretaceous mass extinctions, does not show any impact in marginal-marine biotas. In the same vein, ichnofaunas from deep-water settings do not seem to have been strongly affected by mass extinctions (Uchman 2004). No major crisis has been associated with any of the "Big Five" in the deep sea, other than a reduction in the diversity and abundance of graphoglyptids in the case of the end-Ordovician and end-Cretaceous mass extinctions (Uchman 2003).

16.4 Patterns of Ecospace Colonization

Having established that there are some recurrent ichnologic patterns involving evolutionary radiations and mass extinctions, we may now explore if recurrent motifs can be established in connection with colonization of empty or underutilized ecospace. In other words, is it possible to detect trace-fossil assemblages that recur through geologic time not as a response to environmental constrains (as is the case of ichnofacies), but driven by large-scale evolutionary controls instead? We have attempted to address this question in a previous paper, referring to this particular recurrence of ichnoassemblages revealing common strategies in ecospace colonization as "the Déjà vu effect" (Buatois and Mángano 2011b). In this chapter, we argue that three main types of trace-fossil assemblages can be recognized in connection with exploitation of empty or underutilized ecospace.

The first of these assemblages consists of very small grazing trails (e.g., *Helminthopsis*, *Helminthoidichnites*, *Gordia*) produced by epifaunal or very shallow infaunal vermiform animals, very shallow-tier feeding structures (e.g., *Treptichnus*, *Oldhamia*, *Pilichnus*) of infaunal vermiform organisms, and (in some cases) trackways (e.g., *Diplichnites*, *Stiaria*) of epifaunal arthropods (Buatois and Mángano 2011b). Almost invariably trace fossils occur in association with structures suggestive of microbial stabilization, such as wrinkle marks, palimpsest ripples, and old elephant skin (Noffke 2010; Buatois and Mángano 2012a). The associated primary sedimentary fabric and bedding-plane physical sedimentary structures are superbly preserved (e.g., Buatois et al. 1997). Ichnofaunas reveal superficial and shallow-tier grazing and mining of microbial mats in the absence of substantial infaunal bioturbation. The presence of microbial mats allows preservation of minute trace fossils, displaying delicate fine morphologic features (Buatois and Mángano 2011b). These trace-fossil assemblages occur across a wide range of environmental settings, such as Ediacaran-lower Cambrian shallow-marine (e.g., Gehling 1999; Buatois et al. 2014), Cambrian deep-marine (e.g., Buatois and Mángano 2003), and late Paleozoic continental to fluvio-estuarine (Buatois et al. 1997; Mángano et al. 1997) settings, invariably in connection with empty or underutilized ecospace.

The second assemblage is characterized by shallow-tier burrows (*Spongeliomorpha*, *Halopoa*), trails (*Cruziana*), and resting traces (*Rusophycus*) with well-developed ornamentation, typically bioglyphs. Very shallow-tier burrows and trackways may be present as well. The occurrence of well-preserved bioglyphs and the sharp burrow boundaries suggest emplacement in sediment that was firm at or close to the sea bottom. These trace-fossil assemblages are associated with widespread firm substrates and the virtual absence of a mixed layer (Droser et al. 2004; Jensen et al. 2005; Buatois and Mángano 2011b; Mángano et al. 2013; Hofmann et al. 2015). This is illustrated by two apparently unrelated ichnofaunas: those in Cambrian–Ordovician and Lower Triassic shallow-marine environments. Both deposits are characterized by preferential preservation of epifaunal and very shallow-tier infaunal trace fossils; paucity of mid- and deep-tier trace fossils; absence of mottled bioturbation textures; and dominance of cohesive substrates in open-marine environments (Hofmann et al. 2015). In the case of lower Paleozoic strata, the mixed layer was still incipient and poorly developed (Droser et al. 2004; Jensen et al. 2005; Callow and Brasier 2009; Mángano et al. 2013), whereas in the Lower Triassic the mixed layer may have collapsed as a result of the end-Permian extinction (Buatois and Mángano 2011b; Hofmann et al. 2015; see Chap. 9). The ichnologic responses in both situations were essentially identical.

The third assemblage is characterized by the presence of horizontal branched burrow systems (e.g., *Multina*, *Vagorichnus*) at the base of event sandstone beds (Buatois and Mángano 2011b). These burrow systems are preserved along lithologic interfaces creating virtually no disturbance in the primary sedimentary fabric. *Multina* is common at the base of lower Paleozoic marine tempestites and turbidites, where it records post-event colonization (e.g., Buatois and Mángano 2004, 2012b; Buatois et al. 2009). *Vagorichnus* has been recorded at the base of Jurassic lacustrine turbidites (Buatois et al. 1995, 1996). Although these occurrences are from disparate environments and from rocks of different ages, they are all associated with an increase in burrowing depth reflecting initial exploitation of the infaunal ecospace (Buatois and Mángano 2011b). From an evolutionary standpoint, this incipient colonization of the infaunal ecospace preceded the onset of more intense bioturbation and the establishment of a well-developed mixed layer.

The recurrent presence of these three types of trace-fossil assemblages in rocks of different ages and formed under a wide variety of environmental settings can only be understood under the light of the evolutionary prism. These assemblages reveal a limited repertoire of behavioral strategies that allow benthic faunas to colonize empty or underutilized ecospace. Fossilization of these behavioral strategies in the form of biogenic structures is mediated by a set of preservational conditions resulting from the recurrent opening of a taphonomic window. This window was responsible for the preservation of surface and shallow-tier structures which typically are obliterated by deeper-tier and more intense bioturbation (Bromley 1996).

16.5 Environmental Shifts Through Time

A number of studies published for the most part in the eighties and nineties revealed that the fossil record can be characterized by a recurrent pattern of onshore origination of evolutionary innovations and their subsequent expansion to deeper water, resulting in the proposal of the so-called "onshore–offshore model" (e.g., Jablonski et al. 1983; Sepkoski and Miller 1985; Jablonski and Bottjer 1990; Sepkoski 1991; Sepkoski and Sheehan 1983). In fact, it has been argued that an onshore–offshore pattern is displayed by Sepkoski's evolutionary faunas themselves, as illustrated by the replacement of trilobite-rich communities by mollusk-rich communities in shallow-water niches throughout the Paleozoic (Sepkoski and Miller 1985).

The trace-fossil record provides further empirical support to this model across a broad range of scales. First, an onshore–offshore pattern is evident from individual ichnotaxa, showing either evidence of expansion or retreat. In the first case, an ichnogenus occurring for the first time in shallow water subsequently extends its environmental range into deeper-marine settings without loss of onshore representatives. In the second case, migration into deeper water occurs together with loss of onshore representatives (Bottjer et al. 1988; Stanley and Pickerill 1993). Examples of expansion include *Ophiomorpha* (Bottjer et al. 1988; Tchoumatchenco and Uchman 2001), *Scolicia* (Seilacher 1986) and *Rhizocorallium commune* (Knaust 2013). An example of retreat is *Zoophycos* (Bottjer et al. 1988).

Second, entire groups of trace fossils may display the onshore–offshore pattern. The best example is graphoglyptids, which in the early Cambrian occur in shallow water, but subsequently migrated to the deep sea (Crimes and Anderson 1985; Jensen and Mens 1999), where they became the core component of the *Nereites* Ichnofacies.

Third, the onshore–offshore pattern is also displayed by ichnofabrics. For example, it has been argued that in carbonate settings intense bioturbation first took place in shallow-water settings and only later seaward (Droser and Bottjer 1989). This pattern may reflect the fact that niche partitioning within the substrate first developed in shallow water and subsequently expanded into deeper water.

Fourth, and at a larger scale, the onshore–offshore pattern is displayed in connection with the colonization of empty or underutilized ecospace. This is shown by trace-fossil evidence of original colonization of shallow-marine settings and the progressive subsequent expansion into the deep sea, marginal-marine environments and continental settings. Also, this pattern is apparent within continental environments themselves, as demonstrated by the initial colonization of lake-margin settings and later expansion into subaqueous lacustrine settings (Buatois and Mangano 1993; Buatois et al. 1998; see Chaps. 5 and 6). This is certainly analogous to the migration of plants from upland areas to the lowlands during the Carboniferous-Permian transition (DiMichele and Aronson 1992) and the origination of aquatic insects in running water and subsequent expansion into lacustrine habitats (Wooton 1988).

16.6 Conclusions

Comparative analysis of the ichnologic record of major evolutionary events allows detecting recurrent patterns that may help to further increase our understanding of the underlying evolutionary dynamics of animal-substrate interactions through geologic time. In particular, we have detected recurrent patterns of organism-substrate interactions during evolutionary radiations, benthic fauna response to mass extinctions, strategies of ecospace colonization, and environmental shifts through time. Evolutionary radiations are invariably associated with an ichnodiversity increase, whereas increases in ichnodisparity are linked to the colonization of empty ecospace. Evaluation of mass extinction events suggests common responses from the perspective of animal-substrate interactions, namely a reduction in ichnodiversity, decrease in degree of bioturbation, reduction of bioturbation depth, size reduction, dominance of simple trace fossils in post-extinction strata, preferential survival of ichnotaxa produced by deposit feeders, and selective extinction in shallow-marine ecosystems. The recurrent presence of certain trace-fossil assemblages in rocks of different ages and formed under a wide variety of environmental settings seems to suggest a limited repertoire of behavioral strategies for colonization of empty or underutilized ecospace. The trace-fossil record provides further empirical support to the onshore–offshore model across a broad range of scales.

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