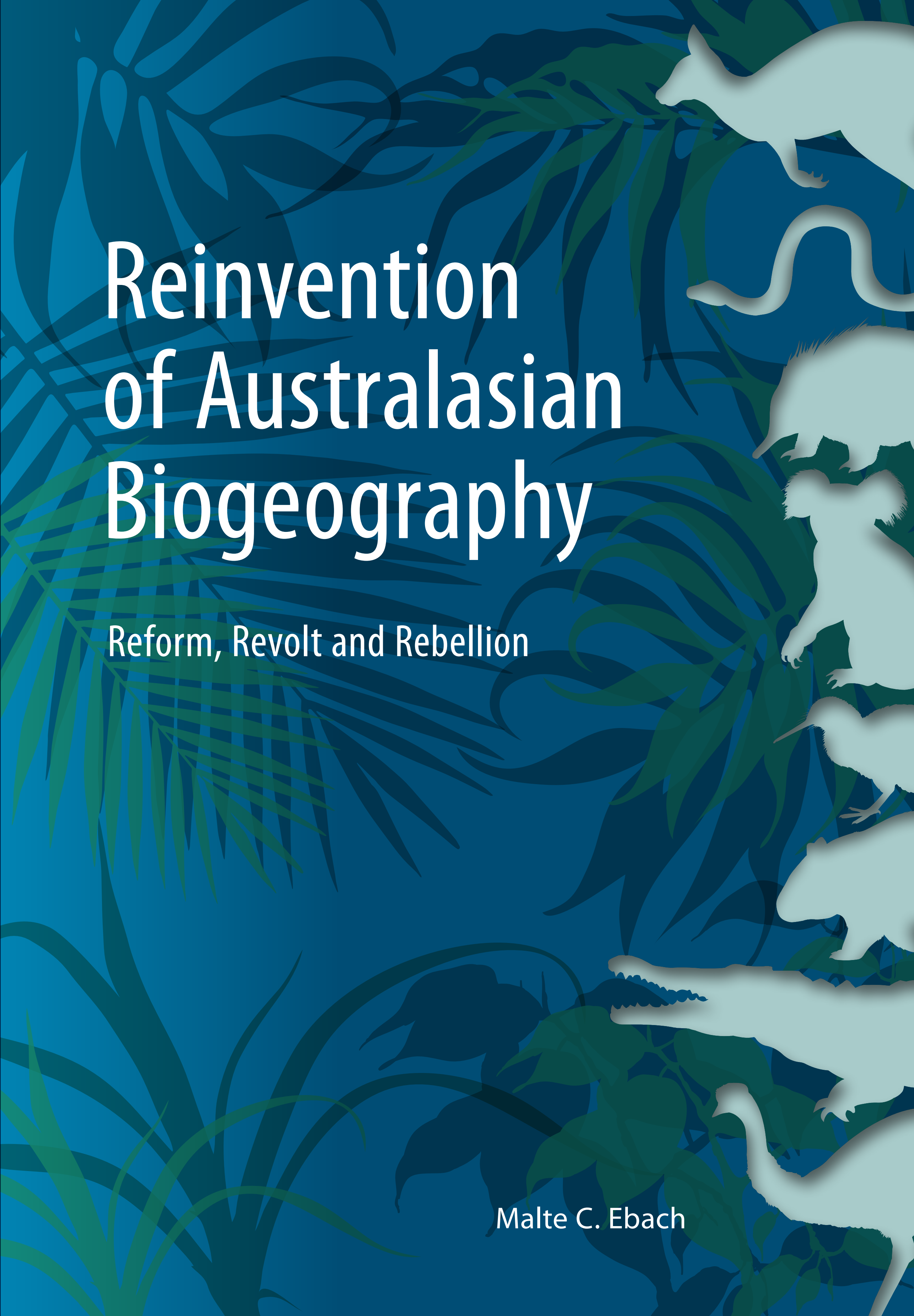

Reinvention of Australasian Biogeography

Reform, Revolt and Rebellion

Malte C. Ebach

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For Melinda

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PUBLISHING

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Foreword

I've dabbled in Australasian biogeography for the last quarter of the 150 years traversed by this book: not as a skilled or particularly insightful biogeographer, but as a lightly educated enthusiast. My first foray in peer-reviewed print – at the end of a taxonomic account of the freshwater red algae in south-eastern Australia published in 1984 – was descriptive, subjective and inconclusive. The affinities of this phycological flora, I said, 'could not be fully assessed'. I had too few collections and too little knowledge of diversity and distribution to make any meaningful comparisons. What I didn't realise then was that I also lacked any scientific method for assessing biogeographical connections, and that at best I was trying to craft an interesting (perhaps) but untestable narrative.

A few years later I wrote an opinion piece for *The Age* about another group of algae I was working on, arguing that the unlikely disjunct distribution of a species, known previously from California but now recorded from the goldfield region of Victoria, might be a case of long-distance dispersal on the shovels of miners. An attractive idea, but again not supported by any scientific theory or method. In 1992 I published my first cladogram and it wasn't until the year 2000 that I published a paper with the word 'biogeography' in the title (using a freshwater algal species to postulate a closer connection between the northern tip of North Island in New Zealand and south-west Tasmania, than both with the east coast of New South Wales). By then I was a convert to Ebach's favoured form of biogeography, announcing optimistically at the end of my paper: 'the presence of diverse and distinct Australasian clades of organisms independent from green plants and animals is good news for cladistic biogeography'.

As with cladistics, I kept abreast of the 'reforms, revolts and rebellions' in historical biogeography, sometimes from primary sources but mostly from (more readable) book reviews and historical summaries. I missed things. The New Zealand passion for panbiogeography failed to capture my full attention despite the beguiling diagrammatic representation of tracks. Within Australia I became little more than an interested bystander. At times I felt excluded by the complexity of arguments and the exclusivity of a club I wasn't sure I even wanted to join. My attempt to write up a 'light-hearted' report of the 1990 Willi Hennig conference held in Canberra for a then largely cladistics-ignorant audience of Australia phycologists was slashed and trashed by (cigar smoking at times, as you'll read) Chris Humphries who somehow found it on the magazine editor's desk. I liked Chris but this response was symptomatic of the discipline. Conversely, meeting Gary Nelson for the first time was transformative and I became, appropriately enough a *transformed cladist*; this despite his favoured method of instruction being to provoke with question rather than provide with answer. Malte Ebach doesn't shy away from the blemishes, biases and bullies of biogeography, particularly in the historical quarter I experienced. He takes no prisoners but the book is prosecuting a case rather than the misguided people who fall along the way.

Like everything written about cladistics and cladistic biogeography, *Reinvention of Australasian Biogeography: Reform, Revolt and Rebellion* will be received variously as heretic or heroic. While Ebach provides an engaging history of biogeography in Australia and New Zealand, and more particularly a perspective on the role of the scientists and biota in these regions in the development of this science, he is really making a robust case for change and reform. Most players in this story stumble and fall, only rarely adding a fragment towards Ebach's grand synthesis. It's a pragmatic approach to history, quickly dispensing with the completely foolish and gathering the occasional fleck of insight from the rest. Despite our author's clear frustration, the central theme is one of possibility and potential.

If we can determine units of biogeography that are testable and informative, we have the basis of analytical biogeography. Having only recently become awakened to Alexander von Humboldt's pivotal and inspirational role in creating the discipline of plant geography, I enjoyed the journey from his recognition of plant formations responding to the climate of a region, through to more inclusive biomes and biotic areas, then to (monophyletic) natural areas. An area of endemism is the unit of historical biogeography, and the grand objective, according to Ebach, is to find the 'single areagram of life [modelled on the predictive "tree of life"] … the relationship of every biotic area that has ever existed'. I was pleased to read that descriptive contributions such as my own can be a reasonable step towards analytical biogeography, and as good a means as any to hypothesise areas of endemism and biotic regions, the classification units favoured by Ebach.

As Ebach reminds us, many scientists end up being more interested in explaining (away) anomalies in their own theories than searching for novel patterns. No one likes to be wrong and it is too easy to resist evidence contrary to what we have published. In this sense we are both flawed human beings and poor scientists. If we are to discover the 'areagram of life', biogeographers have to get over this weakness. Ebach wants hypotheses tested with independent evidence rather than through correlating with popular narratives. This book is an attractive and, to my uncluttered mind, convincing argument for that cause.

Tim Entwisle, Director and Chief Executive, Royal Botanic Gardens Victoria, 18 July 2016

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… to find the primary ontological divisions of the earth's surface
(Sclater 1858, p. 132).

Prologue

The book you are holding (or its digital version) is not a textbook on biogeography, nor is it a historiography. Rather, this book is a series of vignettes of past events in the history of Australasian biogeography made by an Australian biogeographer who works in this field. These vignettes show the development of a scientific discipline seemingly isolated from the academic centres of Europe and North America. In fact, Australasian biogeography has contributed significantly to biogeography over the last 150 years, and has caused much of the innovation and controversy that shaped modern biogeography – Antarctic land-bridges, sunken Pacific continents, panbiogeography, continents reemerging, long-distance dispersal, and Gondwanan distributions. In 1896, Captain Fredrick William Hutton attempted to summarise what was known about Australasian distributions,

> '… a considerable amount of ingenuity has been expended in trying to solve the interesting problem of the distribution of southern faunas. The differences of opinion are due partly to some of the authors having taken only a small number of the known facts into consideration, and partly to constant additions to our knowledge; either by the discovery of new facts, or by the correction of old errors. No doubt our knowledge will still increase, but it seems hardly possible to make any more theories. The problem is a very intricate one, and we may be sure that the true solution is not simple' (Hutton 1896, p. 41).

Thomas G. Sloane continued, 'The quotation above from Captain Hutton's erudite paper … epitomises the position of our present subject in its general bearings as left by Hutton. My intention is only to deal with the zoogeographic sub-regions and districts of the continent of Australia' (Sloane 1915, p. 139). Others, however, had despaired at the prospect,

> 'The origin and composition of the Australian fauna is a time-worn subject. It is an unsatisfactory one, too, because it is so difficult to test the hypotheses that may be built on distributional and morphological evidence. Nevertheless – perhaps, indeed for this reason – those who touch on it become addicts, and cannot leave it alone' (Mackerras 1950, p. 157).

Continuing from Sloane and Mackerras, this book has two aims: the first is to show the growth of biogeography in Australasia – from the first attempts at drawing a natural classification of areas to modern attempts at proposing a unifying synthesis. What is known about the biogeography of Australasia today is to some extent no different from 1896, in 'the discovery of new facts, or by the correction of old errors' and in its inability 'to test the hypotheses that may be built on distributional and morphological evidence'.

As biogeographers, we build syntheses based on many assumptions and after the discovery of new facts, and correct these as we forge ahead. The result is a series of narratives that together form a biogeographical story of a continent – a meta-narrative. The process of constantly reinventing our meta-narrative from generation to generation has become a cycle that we have taken for granted. I term this the reinvention thesis, and here lies the second aim of this book: namely how to break this cycle of reinvention.

In order to fulfil my two aims, I have critiqued several different biogeographic approaches and narratives suggested over the last 150 years. I haven't covered all approaches, such as phylogeography, ecological biogeography (island biogeography) or conservation biogeography. These fall outside my purview and experience. As a cladistic biogeographer, I'm interested in the historical and taxonomic aspects of biogeography, such as testing for area classification, area relationships and the historical processes responsible for the distribution of the Australasian biota. This is why I have focused mainly on the type of biogeography practised by systematists and taxonomists for over two centuries. Some may consider this critique somewhat limited in scope given the popularity of other biogeographic approaches. Regardless, historical biogeography, no matter how limited, holds the key to understanding biotic areas and how they relate to other areas through time. Without a stable and robust area classification, we are reduced to making narratives about *ad hoc* areas or geographic coordinates on a map. The way to test for a stable and natural area classification has always been there, in the taxonomic approach: the very same place from where the idea of a natural area derives. If we have borrowed the concept of a natural area classification from taxonomy, why don't we also borrow the taxonomic approach to find natural area classifications? Alas, science, or at least biogeography, doesn't work like that. With our scientific measurements and observations also come the attitudes and intentions of academics and researchers, all nicely bundled up in popular meta-narratives. Biogeography was a battlefield between different syntheses, such as postgraduate panbiogeographers taking on the established modern synthesists in New Zealand, and Australian cladists taking on evolutionary taxonomists. These battles, however fought and won, give us insight into the inner workings of Australasian biogeography and how new meta-narratives are created and older ones patched up to accommodate new scientific discoveries, such as plate tectonics and genetics.

The book starts with describing the historical biogeography, its early history and approach (Chapter 1). I concentrate on cladistic biogeography and panbiogeography, because these two approaches had made a great impact on biogeographical thinking in Australasia since the 1980s. I will also discuss the first narratives in Australasian biogeography (Chapter 2), and how early biogeographers decided to carve up the natural regions of Australasia (Chapter 3). The role of cladistics in reforming taxonomy (and biogeography) will also be examined (Chapter 4), as well as the revolt of panbiogeographers in New Zealand (Chapter 5), and the rebellion of neodispersalists (Chapter 6). Finally, I will discuss the possible futures of Australasian biogeography (Chapter 7).

The goal of this book, is for the reader – and in particular students or early career researchers – to understand that Australasian biogeography has a long history that goes back to the mid-19th century, and that the same questions, meta-narratives and practices reappear in cycles. The book will show a way to break this cycle of reinvention, and kick-start Australasian biogeography. I have written this book in a conversational style for a general scientific audience and without too much jargon. A concise glossary has also been included containing the scientific terms used throughout the book.

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Chapter 1

Studying the distribution of life on Earth

A biogeographic hiatus ended in the mid-1970s in a flood of analytical and theoretical papers that heralded a new phase of biogeography. For much of the early 20th century, biogeography was thought of as a by-product of evolutionary biology – an artefact of past climatic processes and events that helped shape physiological adaptions and dispersal routes. That was shattered by the acceptance of continental drift that was once rejected as 'absurd'.[1] Continental drift, in the guise of plate tectonic theory, had revolutionised the geosciences, including palaeontology, but it had little overall effect on biologists and how they practised biogeography. Physiological adaptions, mostly to climate, and dispersal routes were all that 20th century biogeography had to offer. Descriptive biogeography (the study of biotic regions and biota) was considered outdated and not in the same league as ecology and population dynamics. Did biogeographers simply dismiss geological processes as occurring over long periods of evolutionary time – too long to have any effect on the distributions we see today? For example, the drying out of Australia over a period of 20 million years was always thought to be due to 'climate' and nothing more. Now we know that this aridity is due to tectonics and fluctuations in the mantle causing the Australian plate to buckle and bend as it slowly moves north. Plate tectonics had usurped climate as the main driver of environmental change. Without the hot molten core and mantle that drives plate tectonics, our planet would resemble Mars: a cold and dead dust bowl. Even by the end of the 20th century, many biogeographers were still struggling with the idea of Earth and life evolving together. But not all of biogeography ignores a dynamic Earth; rather it is how biogeographers define biogeography in which our problems lie. How do you define an undefined field?

Blame 19th century malacologist Hermann Jordan. Not much is known about him, other than he was the first person to use the term 'biogeographie' (Jordan 1883). Like many of the early users of the term 'biogeography', Jordan didn't define it, meaning that it may have been already in use and its definition known. After all, both plant geography (or phytogeography) and animal geography (zoogeography) were already established fields by the 1880s, and there was no umbrella term to describe them.[2] Perhaps the definitions of zoogeography and phytogeography were sufficient enough, but even these terms referred to different practices. A more pragmatic approach is to ask who practised biogeography and work out a definition from there, but there was a snag. Phytogeographers, for example, either studied the distributions of plants (taxonomic groups) or vegetation (plant formations). Zoogeographers referred to either geographical regions or isothermal lines. Which was it? Vegetation such as rainforest consists of many different taxonomic groups. Species within a taxonomic group may be found in multiple vegetation types. Moreover, an isothermal line is based solely on temperature, while a region is based on taxic distributions and geographical barriers. There was no consistency in 1880s biogeography, nor was there a single aim or

The biogeography universe

The multidisciplinary nature of biogeography means it incorporates the aims and methods of various fields (e.g. cladistics, molecular genetics, phenetics, palaeontology and geography). However, much of this book is dedicated to cladistic biogeography, the methods of which are outlined in Parenti and Ebach (2009). Other biogeographic approaches not covered in this book are phylogeography (Avise 2000), palaeobiogeography (Lieberman 2000), ancestral area reconstruction (Ree *et al.* 2005); human biogeography (Harcourt 2012), island biogeography (MacArthur and Wilson 1967, 2001), ecological biogeography (Ricklefs and Relyea 2013) and conservation biogeography (Ladle and Whittaker 2011). The panbiogeographic approach and its impact on New Zealand biogeography is covered in Chapter 5.

method. All zoogeographers and phytogeographers wanted to do was look at different aspects of plant and animal distribution. That tradition has remained until the 21st century. Throw in recent discoveries and innovations, such as genetics, deep-sea thermal-vent faunas, phylogenetics and geospatial technology and suddenly the number of aims and methods multiply, but the definition for biogeography remains the same:

> ‘The branch of biology that deals with the geographical distribution of plants and animals … the characteristics of an area or organism in this respect’ (OED 2015a).

Surely *any* branch of biology deals with the geographical distribution of organisms? For example, botany, entomology, ecology, palaeobiology, parasitology, anthropology, bacteriology and mammalogy all deal with a geographical component. So do related fields such as epidemiology, linguistics and human geography. Perhaps seen as a *multidisciplinary* field, biogeography would make greater sense? After all, what branch of biology doesn’t deal with geographical distribution? Very few indeed.[3] In order to understand what biogeography is, we need to see how biogeography is done.

The search for natural biotic areas

Unless you are reading this in outer space, you are currently in – or driving, riding, flying or sailing over – a natural biogeographic region. The region is defined by the organisms that inhabit it – the biota – which have been formed by millions of years of evolutionary, geographical, geological and climatic processes. This includes the barriers that encapsulate the biota, isolating it from other biota. Over time, these biota diversify and become endemic to areas in which they live. If you are standing in a plain near a troop of kangaroos, for example, you are most likely in Australia. But things get moved around. For instance, you may also be standing in a kangaroo enclosure in a zoo. Biogeography is never clear cut; rather it is messy. Animal and plants tend to move around, either naturally or by human-assisted means, such as the introduction of the cane toad in Australia or eucalypts in Spain.

Identifying which organisms are part of a natural area is incredibly difficult for several reasons. First, not many people work on more than one taxonomic group. A single taxonomic group does not make a biota. Next is the problem of whether your taxonomic group is actually endemic. It might be introduced or naturally cosmopolitan. The biggest hurdle, however, is determining the relationships between the species and genera under study. Without these, you have no independent source of information about the relationships of your areas. The only way to find out what these relationships are is to find the relationships between the morphological or molecular characteristics of your organisms. For much of the 18th, 19th and 20th centuries, this type of information was unavailable. Not until the 1970s were we able to investigate morphological and genetic relationships using numerical methods. Before then, natural areas were assumed, and never tested, given the lack of an analytical method. Without confirmation of natural areas, much biogeography was descriptive; that is, limited to describing and naming areas. There was, and still is, a dominant component to biogeography – the narrative. Knowing the origins and distributional history of species and their genera has been a mainstay of biogeographers since Linnaeus. Narratives about taxic distribution over time, such as dispersal routes for migrations and extinctions, provide a natural history of the organisms in question. Narration is not descriptive or analytical, nor does it necessarily require a method. Over time, our narratives were synthesised in the conclusions to many taxonomic monographs and phylogenetic studies. Biogeography was nothing more than assuming natural biotic areas and telling stories about the distributional histories of its organisms. That is until 1978, when Donn Eric Rosen, an American ichthyologist at the American Museum of Natural History, made a significant breakthrough in how we find the relationships between biotic areas (Rosen 1978). That breakthrough was a result of a new way of doing biological classification – cladistics – and it completely reformed traditional Linnaean taxonomy.

Cladistics: the search for natural taxa and their relationships

Taxonomy is an often-misunderstood field of research. Unlike ecology, physiology and other biological disciplines, taxonomy has no precise methodology – at least not one that has been translated into an algorithm and may be implemented on a computer. Certainly, books detailing the taxonomic method have been written, with an emphasis on how to classify organisms based on characters, how to name them, and so on (e.g. Blackwelder 1967; Winston 1999). These books, however, are not popular and they are rarely cited or used in teaching taxonomy. At first glance it seems that taxonomy is nothing more than a poor cousin of the other more flamboyant biological sciences – ones that use experimental methods, statistics and super-computers. Taxonomy has also been unfairly labelled an 'art-form', much to the chagrin of taxonomists. So what is taxonomy and why on Earth would anyone do it?

Taxonomy is the study of classifying organisms into taxonomic groups: namely taxa (e.g. species, genera, families). Catching butterflies in nets, pinning them onto cardboard and giving them a name is what some people think taxonomists (in this case lepidopterists) do all day. Placing specimens into collections, taking them out again and rearranging them into different groups might also be what taxonomists are seen to be doing, but the act of classification is an intricate process that takes place in the mind. Classification is an instinctive process: something we are born with and something that helps us communicate and survive. Without classification we are lost. There would be no day-to-day language with which we can communicate our feelings and facts to others. This is not to say that giving a name to something defines taxonomy. Taxonomy can be done without names. For instance, we may accurately warn others that the barking thing, with four legs, a tail and sharp teeth, definitely bites. The fact that we can see the characteristics of the four-legged biting thing means we are able to identify it from other things that bite, such as the small buzzing black things that live near the swamp. Giving a thing a name is merely a convenience. Being able to identify what that thing is based on the observed characteristics is the genius of thousands of processes that are occurring in our minds. We can even compare the four-legged barking thing with the four-legged purring thing. They share the same characteristics, such as a tail, teeth and four legs, which probably means that they are more like each other than they are to, say, the buzzing biting thing. That is classification – the ability to identify and categorise organisms based on their observed characteristics.

Classification is something that is inherently human; it is part of us, as much as grammar and touch. This is also why most people trained as taxonomists don't read books on how to do classification, because we have been doing it all our lives. There is no hypothesis to test, nor is there is an experiment. So how do taxonomists know they have got it right? How do they know whether the organisms they classify are in fact natural evolutionary groups? The fact is, they don't. Taxonomy is not an art and taxonomists are unlike, say, art historians. Good art historians are also adept at classifying artwork and have reliable guides for identifying the authenticity of certain types of oil paintings, which they can classify by artist. This is because art historians have access to *provenance* – the art catalogues, gallery labels, auction stamps, and so on. If these are missing, they can date the paint or compare brushstrokes with known originals. But taxonomists have no idea if they do in fact have an 'original' taxonomic group. Rather taxonomists, through comparison, can tell to a certain degree whether a taxonomic group, or *taxon*, is based on natural characteristics called *homologues*, such as feathers in birds and hair in mammals. Taxonomy is classification without provenance, but organisms can be dated (if they are fossils), and we can compare the brushstrokes – namely, the homologues – this is where cladistics comes in.

Cladistics is a methodological approach to biological classification in which the relationships among taxa (e.g. species or genera) are determined by shared relationships between homologues. In short, cladistics is a way to find natural taxa. What makes cladistics important is that it takes away the need for dating (in fossils) and relies on patterns of relationships. In this way, cladistics tests whether our classifications are natural and what other taxa they are related to. Cladistics is a tool used in revising potential artificial taxonomic groups. The most famous example is that of the dinosaurs. Originally described from a fossil claw belonging to *Iguanodon*, dinosaurs were a poorly defined and nebulous collection of taxa. Then in the 1980s, a cladist tested the group and found that some dinosaurs were more closely related to other taxa, such as birds, than they were to anything else, confirming

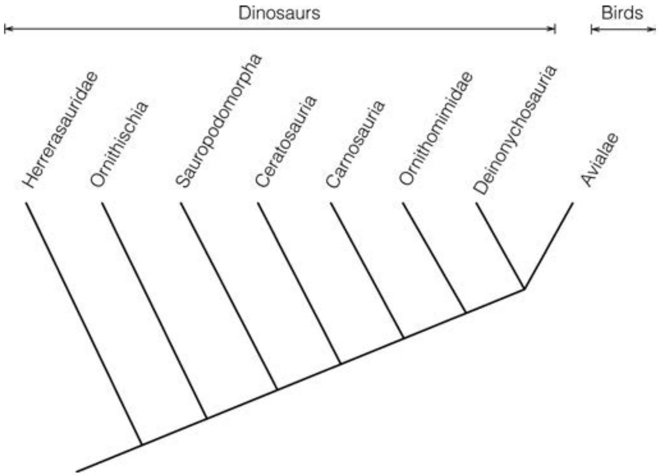
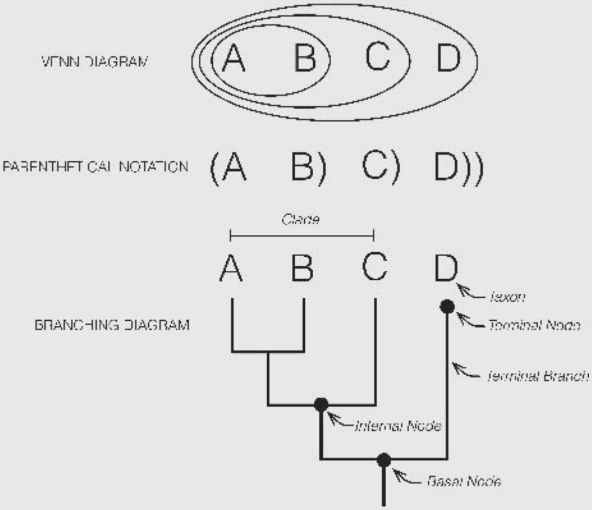


Fig. 1.1. Cladogram depicting phylogenetic relationships among well-known theropods and other dinosaurs. The figure, redrawn from Gauthier (1986, p. 54, Fig. 8), shows that some dinosaurs, such as the theropods, are more closely related to birds (Avialae) than they are to other dinosaurs.

The anatomy of a cladogram

The relationship of homologues is called a homology: namely a relationship. A cladogram is simply a pattern of relationship. The nodes on a cladogram are artefacts of a branching diagram and contain no information. Note that nodes are not present in other types of cladograms, such as in Venn diagrams and in parenthetical notation. A cladogram is evidence for a common history of taxa. Taxa that share a common history are part of a larger natural or monophyletic taxon.



The anatomy of a cladogram.

earlier suspicions (Fig. 1.1). The discovery was reported as dinosaurs being the ancestors of birds. The problem with this statement is that dinosaurs are assumed to be a natural taxon. What the classification, or cladogram, is saying in Fig. 1.1, is that birds have a set of homologues that define them as a natural or monophyletic taxon, while the dinosaurs have no diagnostic homologues and are therefore in desperate need of taxonomic revision. One solution would be to place the birds and dinosaurs into a single group, which would make them monophyletic, but it still leaves us with the problem of what diagnostic homologues make members of birds plus dinosaurs a natural taxon. Rather, a taxonomic revision would involve finding shared diagnostic homologues in order to identify natural taxa within Dinosauria. For example, the theropods may be included in the birds, because they share bird homologues. Ornithischians and sauropods may become two separate monophyletic taxa, and so on. In the end, you will have several monophyletic taxa. The name 'dinosaur' would simply vanish.

Removing the dinosaur name would be a correct and practical solution in biological classification, but it would be incredibly unpopular with the public. The term 'dinosaur', however, does have a practical use in identifying large lizard-like monsters. A sauropod or a theropod may be identified as a dinosaur. So too can cartoon characters and other non-living and non-fossil objects. Dinosaur, like the terms 'unicorn', 'gryphon' and 'leprechaun', is an identifier and serves a useful purpose within a folk classification. If we return to the question of why birds are a natural group and not dinosaurs, we may ask 'name the homologues that relate all birds'. You may say 'beaks', 'feathers' or 'hollow-bones'. Not all birds fly (think of the emu), so 'wings' are not a homologue that relates all birds.[4] Now think of a single homologue that relates all members of the Dinosauria. Some 'dinosaurs' have beaks, but so do birds. In fact, there are *no* homologues that relate all known members of the dinosauria. For taxonomists, artificial or non-monophyletic groups such as the dinosaurs, reptiles and fishes, need revision, but they are incredibly useful to non-taxonomists for identification.

The homologues that do relate taxa, such as hair and lactating glands in mammals, are natural or *homologous* structures. Non-homologous characteristics create the biggest headaches for taxonomists as they may unite unrelated taxa. Consider the wing, for example. Birds, grasshoppers and bats have wings, but in each case they are a different structure that has a similar functional purpose. These are termed analogues and are often used to show similar homologues, such as wings, spines and fins, in distantly related taxa. Although the analogue 'wings' might not relate a homologous structure in grasshoppers and birds, some analogues are in fact homologous, such as the pectoral fins in herrings and catfish, and are useful in determining relationship. Both homologues are part of the vertebrate character 'forelimb' that have a similar function. The trick is to tell which analogues and homologues are homologous, and which are not.

Observing an organism, say a trilobite, describing their characters and finding a homologue and its relationship, is part of the discovery process. In cladistics, monophyly is part of the discovery process. The first step in any cladistic analysis is to compare as many specimens as possible in order to ascertain potential homologous homologues and analogues, and eliminate non-homologous ones. For example, we may find a single homologue 1 is found in two (taxa A and B), of our five taxa (A–E). The relationship between these homologues would result in taxa A and B being more closely related to each than they are to taxa C, D and E. We can denote this relationship as a branching diagram, or as a Venn diagram or as parentheses, namely: ((A,B),C,D,E). Further observation and comparison of our hypothetical group of trilobites resulted in four hypothetical homologues, or characteristics, which we have drawn up as relationships:

Homologue 1: ((A,B),C,D,E)

Homologue 2: ((A,B,C),D,E)

Homologue 3: (A,B,C,D,(E))

Homologue 4: (A,B,C,(D,E))

Upon closer inspection we find that Homologue 3 does not relate any taxa, meaning that the homologue is unique to E. These characters are termed *autapomorphic* and are not useful in cladistic analysis (i.e. they don't relate anything). The next step is to find a common pattern of relationship or a *cladogram*:

Homologue 1: ((A,B),C,D,E) + Homologue 2: ((A,B,C),D,E) = Pattern 1: (((A,B),C),D,E)

If we add Homologue 4, we get a fully resolved cladogram:

Homologue 4: (A,B,C,(D,E)) + Pattern 1: (((A,B),C),D,E) = Pattern 2: (((A,B),C),(D,E))

The three homologues together overlap and form a single unique pattern of relationship, namely, (((A,B),C),(D,E)). In the real world, this rarely happens. Instead, we find that our relationships conflict. For example, let's throw Homologue 5 into the mix:

Homologue 5: ((A,B,C,D),E) + Pattern 2: (((A,B),C),(D,E)) = Pattern 3: (((A,B),C),D,E)

The relationship of D is in conflict because Homologue 5 relates D to A, B and C, whereas in Pattern 2, D is more closely related to E. One of the above homologues may be non-homologous, and there is no way of discerning which is correct. Rather we need more data in the form of Homologue 6:

Homologue 6: (A,B,C,(D,E)) + Pattern 3: (((A,B),C),D,E) = Pattern 4: (((A,B),C),(D,E))

Homologue 6 has the same relationship as Homologue 4, meaning that together, there is twice the amount of evidence for a (DE) relationship. What is important to note is the difference between a relationship, which is a unique relationship between homologues, and a pattern of relationship, which confirms that homologues 1, 2, 4, and 6 are homologous. A homologous relationship of homologues is called a *homology,* and underpins the whole concept of a natural classification. In other words a natural classification is made up of homologies. At this point we can make a clear and precise claim: a homology is part of a natural classification. The next step takes us back to revisionary taxonomy. Our trilobite taxonomy, which was created many years ago, places A–D into genus X and E into genus Y.

Our cladogram, however, shows that taxa D and E are more closely related to each other than they are to anything else, including taxa A, B and C. What claim can we make about genera X and Y? The pattern of relationship shown in our cladogram ((A,B),C),(D,E)), clearly states that taxon D is part of E. Left as just A, B and C, genus X is monophyletic, as it would form a natural taxon. But the inclusion of D make genus X non-monophyletic.

Let us return to our previous claim 'a homology is part of a natural classification'. Monophyly is the discovery of a natural taxon, based on homologies, therefore we may extend our claim as such: homology is part of monophyly, which represents a natural classification, or,

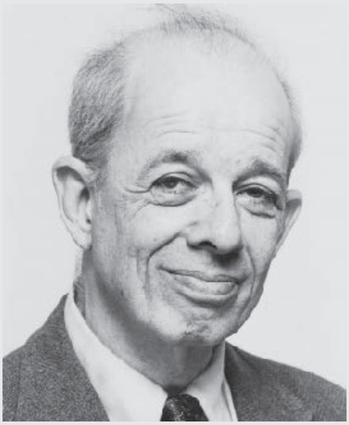
Homology: Monophyly: Natural classification

This claim is called the cladistic parameter and it shows that homology and monophyly are vital, without which we would not have a natural classification (Williams and Ebach 2008). For example, non-monophyly and non-homologous characters are not part of a natural classification. What does this mean for the cladistic method? Essentially the aim of cladistics is to embrace homologous characters and discard non-homologous ones. There is no point in retaining all data if we know that some of it is uninformative. In order to discard that uninformative data, revision of the data needs to take place, meaning that cladistics is the first step in a taxonomic revision. Only then do we have evidence for evolution (i.e. common ancestry) within a named taxonomic group (i.e. monophyly). If we return to our oil painting metaphor, we can say that we have discovered that the artwork is an original and without the need for provenance, namely a record of ownership. In cladistic terms, the 'provenance' are the ancestors and ancestor characteristics that we can never truly identify. In much of the 19th and 20th centuries, identifying ancestors was assumed to be the only way to identify natural taxa, in the same way as establishing the identity of an artist by finding the buyers and sellers of an oil painting. In the natural world, that provenance is lost. We simply do not know the identity of those ancestors and the ancestral characteristics of our taxa. In this way, natural classification remains a powerful way to determine which taxa are natural. What is more, a natural classification is predictive, something that artificial classifications are not. Take the mammals, for example. Any vertebrate with hair and lactating glands is a mammal. That is *any* vertebrate, regardless of its age, or where it is found. All species of mammal that have ever lived and will ever live will be more closely related to other mammals than to anything else, forever. Do you see the problem? What about transitional species? What about ancestors? Where do they fit into this predictive classification?

Classifications and actual phylogenetic ancestor–descendant events are two very different things. Classification is part of communication and it conceptually helps us understand a complex world. Real phylogenetic ancestor–descendant events are unobservable realities for which we have no evidence. Unlike experimental science, we can't replay millions of years of evolution in a laboratory – we may be able to model it, but we will never replicate it – ever. Making sense of the world and being able to communicate the idea of a mammal, for example, is one reason why we classify. By replicating the complex world, we learn little from it, other than confirming that it's complex. Tourist maps, for instance, communicate a complex terrain in a handy foldout drawing, in which important and relevant structures are identified and related. Underground train lines may be drawn out in red, bus stops drawn in blue and certain types of eateries categorised by national cuisine. The map helps us translate a complex city into information we need to travel and eat. Now imagine Lewis Carroll's fictional map 'on the scale of *a mile to a mile!* […] It has never been spread out, yet [and] it would cover the country, and shut out the sunlight! So we now use the country itself, as its own map, and I assure you it does nearly as well' (Carroll 1893, p. 169).[5] Jorge Luis Borges called this map 'useless' (Borges 1974). A mile for mile map is nothing more than a 1:1 replication. It serves no practical purpose, nor does it communicate ideas. The same is true for identifying ancestors or transitional species. For example, in 2012 Japanese scientists discovered a single microbe collected from a deep-sea vent at a depth of 1240 m. The microbe, *Parakaryon myojinensis,* stumped the microbiologists describing it because it places 'neither with the prokaryotes nor with the eukaryotes' (Yamaguchi *et al.* 2012, p. 424). *Parakaryon myojinensis* was identified as 'an indication of a potential evolutionary path between prokaryotes and eukaryotes' (Yamaguchi *et al.* 2012, p. 423). Many transitional fossils are identified as being part of more than one taxon, such as *Archaeopteryx* (part reptile, part bird) or the platypus (part reptile, part mammal). But we know that reptiles are non-monophyletic and that birds and mammals are monophyletic. Clearly the 'part reptile' means that some 'reptilian' taxa share a closer

Donn Eric Rosen (1929–1986)

The founder of vicariance (later cladistic) biogeography, along with Gary Nelson and Norman Platnick, Rosen was a fish taxonomist at the American Museum of Natural History (AMNH) in New York. His focus on poeciliid fishes (e.g. guppies and swordtails) and their distributions was instrumental in kick-starting vicariance/cladistic biogeography. Nelson and Rosen (1981) were also responsible for organising the first vicariance symposium at the AMNH in 1979, where many of the first discussions were held concerning biogeographic patterns in cladograms.



Donn Eric Rosen (1929–1986) in Nelson *et al.* (1987, p. 542). ©Copeia.

relationship to birds than they do to other members of the Reptilia. The microbe *Parakaryon myojinensis* is no different. Eukaryotes are a monophyletic taxon, but prokaryotes are non-monophyletic, meaning that *Parakaryon myojinensis* most likely belongs to a taxon that is more closely related to eukaryotes than it is to other members of the prokaryotes. The solution is taxonomic revision, to improve our way of communicating what *Parakaryon myojinensis* is, rather than by trivialising matters. In other words, Yamaguchi *et al.* see the world as complex, in which prokaryotes make no sense (because they are assuming prokaryotes are a real taxon), so they complicate matters further by trying to replicate that complexity. No discovery is made beyond that of a single microbe. Transitional fossils are nothing more than attempts at explaining the relevance of non-monophyletic taxa. Ancestors, however, are real and they too relate to other taxa that are not ancestors. Ancestors are as much part of a natural group, as a father or mother is part of a family unit. Mothers and fathers are merely designations for the progenitors of sons and daughters. Being a parent, just like being an ancestor, is not a characteristic, it does not form a relationship or a pattern, and it certainly is not part of the cladistic parameter. Identifying taxa as potential ancestors, and homologues as ancestral characteristics, are not discoveries – rather they are untestable hypotheses. Our taxonomies are the hypotheses and the cladistic parameter is the test for natural classification. As hypotheses of taxa, dinosaurs, reptiles and prokaryotes fail that test. But can the cladistic parameter be used to test for natural biogeographic areas? Here we return to Donn Eric Rosen and the beginning of cladistic biogeography.

Cladistic biogeography: the search for natural areas and their relationships

By the early 1970s, biogeography had been in a decades long hiatus. The ideas of early 20th century scientists, such as George Gaylord Simpson and Ernst Mayr, were still the mainstay of biogeographic theory and methodology. Cladistics had reformed natural classification by showing that homologues and homologies alone could be used to discover natural taxa and their relationships. The idea that ancestors were needed, let alone even necessary, in identifying natural taxa had diminished, but strangely not in biogeography. Even die-hard cladists insisted that ancestors were fundamental to understanding biogeography. The 'ancestors' in this case were dispersal events and ancestral areas (or vicariance). Studying distribution by itself was considered to be old-hat – a 19th century pursuit that ended at the dawn of the evolutionary age. Established scientists such as Mayr were quick to dismiss it as a dusty old science, such as taxonomy, until 'Eventually it was realised that the whole method of approach – *Fragestellung* [question] – of this essentially static zoogeography was wrong. Instead of thinking of fixed regions, it is necessary to think of fluid faunas …' (Mayr 1946, p. 5). 'Static zoogeography was wrong'? What was Mayr thinking? It was taxonomy and 'static zoogeography' that led to the discovery of evolution! Why, then, are evolutionary biologists, such as Mayr, so keen to dismiss it?

This question returns us to the problem of identification and classification. We may identify hypothetical events, processes or objects, such as identifying the ancestor to all primates, as did Franzen *et al.* (2009). The discovery of a fossil primate called Ida, and the media-circus that followed, attracted worldwide attention – even Google changed its logo for that week. Now compare this with classification, which remains silent about events, processes and ancestors. If we discover tomorrow that prokaryotes are in fact monophyletic, it may attract a small 200-word editorial in *Science* or *Nature*. You get to speculate a lot more when you describe and explain away hypotheticals, as opposed to discovering whether something is natural or not. This had been the downfall of taxonomy – its inability to comment on specific evolutionary events and processes. Rather than herald taxonomy (and later cladistics) as a way towards discovery, they were written off as 'static' and dusty: a 19th century pursuit worthy of 19th century naturalists.

Mayr's 'static zoogeography', was the search for a natural area classification – essentially an area taxonomy. Why it had proven old fashioned was its inability to test for natural classification. While taxonomists had robust homologues to use as evidence for their hypothesised natural classifications, biogeographers had an endless supply of worthless narratives that appeared dynamic, rather than 'static'. What biogeography needed was reform, in the same way that taxonomy had, through the adoption of the cladistic parameter. More still, biogeography needed evidence, not more hypothetical reasoning. Donn Rosen saw part of this reform coming from cladistics and the other from the work of Italian botanist Léon Croizat, who considered geography and geology as the homologues in biogeography. If biogeographers recognised that 'geology and biogeography are both parts of natural history and, if they represent the independent and dependent variables respectively in a cause and effect relationship, that they can be reciprocally illuminating. But for there to be reciprocal illumination between these two fields there must be a common language' (Rosen 1978, p. 187). This language, Rosen explains, is cladistics. But how do you combine cladistics, geography and geology?

From the very start, cladistic biogeography had two conflicting goals. Life and Earth evolve together is a great concept, but where do geology and geography fit in? Take the path paved by Croizat and we should be looking at geographical distance, geological structures, ocean basins, and so forth (see Chapter 5). Viewed from the cladistic side, we should be using the homologues and taxa from our monophyletic taxa. You can't do both, so what is going on? Cladistic biogeography started off as a methodological approach in cladistics, rather than as an independent biogeographical method, meaning that the sole focus is on taxa and homologues. Seen from a biogeographic perspective, such as that of Croizat, the emphasis is on geographical and geological processes, leading to the problem of what are the taxa and homologues in biogeography?

What is an area? Establishing the cladistic biogeographic method

The history of cladistic biogeography is that it is both complicated and convoluted. Even the name, cladistic biogeography, is derived from the work of vicariance biogeographers. From its inception in 1978, cladistic (vicariance) biogeography is representative of biogeography as a whole – a multidisciplinary field with many different, and at times conflicting, aims and goals. The reason, I believe, is that cladistic biogeography was introduced as a cladistic approach rather than as a totally new approach in biogeography. The emphasis was on determining the dispersal pathways and the ages of vicariant events within existing cladograms. Rather than reforming biogeography in the same way cladistics had reformed taxonomy, biogeography was nothing more than an evolutionary biology add-on. Mayr's ideas ran rampant across the branches of cladograms – where ancestors had been used as any other taxon along the tips of the branches, they were now firmly placed at its nodes. To the outsider, cladistic biogeography looked like an undisciplined technique without any theoretical justification. But this is not surprising given that the main text cited in early cladistic literature, Hennig (1966), introduced these ideas, which were popularised by Lars Brundin in the same year. The main thrust of Hennig and Brundin's work was that the direction of dispersal could be worked out from looking at the position of taxa and the areas they inhabit on a cladogram. Hennig termed this the 'progression rule', and it meant that taxa at the base of the cladogram were closer to the ancestral area and taxa further up in the terminal nodes were the descendants, which were located further away geographically. But this form of reading ancestors off a tree was an anathema to Rosen and his colleagues Gary Nelson and Norman Platnick. Clearly cladistic biogeography looked in such utter disarray not because it has no theoretical grounding, but because its aims are in total conflict. Hennig and Brundin wanted a way to interpret the geographical history of their taxa, while Rosen, Nelson and Platnick wanted to apply the cladistic parameter to areas. The clash between these two different approaches, which share little other than same name, became apparent at the Symposium of the Systematics Discussion Group of American Museum of Natural History held at the AMNH in New York between 2 and 4 May 1979 (Nelson and Rosen 1981). There Brundin (1981a) stood up to Rosen's vicariance biogeographers (Platnick 1981) and defined his progression rule by disassociating himself from the whole topic: 'A more adequate name for my biogeography would be "Phylogenetic biogeography according to the vicariance/dispersal model"' (Brundin 1981b, p. 153).

At the heart of the issue was whether vicariance/cladistic biogeography has the means to function as a biogeographic approach, separate to that of cladistics. Rather than an add-on to cladistic analysis, would cladistic biogeography move beyond a taxon-driven science to an area-driven one? The critical element was identifying the unit of classification or, more accurately, what was vicariance/cladistic biogeography trying to do? At first the name seemingly betrayed the approach – vicariance was seen incorrectly as the opposite of dispersal. Ideas about dispersal hadn't changed much since the early 18th century when naturalists talked of animal distributions deriving from some ancestral stock. Dispersal is dependent on ancestor–descendant narratives and time. Like a hypothesised evolutionary lineage in palaeontology, dispersal was unobservable and impossible to test (and remains so today). Vicariance, on the other hand, focused on the breaking up of an ancestral area. Like ancestors in taxonomy, both dispersal and vicariance suffered from a lack of evidence. Or so it seemed. Although ancestors cannot be seen, we can still infer them from monophyletic taxa. If two or more taxa are more closely related to each other than they are to anything else, they probably share a common history. That common history could be inferred to be a common ancestor. Translate this into cladistic biogeography and you have a hypothetical ancestral area. Vicariance *could* be tested, but the events *could not* be identified. In effect you have half the story, but if you are looking at areas rather than individual taxon histories, then you have what is needed. But for many biogeographers in the 1970s this wasn't enough. Most biogeographers did biogeography because they wanted a model of their taxon's geographical history. Areas were of minimal significance, leading us back to the question, 'what is an area?'

Donn Rosen, who was interested in the distributions of his poeciliid fish (tropical fish), argued that a biogeographic area was an endemic area. When Rosen discovered that two of his fish genera (*Heterandria* and *Ziphophorus*) had overlapping endemic areas, he concluded it was probably because they shared a similar geographical history in which their distributions were effected by the same geographical events. Rosen's 'cause and effect relationship' is 'reciprocally illuminating', meaning that overlapping endemic areas or biotic areas represent past geographical or geological events. If these geographical events isolated Rosen's fishes in the same way over the same time period, then these taxa will share the same relationships. For Rosen, the areas were not geographic in the sense of streams and lakes and mountains, but biotic – that is, the space inhabited by a biota, which is shaped by geography. Look for the relationships between biota and you have found geographical congruence.

Rosen's approach makes cladistic/vicariance biogeography a purely biogeographic approach, which is separate from the cladistic focus on taxa. But for cladistic biogeography to work using cladistic methods, the translation from taxa to areas had to be clear. The unit of study in cladistics is the homologue, and in cladistic biogeography it is the endemic area. If the overlapping relationships of homologues find our natural taxa, then overlapping relationships of endemic areas will discover natural areas (Table 1.1). Cladistic biogeography was no longer a technique applied after cladistic analysis to generate a narrative; rather it was a biogeographical approach that looked at the inter-relationships of biota using cladistic techniques. The independence of cladistic biogeography was final, much to the confusion of other cladists. Seen as a technique applied after a cladistic analysis, many cladists saw cladistic biogeography as obscure, even inflammatory. For example, the lack of any dispersal hypothesis was seen to be a major flaw in cladistic biogeography. Ironically, evolutionary biologists such as Mayr saw cladistics as a failure because it did not identify ancestors. The independence of cladistic biogeography as a way to find and test for natural area classification has been, and still is, misunderstood. Regardless, Rosen, Nelson and Platnick's cladistic biogeography was truly a reformation of biogeography, making it independent of evolutionary biology and the geographical 'ancestry' of taxa or 'lineage geohistory' (Ree *et al.* 2005).

Table 1.1. Equivalence table of terms used in cladistics and cladistic biogeography.

Cladistics	Cladistic biogeography
Taxon	Biota
Homologue	Endemic area
Homology	Endemic area relationship
Monophyly	Geographical congruence
Ancestor	Ancestral area
Common ancestors	Vicariance
Ghost lineage	Dispersal

Biota are the organisms that inhabit a geographical area that share the same history. Treating biota as taxa and endemic areas as homologues makes cladistic biogeography highly effective in finding natural biotic regions. Geographical congruence, that is area monophyly, is the evidence for a natural biotic area. Few discoveries of natural biotic areas have been made since Latreille (1815) and Candolle (1805, 1820) who were among the first to propose endemic areas and natural biogeographic regions. The lack of such discoveries might astound, but the rocky history of cladistic biogeography had rarely shown the practical applications of natural biotic areas. Rather the opposite was true. Cladistic or vicariance biogeographers had one problem – a lack of good quality and overlapping cladograms. Rosen's example was unique, and few had the data to make cladistic biogeography practical. In hindsight, it may seem that cladistic biogeography had arrived too early, like the light bulb arriving before electric wiring. Even with sufficient data, geographical congruence is often difficult to find. This had led to many abandoning the approach in favour of narrative approaches. In doing so, cladistic biogeographers were unable to test their methods on real data, meaning that most theoretical and methodological studies were either based on hypothetical examples or the same data, namely Rosen's poeciliid fishes. Cladistic biogeography was a brilliant method, but few biogeographers had enough overlapping data to use it, and fewer still were interested in finding natural biotic areas. Even today the particular application of natural biotic regions to biogeography is unknown, particularly in the ancestral modelling community, where arbitrary areas are used to create intricate biogeographical models. What use is a model that is based on an arbitrary area, particular when the model changes once the areas are changed? Surely a way to test for natural biotic areas would be a must in such a case? Could we say that since 1978, vicariance/cladistic biogeography hasn't reached an appropriate audience? Has the reform of biogeography simply been delayed and is yet still to come?

How to do cladistic biogeography (or how to start reforming)

Before answering any question on biogeographic reform, I wish to show how a cladistic biogeography is done in principle. Like taxonomy, I wish to show that cladistic biogeography is *area taxonomy* – a scientific approach that is best shown (or described in this case), rather than argued at the narrative level. A cladistic biogeographic study can be done in three steps, as described below.

1. Propose endemic areas

Like species concepts, area definitions are rife in biogeography. In 2009, Lynne Parenti and I counted 22 definitions for the term 'endemic area', the majority of which were largely defined as the overlap of two taxon distributions. A biota refers to all the taxa that live in that endemic area. How then do you find an endemic area? Like species in taxonomy, the endemic area is subjectively proposed by the classifier. Although there are morphometric programs that can do something similar for you, they too are subjective because not all phenotypic measurements are homologous. The same is true in defining areas. Although there are many sophisticated ways to propose an endemic area using geospatial software, for example, they still remain subjective because areas change over time. Consider a species of crayfish endemic to a meandering river. Over time, the endemic area would cover much of the floodplain over which the river meanders. Over time, both the crayfish and the trees either side of the river bank share the same endemic area, meaning that a region we see today may not be the whole area. In any case, arbitrary endemic areas remain as the basis for a cladistic biogeographic study and are the equivalent of an area homologue. In our hypothetical study we have five areas: A–E.

2. Find geographically overlapping endemic areas

Choosing geographically overlapping endemic areas in different cladograms is paramount. Once the endemic areas are proposed, the names of the taxa that occur are replaced by the names of their endemic areas. The result is an areagram – namely, a branching diagram that shows the relationships between the areas. Any information regarding the taxa, such as shared homologues, is no longer considered. The areagram is an area homology. In our analysis, we have three areagrams that share our proposed five areas – namely:

Areagram 1: (((A,B),C),(D,E))

Areagram 2: ((A,B),(D,E,(D,E)))

Areagram 3: ((A,B),(D,(D,E)))

Note that in areagram 2 a single taxon is found in two areas, D and E. The resulting structure is called a mast (multiple areas on a single terminal-branch), and represents a single taxon. Similarly in areagram 3 we have a duplication of area D, meaning that two taxa occupy the same area. Area duplication is called geographic paralogy. Given that we are viewing life as monogenetic – that is, a single species stems from a single place – then only one area can occupy a single terminal-branch at a single time. Geographical paralogy is problematic because it is duplication of the same area on different branches. An effective way to eliminate paralogy is to simply reiterate the relationship. In areagram 3, for example, D is more closely related to E than it is to either A or B, and A and B are more related to each other than they are to either D or E. In other words, ((A,B),(D,E)). The area relationships do not have to conform to the same branching structure as the parent cladogram: only the relationships need to be the same. Masts are harder to eliminate because they contain potential information. In areagram 2, for instance, we do not know whether D or E is paralogous. The trick is to write out the relationships separately as two areagrams:

Areagram 2a: ((A,B),(D,(D,E)))

Areagram 2b: ((A,B),(E,(D,E)))

Once we reiterate the relationships, we find that both D and E are paralogous and that, in each case, D is more closely related to E than it is to either A or B, and A and B are more related to each other than they are to either D or E. The informative relationships, then, are:

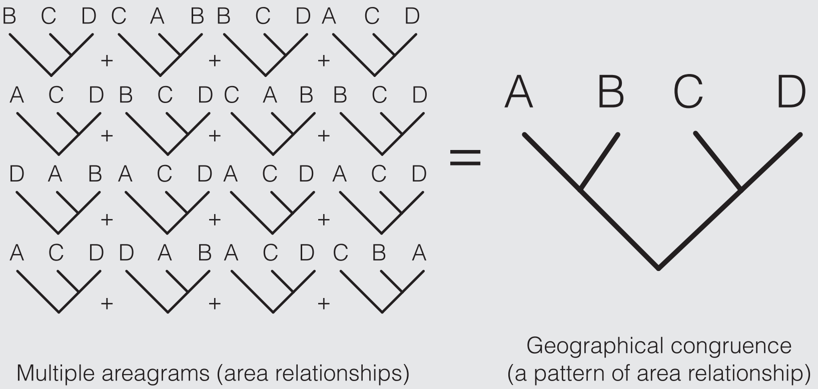
Areagram 1: (((A,B),C),(D,E))

Areagram 2: ((A,B),(D,E))

Areagram 3: ((A,B),(D,E))

Relationship of distributions

An areagram is the relationship of natural distributions (endemic areas). A pattern of area relationship (general areagram) is acquired when two or more overlapping areagrams are combined. This pattern is termed *geographical congruence*, and is evidence for a common biotic history. Areas that share a common biotic history are part of a natural biotic area.



Multiple areagrams (area relationships)

Geographical congruence (a pattern of area relationship)

Relationship of distributions and a pattern of relationship.

3. Find geographically overlapping endemic area relationships

In order to find geographical congruence, namely area monophyly, we add the areagrams together:

Areagram 1: (((A,B),C),(D,E)) + Areagram 2: ((A,B),(D,E)) + Areagram 3: ((A,B),(D,E)) =
General areagram 1: (((A,B),C),(D,E))

The general areagram is a pattern and a discovery – namely that D is more closely related to E than it is to either A or B, and A and B are more related to each other than they are to either D or E. The problem here is area C, which is only based on a single relationship in areagram 1. Although area C fits into the general areagram, there is no evidence to suggest that it either conflicts or agrees with the overall pattern. Until another areagram is added, we cannot be sure where C fits into the general areagram.

The approach may appear simple, but the reality of proposing endemic areas into which the distributions of taxa fit neatly is extremely difficult. Moreover, finding overlapping areagrams is equally difficult. The analysis of removing paralogy and resolving masts is easy, as is finding the general areagram. Where things become complicated is when the approach is used in areas that may contain temporal holdovers.

A holdover is a common phenomenon in palaeobiogeography. When a fauna or flora of one period is found to exist in another, possibly due to low extinction rates, it intermingles with the newer biota. The problem with a temporally mixed biota is that it has two different histories, which may not share the same area relationship. What is more, temporally mixed biota overlap geographically, meaning that two biotic areas share the same geographical space. For example, we may find that areagram 4 and areagram 5 share different relationships, namely,

Areagram 4: ((A,(B,C)),(D,E))

Areagram 5: ((A,B),(C,(D,E)))

Added together the pattern shows that area C is in conflict:

General areagram 2: ((A,B),C,(D,E))

We find that area C contains two temporally and geographically overlapping biota, C_1 and C_2. Given this the areagrams are rewritten as:

Areagram 4: $((A,(B,C_1)),(D,E))$

Areagram 5: $((A,B),(C_2,(D,E)))$

Together the areagrams form a single pattern:

General areagram 2: $((A,(B,C_1)),(C_2,(D,E)))$

Although areas C_1 and C_2 inhabit the same geographical space, they are not more closely related to each other than they are to any other area. This technique is referred to as time-slicing and can be used to resolve potential area conflict (Humphries and Ebach 2004). In the example above, we are still faced with the problem of finding further evidence to support or deny the relationship of C_1 and C_2 to the other areas.

The prospect of there being temporally and geographically overlapping areas also means that all biotic areas – that have ever existed and will ever exist – are related to each other. That relationship could be theoretically expressed as a single *areagram of life*, in the same way taxonomists refer to a 'tree of life'. The aim of cladistic biogeography is to find that single general areagram of life that shows the relationship of every biotic area that has ever existed. Just as it is impossible to find the complete tree of life the same is true for the areagram of life. Yet, we can find fragments and piece these together to get a good understanding of taxic, as well as biotic, relationships. The National Science Foundation in the United States has poured millions into finding the tree of life (Cracraft *et al.* 2000), why not do the same with the areagram of life?

With geographical congruence as the goal and cladistics as its method, cladistic biogeography has the ability to reform biogeography, moving biogeography beyond a narrative-based approach into an analytical or evidence-based approach. Pattern – in this case geographical congruence or area monophyly – is the evidence for natural biotic areas. How, then, can we monitor any reform within biogeography? English biologist Ian Ball saw biogeography 'as passing through three phases: the descriptive or empirical phase, a narrative phase, and an analytical phase, the last two comprising of historical biogeography' (Ball 1975, p. 408). The historical biogeography that Ball refers to includes cladistic biogeography. Ball's phases could be used as an indicator to monitor reform considering that the analytical phase relies on more than just a narrative.

Ian Raymond Ball (1941–2000)

Ian Ball was an English flatworm taxonomist who worked at the National Museum of Natural Sciences in Ottawa and the Royal Ontario Museum in Toronto, Canada, as well as the Universities of Amsterdam and Newfoundland, before accepting a position at the University of the West Indies in Kingston, Jamaica. Ball is world-renowned for his work on taxonomy and for his famous 1974 contribution to the phylogeny and biogeography of freshwater tricalads (Ball 1974). In 1990, Ball produced an update to his three phases in which he proposed three facets in framing biogeographic hypotheses in regards to vicariance (cladistic) biogeography and monophyly – namely *clarity*, *comparability* and *rigour*. Together, these facets can test for a general history across multiple monophyletic taxa. Ball (1990) also recognised that unique histories of individual taxa are not compatible nor do they offer clarity in terms of a common history or rigour. These individual narratives 'rely on "expert authority" for their survival; usually die with their protagonists' (Ball 1990, p. 5).

Ian Raymond Ball. Photo taken at the Third International Symposium on the Biology of the Turbellaria Diepenbeek, Belgium (in Schockaert and Ball 1981, p. X).

Reform and the three phases of biogeography

Ball's biogeography is a very different beast. Rather than focusing on classification, it refers to a hypothesis-based approach in an 'explanatory historical biogeography' – one that asks questions beyond 'are my areas part of a natural classification'. In the period when Ball erected his three phases – the descriptive, narrative and analytical – Rosen (1975, 1978) was coming to grips with geographical congruence, and the principles of vicariance/cladistic biogeography were emerging in the works of Nelson and Platnick (Platnick and Nelson 1978; Nelson and Platnick 1981). In hindsight, one gets the feeling Ball wrote his piece decades too soon. In 1976, biogeography was only about erecting narratives based on untestable assumptions, something which invoked the ire in Ball (1975),

> 'In erecting a biogeographical hypothesis we have a responsibility to do more than simply explain the facts at our immediate disposal' (Ball 1975, p. 423).

Ball saw that many biogeographical hypotheses were untestable, such as chance dispersal. His own solution was to use the hypothetical deductive method of Popper (1959), which allows hypotheses to be tested via the elimination of error. But how do you falsify a hypothesis that refers to an unobservable process? If, for instance, we say that this fossil in my hand is the oldest known trilobite, we would have to find an older trilobite in order to falsify this hypothesis. What if an older trilobite was not preserved, or not found? We simply do not know whether we are holding the oldest trilobite. Given that most hypotheses in historical science are based around unobservable processes and events, such as the 'oldest' species, we are stuck in a cycle of proposing untestable hypotheses and using a narrative to ensure its veracity. Effectively, the reinvention thesis is part of Ball's narrative phase – namely to test explanatory hypotheses. Ball intended to use Popper's method to test these explanatory hypotheses in his analytical phase. But, rather than sort good hypotheses from bad, Ball identified a serious problem – untestable explanatory hypotheses. What do you do with untestable hypotheses? Ball's analytical phase found no solution.

Let's take Ball's descriptive and narrative phases and adopt cladistic biogeography, and geographical congruence, as part of a new analytical phase, as Ball (1990) did – the phase of reform. Together these three phases form a procedure, or steps, within the reformation of a scientific discipline. As steps, there is no single direction or temporal succession. The analytical phase is both the beginning and end of the reform. Natural classification, the goal of cladistics and cladistic biogeography, was also the first goal of early naturalists, such as John Ray, Joseph Pitton de Tournefort and Michel Adanson who sought a natural classification for plants, and Carl Linnaeus and his followers, who as pragmatists saw it as unachievable. Ray, de Tournefort and Adanson failed to find a natural classification. Linnaeus's victory was Pyrrhic, because he too wanted a natural classification, but instead created a partial artificial classification, albeit one that worked for identification purposes. The anticipation of natural classification kick-started the analytical phase – the search for a method occupied the minds of early plant geographers such as Alexander von Humboldt and Augustin de Candolle. The descriptive phase of recording measurements, producing maps and statistical lists was all they could do instead. Humboldt mapped and measured vegetation across present day Colombia and Ecuador and de Candolle mapped the flora of France and proposed the plant regions of the world. The narrative phase came with explanations as to how organisms got to where they are and gradually evolved with the descriptive phase. As Alfred Wallace mapped the zoological regions of the world, the narrative phase became more complex, with explanatory detail as to how animals in both the Nearctic and Palaearctic looked so alike that perhaps it was a single region, the Holarctic. The descriptive and narrative phases evolved together to form what we have today: a complex morass of maps and measurements with even more complex explanations that can only be processed by a computer algorithm. Technology has not helped. Models are now so complex that many biogeographers have no idea what these computer programs do. The trend has been consistent over 200 years, and in between, there have been attempts at establishing analytical phases. These attempts at reform failed because they were not concerned with making sense of complexity and deriving meaning from noise. Instead, they have been calls for further integration of more and more fields: ecology, conservation biology, human geography, and so on. Biogeography has grown, not only in size but also in its aims and goals and approaches.

Australian and New Zealand practitioners played an important part in the development of biogeography, from the discoveries of Australasian taxa to the more complex methods of today. The attempts at some type of reform – a way to make sense of biogeography as a whole – has been largely based on narratives. Also, Australasian biogeography has developed its descriptive phase, by endlessly reinventing the Australasian biogeographic regions. This book is about the development of Australasian biogeography through the descriptive and narrative phases and attempts at reform: the analytical phase. Early New Zealand biogeographer Captain Fredrick W. Hutton thought that by finding a sunken Pacific continent, he would unify biogeography and help explain the odd distributional relationships between Australia, Antarctica and South America. Charles Hedley, an Australian malacologist, was more pragmatic and dismissed Hutton's sunken continent. Rather he saw area classification as a way to make sense of Australasian plant and animal distributions. A student revolt in 1980s New Zealand was perhaps the most daring attempt at reform in the history of biogeography. Followers of Croizat, the panbiogeographers, nearly overthrew an establishment (Chapter 5). A revolt against the panbiogeographers saw New Zealand biogeography returning back to Hutton, but this time in a more dramatic sense – the total drowning of New Zealand 30 million years ago (Mya), and the emergence of a new biota, one without relict taxa. This effort at a reform had only stirred the ire in many biogeographers, who, like Hedley, were quick to quash any notion of sunken continents. Yet, as we explore the depths of the oceans and the far reaches of the Antarctic, we find that life too has settled in these extreme places. Biogeographers, rejoicing in these new discoveries, have a unique chance at doing something that only 19th century plant and animal geographers had experienced – the discovery of new biogeographical regions.

But reform still has not come to Australasian biogeography. Perhaps it is there in the making, either through the pursuit of natural classification or in the discovery of an ultimate biogeographical synthesis, like plate tectonics in geology. Like their colleagues across the planet, Australasian biogeographers continue to work towards breaking through cycles of reinvention and reforming biogeography. The journey of biogeographic discovery is still in the making.

Chapter 2

Biogeography comes to Australasia

In order to better come to grips with the reinvention of Australasian biogeography (herein the reinvention thesis), we need to look at how early biogeographers practised plant and animal geography and why biogeographers keep returning to the same old concepts that were previously rejected. For instance, the first biogeographical treatment by Joseph Dalton Hooker set the scene for the early hypotheses on the origins of the Australian flora, many of which have been reused in the 20th century. In particular is the use of the terms biome and elements, in favour of regions. The distinction between biogeographical areas and biomes is most likely due to the tension between taxonomic and ecological biogeographic approaches. Certainly by the early 20th century, plant geography had distanced itself from traditional taxonomic principles and classification, leaving a conceptual gap between zoogeographers and phytogeographers – one that still persists in current Australasian biogeography.

Biological classification and biogeography: a condensed history

A common misunderstanding in modern biogeography is that plant and animal biogeography share a common history in single works or people, most notably Charles Darwin, Alfred Russel Wallace or Alexander von Humboldt. Strangely, few have seen the paradox: why would three people doing three different things at different times be considered points of origin for a single common subject? Darwin was interested in species and their origins; later in life, Wallace was interested in the natural regions of the world; and Humboldt was interested in vegetation formations. If we dig further, we also notice that the term ‘biogeography’ has different origins. Herman Jordan, a forgotten German malacologist, was first to coin the term ‘biogeographie’ (Jordan 1883) when comparing regions of Schmarda (1853), Grisebach (1872), and Wallace (1876). Later, Friedrich Ratzel (1891), a German geographer, called to unify plant and animal geography under a common field, ‘allgemeine [general] biogeographie’ – one that falls under the science of geography. A year later, the term ‘biogeography’ first appeared in English to define life zones – the geographical regions of North America (Merriam 1892). What is striking is that the term ‘biogeography’ was never once defined. With these historical facts in mind, one wonders whether biogeography actually has a single origin at all. But in each of the cases above, the mention of the term biogeography did involve an area classification: Jordan and Merriam debated the merits of Wallace’s Sclaterian areas, while Ratzel investigated how human geography would fit into existing biogeographic regions.

Area classification has been a driver of plant and animal geography – one that had its origins in animal and plant taxonomy and in Humboldt’s plant geography. The resulting dichotomy in area classifications is perhaps the great legacy of 18th and 19th century plant and animal geography – one that still persisted throughout the 20th century and is still with us in the 21st. The aims, goals, methods and hypotheses of 21st century biogeography, however, have their origins in the mid to late 20th century. Island biogeography (MacArthur and Wilson 1963, 1967), for instance, has its origins in population dynamics, rather in Wallace's own biogeography of islands (Wallace 1881).[6] Cladistic biogeography has its origins in the work of Donn Rosen, Norman Platnick and Gary Nelson (Rosen 1975, 1978; Platnick and Nelson 1978; Nelson and Platnick 1981); phylogenetic biogeography in Hennig (1966) and Brundin (1966); and phylogeography in molecular systematics (Avise *et al.* 1987). More recent methods, such as ancestral reconstruction, have their origins in even later work (Bremer 1992; Ronquist 1997). Few methods have a 19th century, let alone early 20th century, origin, other than area classification and the pursuit for natural biotic areas.

The two area classifications: the triumph of Humboldt's plant geography

Traditionally, practitioners of plant and animal geography, particularly in the 18th and 19th centuries, used ideas and approaches intrinsic to their own fields. Taxonomists such as Augustin de Candolle (1805, 1820), Pierre André Latreille (1815) and William John Swainson (1835), used areas based on taxic distributions. They explained their distributions through soils, climate, dispersal ability, and so on. Taxonomic area classifications, then, were based on overall distribution, regardless of the mechanism that caused these distributions – after all, 19th century naturalists thought that the Earth, with its fixed continents, underwent gradual climatic changes. Alexander von Humboldt turned the tables. Nature, particularly the plant world, was defined by the climate, temperature and rainfall. A rainforest plant, for instance, was tall with a large canopy and lived in a warm tropical environment. Nature herself had created the plant form (the tall canopy tree), and the vegetation formation (the rainforest). Humboldt had discovered a new way to classify plants based on where they are found and in doing so had created a geography of plants (von Humboldt and Bonpland 1807). The only role taxonomy had to play in his geography of plants was to identify the species that made up vegetation formations. In fact, you could even do the geography of plants using unidentified species: something that would have been impossible to do using de Candolle's botanical geography.

The botanical geography of de Candolle counted the number of endemic species and genera within an area. A smaller area would accommodate endemic species, while a larger region, such as a continent, would contain endemic genera. The distributional mechanisms for each differ: species in smaller areas are directly influenced by the environment they are found in, while genera are a result of older geographical or geological processes (Nelson 1978). At first this seems to overlap with Humboldt's version of plant geography, but there is a significant difference – Humboldt was looking at *plant forms* not species. A plant form is any plant that has a similar shape and functions in a similar way within a vegetation. For example, in the Australian subtropical rainforest, the coachwood (*Ceratopetalum apetalum*) and the sassafras (*Doryphora sassafras*) would be classified as the same plant form, even though they belong to two different families: the Cunoniaceae and Laurales, respectively. Moreover, the same plant form can be found in any rainforest, meaning that there would be no difference between the plant forms of, say, the Atlantic forests in Brazil than the south-eastern Australian forests, while the species compositions would differ dramatically. By the early 19th century, plant geography had two very different classification schemes that were used in conjunction: vegetation and taxic distributions. But how did they differ to a practitioner living in the early 19th century? Humboldt's approach was largely empirical. It required measuring temperature, air pressure, altitude and rainfall, as well as determining the physiognomic characteristics of the vegetation. The approach of de Candolle simply meant counting the numbers of unique taxa in a proposed region and determining whether the region is endemic or not. Consider the practical application of both approaches in terms of time and money. Humboldt's own study of Mount Chimborazo in present day Ecuador was part of a 5-year expedition through South America, measuring and collecting. Moreover, Humboldt was a wealthy aristocrat and had spent the lion's share of his inheritance on the expedition. In comparison, de Candolle could divide the natural world into 20 plant regions using nothing but a library or herbarium. The difference between both methods is one of practicality. Few naturalists in the 19th century had the time or money to embark on large expeditions, which were usually reserved for teams of scientists, as they are today. In fact, it was easier and cheaper to trawl through travelogues and textbooks, than travel and measure temperature and soil moisture.

Animal geographers of the early 19th century had other challenges. They were chiefly concerned with the nature of species and their distributions. The animal kingdom didn't have faunal formations or animal forms. There was no equivalent Humboldtian method in early 19th century animal geography. For example, a desert fox and arctic fox were very much alike, so too are black bears and polar bears. Rather, the debate focused around the concept of species and race. For instance, a polygenist would consider animals to be created in the places where they were found, while a monogenist would face a greater problem of understanding how species of the same genus got to the far-flung places where they are found. The same problem could also be said of vegetation and the distribution of plant taxa. A vegetation is created in the place where it is found, while the distribution of plant taxa needs a law of distribution, beyond what can be observed and measured. How then can a 19th century plant or animal geographer explain the distribution of a widespread species or genus?

Distributional laws for vegetations were simple to quantify, but the distributions of species were not. Humboldt had the foresight to understand this problem and classified his own method as geographical and the distribution of taxa as historical. You needed historical processes that are not directly observable or measurable to understand the historical distribution of plant and animal taxa. With the plethora of travelogues being published throughout the 19th century, which included measurements of vegetations, ocean currents and weather patterns, Humboldt's geography of plants, like de Candolle's method, became a far more practical method – one that anyone could do with access to a library. The historical approach of de Candolle became too complicated, possibly due to a lack of data, but most likely because there was no satisfactory fundamental law of plant distribution. In 1855, de Candolle's son, Alphonse, rejected his father's approach as being 'too arbitrary' (de Candolle 1855). By the mid-19th century, taxonomic plant geography died. Alphonse preferred the

Humboldtian or proto-ecological approach for smaller areas, and endemism for larger areas – one that factored in an evolutionary law of distribution.

By the mid-19th century, zoogeographers too were attempting to adopt a Humboldtian approach for animals. Karl Ludwig Schmarda attempted a bioregionalisation based on climate and animal distributions (Schmarda 1853). But the approach was not successful, nor was it widely adopted. At the same time, Philip Lutley Sclater attempted a hierarchical classification of the bird regions of the world (Sclater 1858). His classification was to change how zoogeography was done for almost a century. Rather than investigate distributional laws, he set the seed for natural zoogeographical regions, something that appealed to Alfred Russel Wallace. Sclater's regions were adopted by Wallace (1876), and by the whole zoogeographical community by the late 19th century. What made the classification successful was that it united zoogeographers with differing views on distributional laws. Sclater was a polygenist, whose areas were adopted by a monogenist. In fact, the Sclaterian regions of Wallace are still with us today (see Holt *et al.* 2013); however, our laws of distribution have changed considerably since the late 19th century. If Wallace's regions are compared with the plant regions defined by vegetation formations, we see that between 1858 and 1899, Wallace's area essentially remained the same, while new classifications of vegetation formations were being proposed over and over again (Grisebach 1872; Drude 1890; Warming 1895; Cowles 1899). German botanist Oscar Drude (1890) believed that the fault lay in the hierarchical nature of the classification system. Although vegetative formations were fairly stable in the classification, it was the higher units that posed the problem. These units were based on the distribution of key taxa, families and genera that to Drude belonged in an artificial Linnaean taxonomic system. Instead, Drude (1890) proposed that all levels within a natural vegetation classification discard taxonomy and employ vegetation classes. These 'considerations', Drude argued, would 'lead to the implementation of an autonomous biological system' (Drude 1890, p. 62, translated in Ebach 2015).

Drude had proposed a hierarchical natural classification system of vegetation, of which the most important unit is the formation. In criticising the Linnaean system of classification, Drude had little idea of how much the concept of a formation could vary between practitioners. In 1916, American ecologist Frederic Clements listed seven different definitions of a formation, which suggests an unstable classification system. In contrast, the taxonomic system remains stable *because* it does not rely on a single definition of a species or genus. These multiple definitions didn't deter Clements, who simply redefined formation once again.

Clements (1916) first coined the term biome, which referred to 'human evidence of past climates and biotic communities', namely 'the biome or plant-animal formation is the basic community unit', that is, 'a logical outcome of the treatment of the plant community as a complex organism, or super-organism, with characteristic development and structure. As such a social organism, it was considered to possess characteristics, powers, and potentialities not belonging to any of its constituents or parts' (Clements and Shelford 1939, p. 20). Had ecologists finally found a stable unit of classification? Unfortunately not.

Many ecologists, particularly English ecologist Arthur Tansley, rejected Clement's 'complex organism' and 'biotic community'. 'Clement's earlier term "biome" for the whole complex of organisms inhabiting a given region is unobjectionable, and for some purposes convenient. But the more fundamental conception is "… whole complex of physical factors forming what we call the environment of the biome – the habitat factors in the widest sense"' (Tansley 1935, p. 299). Here we start to see what is a modern concept of the biome, the 'plant and animal community of a major climatic region or type of habitat' (OED 2015b), or is it the 'plant formations with the animal constituents integrated' (Shelford 1978, p. 16)? The definitions and uses of biomes vary, leading one leading ecologist, Paul Colinvaux to state, 'The word biome is useful for impressing the layman with superior and mysterious knowledge, but otherwise it is unfortunate. The word is redundant, since "the tropical rain forest biome" conveys no more to the reader than does "the tropical rain forest"' (Colinvaux 1973, p. 57). Why then use the term? Colinvaux gives a sensible answer,

> '… the great technical difficulty of plotting the distributions of animals has led ecologists to forebear developing maps of animal distributions very far. Instead, they have conceded that the distribution of animals is so tied up with the distribution of the vegetation in which they live that it is best to accept the formation boundaries and to include the animals in the formation descriptions. The formations then become biomes, and people speak of the tropical rain forest biome instead of just the tropical rain forest' (Colinvaux 1973, p. 57).[7]

Australian biogeography has done exactly this since the late 19th century – namely, tie up the distribution of animals with the distribution of the vegetation. In doing so, the vegetation describe animal distributions, but remain silent about the distributional history of animal and plant taxa, such as their origin and migration routes. To compensate for a lack of historical biogeography, the term 'elements' had been used to identify parts of the biome that have their origins elsewhere. This duplicitous system of biomes and elements is both contrary and confusing. A biome with different elements would imply that it has different origins, in the same way that a non-monophyletic taxon has multiple origins. A non-monophyletic biome is not representative of a biota, then why confuse biotic areas and biomes? I will attempt to answer this using Australasian biogeography as an example.

Australian biogeography: flora, fauna, elements and biomes

Ironically, biologists are not fond of neologisms, but coin more terms than they really need. In the 19th century alone, the study of the distribution of plants has been called 'phytogeography', 'plant geography', 'geography of plants', 'historical plant geography' and 'biogeography'. When authors coined these terms, only a vague description accompanied each. Regardless, biogeography is full of such terms and one that is used often by Australasian authors since the 19th century is 'element'.

Like the term 'biogeography', 'element' was never formally defined in the literature and is used in various ways by different authors. For late 18th and early 19th century naturalists an element was an actual inorganic component inhabited by an organism:

> '… their element being for the greatest part the water' (Pennant 1781, p. viii)

> '… elements in which they naturally dwell' (Agassiz 1850, p. 194)
>
> '… no fish can exist unless in its own element' (Swainson 1835, p. 250).

To others it represented a taxonomic group:

> 'The Rodents also form a very conservative element of the Upper Eocene group of animals' (von Zittel 1893, p. 411)
>
> '… elements of a continent fauna' (Hutton 1873, p. 227).

The most common usage is that of a taxonomic assemblage typical of an endemic or foreign biota:

> '*Acacia* species belonging to the tropical-African Element, are separated from southern African species' (Drude 1890, p. 146, my translation)[8]
>
> '… presence of a Notogaeic element in the fauna of Neogaea' (Lydekker 1896, p. 127).

Most frustrating of all is that not all authors use the term in exactly the same way (or if at all), as in the case of Hedley or Wallace. In Australian botany, the term element is useful in determining the origins of plants that make up Australia's flora. In fact, 'It is customary to regard the Australian flora as consisting of three main elements: the Australian or Autochthonian, the Antarctic, and the Malaysian (sometimes called the Indo-Malayan or even the Indo-Melanesian)' (Burbidge 1960, pp. 91 and 167). CSIRO botanist Nancy Burbidge represents a milestone in mid-20th century plant geography. Her 1960 monograph, *The Phytogeography of the Australian Region*, a citation classic and often used by biogeographers, is representative of early 20th century Australian botanical biogeography. Published on the eve of the plate tectonics revolution, Burbidge did attempt to incorporate continental drift into her hypothesis, noting that 'drift does not solve all the difficulties, especially within the available portion of the time scale' (Burbidge 1960, p. 156; also see Chapter 6). What Burbidge did do was redefine Australia's botanical regions in light of distributional hypotheses current at the time. The result was interzone areas, or regions of overlap, which included the McPherson–Macleay overlap zone. Burbidge did, however, refer to elements, and in doing so, may have unwittingly created a popular myth[9]:

> 'It was Hooker [1859] who first drew attention to the relationships between genera of isolated land masses in the southern hemisphere and to the presence, in the Australian flora, of elements that could be referred to as "Antarctic"' (Burbidge 1960, p. 155).
>
> 'Nancy Burbidge's own great summary in 1960 of the phytogeography of the Australian region was the apotheosis of a conventional interpretation that had continued from the time of J.D. Hooker' (Schodde 1989, p. 2).

Burbidge's claim may have started off the erroneous assumption that Joseph Dalton Hooker 'thus identified three elements in the Australian flora [i.e. Autochthonous (Australian), Indomalayan and, Antarctic]' (Barlow 1981, p. 26; see also Beadle 1981,

Nancy Tyson Burbidge (1912–1977)

British-born Nancy Burbidge was a botanist who worked for the Plant Industry Division at CSIRO. Her monograph *The Phytogeography of the Australian Region* is considered a landmark in Australian biogeography. Burbidge is also instrumental in suggesting that climate, and not continental drift, is responsible for plant distributions in Australia. Although Burbidge did support the invasion hypothesis, she did also consider the possibilities of overlap zones, such as the McPherson–Macleay overlap zone in eastern Australia. In 21st century Australian phytogeography, Burbidge's work is still important in providing an explanation for possible zones of overlap in south-western Australia.

Nancy Tyson Burbidge. Photographer: Colin Totterdell, CSIRO Science Image.

p. 409). While the misattribution is trivial, it does highlight the ecological rather than taxonomic nature of interpreting Australian biogeography.

Hooker described seven floras (including plants) and three 'features of the Australian Vegetation': 'Tropical Australian Flora', 'Flora of Extratropical Australia', 'Flora of the countries round [sic] Spencer Gulf', 'Tasmanian Flora', 'New Zealand and Polynesian features of the Australian Vegetation', 'Antarctic Plants of Australia', 'South African features of the Australian Vegetation'; 'European features of the Australian flora'; 'Fossil flora of Australia' and 'Naturalised Plants of Australia' (Hooker 1859, pp. vi–vii). Moreover, Hooker also described three undefined geographical distributions, namely, 'South-east', 'South-west' and 'Tropics' (Hooker 1859, pp. xxxiii–xxv; see also Crisp *et al.* 1999). Together these form 13 floristic units. Moreover, Hooker used the term 'element' loosely and not in the way that later authors would in describing Autochthonous (Australian), Indomalayan and Antarctic elements. Where then did the concept of the three Australian floristic elements come from?

The Autochthonous, Indomalayan and Antarctic elements were proposed by German ecologist Ludwig Diels, and not the taxonomist Hooker:

> 'Floristic elements are well-known, however, little is understood about their arrangement within a vegetation formation [Vegetationbilde]. Hooker had already separated them based on their exterior affinities … An analysis of the

> Australian flora, to whom we can thank Hooker and von Mueller for providing the foundation, results in three main elements distinguished as the Australian, Malayan and Antarctic' (Diels 1906, pp. v and 31, translation in Ebach 2012).[10]

In a way, the involvement of Diels means that elements are simply large taxonomic assemblages that group vegetations.[11] The taxonomic approach of Hooker was by and large subsumed by the ecological approach of Diels. Twentieth century Australian botany has had a largely Humboldtian approach, as seen in the use of vegetations to define biogeographic areas. For example, consider von Mueller's first attempt at dividing up Australia's flora into 'distinctive features of the vegetation':

'1. Plants of the dense coast forests.
2. Plants of the Brigalow scrub.
3. Plants of the open downs.
4. Plants of the desert.
5. Plants of the sandstone table-land.
6. Plants of the sea-coast.
7. Plants of the banks and valleys of rivers' (von Mueller 1858, p. 146).

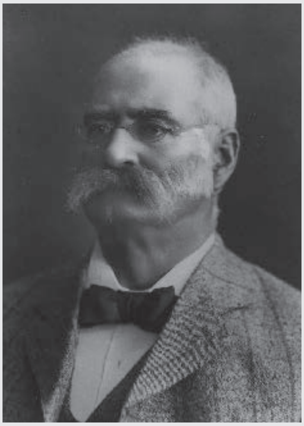
These are not plant regions based on taxonomic distributions, but areas defined by vegetation or type (e.g. Brigalow scrub) or ecology (e.g. desert). Even the approach of Ralph Tate, who proposed Australia's first plant regions (see Chapter 3), was based on floristic elements:

> 'The flora of Australia consists of the following constituent elements:
> I. – An immigrant portion, derived from at least two separate sources.
> (a) Oriental, which is dominant in the littoral tracts of tropical Australia; but despite the large assemblage of Asiatic species, the Australian character is deeply impressed by numbers, specifically and individually, of *Eucalyptus*, *Grevillea*, Phyllodineous *Acacia*, and others.
> (b) Andean (including also certain species of the cool and temperate regions of the North Hemisphere [sic]). For the most part this type of vegetation is restricted to the high mountains of Tasmania, Victoria and New South Wales. The peculiarity of the Tasmanian flora is only in its alpine types.
> II. – An endemic portion, a localised type of which occupies the extreme south-west of the continent' (Tate 1889, p. 313).

The last floristic element was divided into three types, the Autochthonian, Euronotian and Eremaean, based on temperature and moisture, rather than taxonomic distribution. Effectively Tate proposed three Australian floras using the same method ecologists at the time used to create vegetation types. The problem is two-fold. The climatic areas are generally based on vegetation, climate and topography (i.e. biomes). The origins of vegetations, rather than taxa, are founded on the very data from which they were created. A tropical vegetation, for instance, originates because of high rainfall, warm temperature and moist soils. In other words, vegetations are self-defining. Hybrids, such as the types Tate created, only served to confuse matters more (see Chapter 3).

Ralph Tate (1840–1901)

British-born geologist, botanist and malacologist Ralph Tate was based at the University of Adelaide. Tate created the first biogeographic map of plant regions (Tate 1889), which was used by Charles Hedley and Walter Baldwin Spencer to map animal regions (Hedley 1893a; Spencer 1896). Tate's regions are still used today in both animal and plant biogeography and are gaining popularity in modern geospatial studies.



Ralph Tate. Photograph courtesy of University of Adelaide Archives, Series 1151 University Photographs and Glass Slides: http://hdl.handle.net/2440/50055.

The concept of elements in New Zealand biogeography is by far a more orderly affair. New Zealand 'Botanists and zoologists' Fleming tells us 'on the whole have agreed on the main elements in the biota, classified according to their geographic relationships and probably origin' (Fleming 1975, p. 69). These elements, however, also have their origin in the ecological work by Cockayne (1921).

Influenced by German botanical ecologists Adolf Engler and Ludwig Diels, Leonard Cockayne produced a monographic ecological treatment *The Vegetation of New Zealand* Cockayne (1921). In it, Cockayne proposes the seven elements of the flora (i.e. endemic, palaeozelandic, Australian, subantarctic, palaeotropical, cosmopolitan and Lord Howe and Norfolk Islands), which were revised as six elements by Fleming (1962, 1975). Cockayne's elements were defined by taxic distributions, meaning that both the Australian and New Zealand elements were defined in the same way – namely, as taxonomic assemblage typical of a biota.[12] Fleming's revision of Cockayne's botanical elements to include all organisms had a dual effect – it had helped keep the classification approach active in New Zealand until the present day and it helped cement the idea of elements as result of dispersal in the minds of many New Zealand biogeographers (see Chapters 5 and 6). Conversely, the element classification system in Australian biogeography had only survived in isolated cases, mostly in botany and in some invertebrate groups. Only until recently have elements and biomes been considered across all Australian taxonomic groups (e.g. Byrne *et al.* 2008; Bowman *et* *al.* 2010). The rediscovery of biomes has led to the next cycle of reinvention within the Australasian biogeographic research program.

Australasian Biogeographic Research Program: the search for origins, regions and biomes

The mid-1970s to the early 1980s was perhaps the most dynamic period in Australasian biogeography. The four influential works by Williams (1974), Kuschel (1975), Keast (1981) and Gressitt (1982) appeared in the *Monographiae Biologicae* series by W. Junk Publishers. Fleming's revised work *The Geological History of New Zealand and Its Life* appeared in book form (Fleming 1979), the first volume of the *Flora of Australia* was published, which included an updated phytogeography of Australia (Barlow 1981), followed by the release of *Vertebrate Zoogeography and Evolution in Australasia* (Archer and Clayton 1984). These volumes included a new interpretation of Australasia: one that had adopted plate tectonics, new discoveries in palynology and phylogenetics. It heralded a new era and a new Australasian research program, which focused on an older endemic flora and fauna that existed on a dynamic geological plate of Gondwanan origin. While the origins of Australasia's flora and fauna were challenged, the distribution mechanisms were not:

> 'For many taxa with dispersibility, the positions of the continents have little effect on distribution, and plate tectonics may be unimportant' (Barlow 1981, p. 40).

Barlow's statement is echoed through the literature of the 1970s and 1980s: the flora and fauna of Australia, New Zealand and New Guinea originated partly on a larger super-continent; their distributions, however, were not Gondwanan. Rather, during the break up of Gondwana, many biotic elements, formerly isolated from one another, intermingled to form the biotic compositions we see today. The differences between earlier biogeographical hypotheses are the addition of tectonics and more precise quantitative measurements from another source formerly excluded from earlier studies – plate movement and uplift. Tectonics hadn't replaced existing biogeographical dispersal hypotheses – it just added a few more, particularly to palynological and palaeontological studies. With more hypotheses, Australasian biogeography was drowning in a multitude of equally plausible narratives – but where were the tests? Fleming in his 'third attempt to describe the history of life in New Zealand' emphasised an important point – namely 'that tentative conclusions are hypotheses for testing and that the gulf between raw data and paleogeographic conclusions has often been crossed by a rather flimsy bridge of projection and extrapolation' (Fleming 1975, p. 77; Fleming 1979a, p. 114). Where were these tests and what do these narratives tell us? Fleming, for instance, still used the term 'biotic element' to classify New Zealand organisms based on their geographic affinities.[13] But Australian terrestrial biogeographers used biogeographic areas, rather than elements, to determine how the flora and fauna inter-relate. Elements and areas are two different approaches: the first tells us about successive biotic invasions from a centre of origin, usually a mainland, to an island; the other tells us about the area relationships between continental areas and former biotic connections. If we were to draw an analogy between biogeography and systematics, an element would be an ancestral form: something

Charles Alexander Fleming (1916–1987)

Fleming was a New Zealand-born naturalist, specialising in geology, palaeontology, ornithology and marine invertebrates, who worked for the Geological Survey Branch of the DISR. For 30 years, Fleming contributed an evolving text on New Zealand biogeography, first as a short paper in *Tuatara* 'The Geological history of New Zealand' (Fleming 1949), which over time developed into 'New Zealand Biogeography. A paleontologist's approach' (Fleming 1962), also published in *Tuatara*, then as a book chapter 'The geological history of New Zealand and its biota' (Fleming 1975), and finally as a book *The Geological History of New Zealand and its Life* (Fleming 1979a).

Charles Alexander Fleming (*c.* 1971). Ref: 1/2–055789-F. Alexander Turnbull Library, Wellington, New Zealand. http://natlib.govt.nz/records/22679922.

that is fairly meaningless in a classification. Regardless, elements have been key components in explaining biogeographical classifications, particularly in that of Burbidge (1960), Fleming (1975) and early Australasian biogeographers (e.g. Tate 1889, Cockayne 1921). The move away from vegetation formations to biotic elements (and later regions), helped Australasian biogeography establish a narrative phase – the search for origins.

From vegetation formations to biotic elements: establishing the narrative phase

Australasian phytogeography has its roots in ecology and in the establishment of a vegetation formation classification, in which taxa are grouped based on climatic and physiological characteristics. It is commonly believed that taxic distributions were bounded by ecological barriers: a desert species would not, for instance, be found outside the desert biome (i.e. Eremaean). By understanding the development of an ecosystem and climate, one will have a history of its inhabitants. The only downside to this practice are the phylogenetic relationships between taxa. Not all species of a single genus reside in the same ecological niches. In fact, several species of a single genus may not only have vastly different ecological preferences, but they may also found in different continents. The need to account for these 'elements' is where the story of the origin of the Australian flora and fauna is told. But this is where Australian biogeography becomes rather complicated. First, the elements of the Australian biota are believed to be both Austral and Indo-Malayan. Second, Australia lacks the isolation caused by geographical barriers found in most other continents such as North and South America (e.g. Andes, Rocky Mountains). Isolating barriers tend to be based on climate, such as deserts, meaning that the distributions of many Australian taxa seemingly overlap with larger ecological areas. Horton (1973) noticed this also and concluded,

> 'On this basis the north of Australia above about latitude 15°S with its tropical monsoon influence, and the south-west corner of Western Australia with its cool temperate climate could both be separated from central and western parts of the continent with their semiarid and arid climates' (Horton 1973, p. 193).

Perhaps this explains the ecological/distributional regions of Tate (1889)? Like Tate, early Australian biogeographers tended to use rainfall and vegetation to justify their biogeographical regions. Zoogeographers, however, were focused on taxic distributions. For example, the drover and outback entomologist, Thomas Sloane, described the Riverina district 'to take in the whole of the basin of the River Darling, its western boundary being the watershed between the Darling and Barcoo Rivers. Its chief distinctive character is the prevalence of immigrant forms from the Bassian and Torresian sub-regions' (Sloane 1915, p. 146). Neither climate nor elements were used to define and describe zoogeographical sub-regions. For this we have to thank in part Charles Hedley and Sir Walter Baldwin Spencer. In adopting Tate's plant regions for a universal biogeographical classification, Hedley divided the Euronotian into northern and southern sub-regions, 'a separation of Australian life into Papuan and non-Papuan seems to the writer to be the primary divisions into which fall the Australian fauna and flora' (Hedley 1893a, p. 445). Spencer also emphasised the connection of the Australian fauna to areas outside of the continent:

> 'Owing, in the first instance, to the northern connection with Papua (and also Polynesia) and to its southern connection with an Antarctic land and, to a lesser extent, to differences in temperature …' (Spencer 1896, p. 197).

Spencer's (1896) three regions, the Torresian (formerly Hedley's Papuan), Bassian and Eyrean, overlapped closely with Tate's Euronotian and Eremaean (Table 2.1).

The regionalisations of Hedley, Spencer and Sloane are characteristic of zoogeographic practice, none of which had influenced Australian phytogeography. Rather the opposite was true. Zoogeographers, such as these, not only adopted the phytogeographical regions, but also the use of elements to determine the origins of their biota.

Elements, such as ancestral taxa in systematics, are ideal ways to both identify a relationship and determine provenance – elements are the artefacts of the dispersal process. In fact, Crisp *et al.* (1999) draw an analogy between elements and panbiogeographic tracks, a term Burbidge (1960, p. 141) also used to describe migration (dispersal) routes of communities rather than a single taxon (Ladiges 1998).[14] Fleming had also referred to elements as a 'given dispersal avenue' that 'implies their immediate place of origin' (Fleming

1963, p. 15). In Ball's narrative phase, elements function as a narrative explanation – one that is part of a scientific discussion – but did not make a discovery nor confirm a new law or establish an empirical fact. Narratives did not make 'predictions about what may be found in future investigations'. 'This', Ball said 'is precisely the status of many biogeographical theories' (Ball 1975, p. 409). Narratives, however, are the drivers of biogeographic discussion and were often used to validate one regionalisation over another. Alone, regionalisations, although important as distributional hypotheses, 'rest purely on an inductive base of the sort that predicts that kangaroos will not be found in Europe because they have been seen, in the wild, only in Australia' (Ball 1975, p. 408). What is stopping biogeography from progressing is the confusion over concepts (e.g. elements), how these influence research programs and what biogeographic methods are derived from them.

Elements have been the driving force of an Australasian narrative biogeography for much of the 20th and 21st centuries. The added benefit of describing the origins of faunas and floras as elements means that there is less emphasis on other distributional mechanisms, such as vicariance. For early practitioners, chance dispersal (e.g. trans-oceanic migration) was the only distributional mechanism. If there was an Oriental element in Australia, then it obviously migrated south from Asia. But the more isolated a biota was, the harder it was to explain. The distribution of Melanesian, South American and Australian elements in New Zealand, for example, led to hypotheses of former land connections via land-bridges over Antarctica and the sunken Pacific continents (see Chapter 6). While popular during the late 19th and early 20th centuries, little geological evidence was found to support such land connections. Instead, biogeographers turned to oceanography (e.g. west wind drift; Fell 1962) to explain disjunct oceanic distributions. For continental faunas and floras, however, many hypotheses appeared during the 19th, 20th and 21st centuries. These may be separated into four meta-narratives: (i) invasion hypothesis; (ii) Gondwanan hypothesis; (iii) refugia hypothesis; and (iv) the New Zealand Oceanic Island hypothesis (see Chapter 6). Each of these hypotheses had a role in changing how biologists and palaeontologists viewed the evolving Australasian biota.

Invasion hypothesis: biomes, young endemic elements and widespread older elements

The main ideas discussed by proponents of the modern invasion hypothesis, such as Burbidge (1960) and Heatwole (1987), differ from the older invasion hypothesis of Hedley (1899) and Hooker (1859). While both acknowledge older Gondwana or Mesozoic elements, the modern invasion hypothesis acknowledges the fallacy of land-bridges and sunken continents. In either case, elements were an important part of describing the Australian biota in terms of migrations and origins. For instance, Burbidge (1960) considers climate, and to a lesser degree geography, to be the main driver of Australian phytogeography. This is evident in the way organisms are referred to as vegetation types or 'forest dwellers'. The invasion theory holds that Australia's biota is resultant of waves of migrations from northern areas into Australia along ancient corridors dating back to the Mesozoic.[15] Once here, these newer elements radiated through the Australian continent, forming two predominant biota – an arid interior and a moist peripheral biota. These biota arose independently since the

Table 2.1. Examples of elements in the Australian biota.

T = type of biota (P = phytogeographic, Z = zoogeographic).

Authors	T	Elements								
Hooker (1859)	P	Tropical	Extra tropical	Spencer Gulf	Tasmanian	NZ, Polynesian	Antarctic	South African	European	Fossil
Wallace (1881)	P	Australian	European	Arctic	Indo-Malayan					
Tate (1889)	P	Endemic	Oriental	Andean						
Drude (1890)	P	Tropical-asiatic	Malayan-Melanesian	Antarctic						
Hutton (1896)	Z	Australasian	Northern	South-tropical	South-temperate					
Spencer (1896)	Z	Papuan	Asian	Austro-Malayan	South American					
Diels (1906)	P	Australian	Malayan	Antarctic						
Sloane (1915)	Z	New Holland	Pacific	Austro-Malayan	Antarctic					
Cockayne (1921)	P	Endemic NZ	Palaeozelandic	Australian	Subantarctic	Palaeotropical	Cosmopolitan	Lord Howe, Norfolk Island		
Tillyard (1924)	Z									
Harrison (1928)	Z	Autochthonous	Indo-Malayan	Leumurian						
Schwarz (1928)	P	Australian	Melanesian	Indo-Malayan						
Herbert (1932)	P	Australian	Palaeotropical	Antarctic						

Authors	T	Elements								
Burbidge (1960)	P	Australian	Melanesian	Indo-Malaysian						
Good (1964)	P	South Circumpolar	Melanesian	Afro-Australian						
Fleming (1962, 1975, 1979a)	P & Z	Australian	Austral	Malayo-Pacific	Endemic	Holarctic	Cosmopolitan			
Specht (1981)	P	Endemic Australian	Australasian	Indo-Malayan-Australasian	Afro-Indo-Malayan-Australasian	African-Australasian	Southern continents	South American-Australasian		
Beadle (1981)	P	Gondwanan	Intrusive							
Heatwole (1987)	Z	Pangaean	Gondwanan	Asian Tertiary	Modern					
Schodde (1989)	P & Z	Torresian	Bassian	Eyrean	Tumbunan	Irian				
Bowman *et al.* (2010)	P & Z	Australian								

Pleistocene, when the Australian continent had a climate similar to that of today (Cracraft 1991, p. 223). Although older elements arrived earlier, they existed as relict biota and had their origins in far-flung places. When an ecological hypothesis for plant distributions becomes problematic is when geographically disjunct phylogenetic relationships reveal themselves: 'The generic relationships and affinities between Tasmania, south-eastern Australia, New Zealand, and South America pose a phytogeographic enigma' (Burbidge 1960, p. 202). Ecological processes cannot account for distinct distributions between closely related taxa, hence the use of elements. With elements you can identify part of a biota as originating elsewhere, making the invasion hypothesis tenable. Clearly processes other than climate and geography are involved and that some biota have distributions that span over long distances. Heatwole considers this to be the result of older Gondwanan fauna that 'has been in Australia a long time and has had a longer time to disperse and, at least at some taxonomic levels (genus, family), would be expected to have broader distributions (Heatwole 1987, p. 130). Heatwole was of course referring to faunal elements, not floras, which 'despite the longer time range taken into account by the zoologists' Burbidge accepts 'there is evidence that there are similar trends' (Burbidge 1960, p. 201).

The ecological approach of combining climatic and physiographic barriers in order to determine vegetation formations and larger biomes seemed to mid-20th century biogeographers to overlap significantly with animal and plant distributions. Given this, the elements that make up Australia's biota are mostly young, with some Gondwanan elements distributed widely across both Australia and the Southern Hemisphere.

Gondwanan hypothesis: older endemic elements and younger immigrant elements

The overwhelming acceptance of plate tectonics had a major effect on the biogeographical history of Australia. In addition to palaeontological and geomorphological evidence of a wetter and cooler temperate Australia in the Palaeogene, plate tectonics had not only explained the major disjunct distributions between closely related taxa, it had also provided a mechanism for the drying out of the Australian interior. One would imagine that plate tectonics had dethroned the invasion hypothesis once and for all, except for one aspect – time. The super-continent of Gondwana started to split up during the mid-Mesozoic, with New Zealand becoming isolated ~60 Mya and Australia finally being separated from Antarctica at the end of the Cretaceous to the late Eocene (~50 Mya). Biogeographers had a problem: was the Australian biota really that old?

Terrestrial fossils, unlike their marine counterparts, are uncommon. This is because most terrestrial environments are erosional, not depositional, and usually not ideal for the preservation of fossil material. The lack of depositional environments means a lack of fossil data and a glimpse into Australia's biotic past. The discovery of a fragmentary palynological record had helped establish an approximate age of the beginnings of Australia's fossil flora. By the Miocene, Australia stated to dry out – that is 23 Mya, ~40 million years after Australia became isolated. During this time, modern plant genera first appeared in the pollen record, such as *Acacia* and *Eucalyptus*. Older taxa such as *Nothofagus* had older pollen records, signifying that Australia had biotic histories of different ages. Those like Cracraft (1991) and

Crisp *et al.* (1999) understood the varied history of the Australian biota. But biogeography had moved on and, for the first time, developed a systematic methodology: one that could discover historical patterns. What, if anything at all, did the discovery of historical patterns mean for biogeography?

The history of biogeography divides the field into two sub-disciplines: (i) ecological biogeography, which looks at recent ecological processes and ecological classification (e.g. vegetation and communities); and (ii) historical biogeography, which investigates geographical processes over time and focuses on taxa (Nelson 1978). A newly revised history, together with a new methodology, saw the rise of cladistic biogeography (as described in Chapter 1) – one that treated the endemic areas of plant and animals as taxa and translated phylogenetic relationship between taxa as area relationship (Rosen 1978; Nelson and Platnick 1981). Cladistic biogeography removed the need for ecological biomes and their elements. Rather, endemic areas and their relationships replaced the need for ecological biomes and elements. Australian historical biogeographers, however, still referred to elements (or tracks) as testable hypothetical histories (Crisp *et al.* 1999). Here I return to Ball (1975) who regarded the narrative and analytical phase as 'comprising historical biogeography' (Ball 1975, p. 408). Ball was unclear as to what the analytical phase meant to biogeography. By 1976, cladistic biogeography was establishing methodological principles, most of which had not been quantified until the mid-1990s (i.e. Nelson and Ladiges 1996). By then, there had been attempts at generating patterns to test distributions in both marine and terrestrial taxa, but together the data lacked the necessarily geographical overlap to successfully work out a general pattern (i.e. general congruence). With many phylogenies and methods quantified, this would have been increasingly frustrating. In the late 1990s the frustration was showing,

> 'Some studies, unfortunately relatively few, have looked for general patterns through combined analysis of multiple taxa' (Crisp *et al.* 1999, p. 332).

Why couldn't biogeographers get their act together? Even Australian botanists such as Mike Crisp, Judy West and Pauline Ladiges, adopted the animal endemic regions of Cracraft (1991) – possibly the first and only time zoogeography had any influence on Australian phytogeography (e.g. Crisp *et al.* 1995). The climatic biomes – Eremaean, Euronotian and South-western – popular in the 1960s, 70s and 80s, were dropped in favour of endemic areas.[16] Elements also disappeared in favour of the analogous panbiogeographic track, but even so 'efforts to trace general floristic tracks within the continent, and to find phylogenetic relationships among areas, have not been very successful' (Crisp *et al.* 1999, p. 355). Even by moving into a historical biogeography, Australian phytogeographers were stuck. The problem with Australian historical biogeography was not its cladistic methods, but rather the assumption that Australia biota had seemingly evolved at the same time.

Australian historical biogeography, even with all its bells and whistles, came to a grinding halt by the early 2000s. No attempts were made to find a general pattern across multiple taxa. Rather, due to the prevalence of phylogeography and single taxon studies, historical biogeography had lost its analytical side – the search for patterns – and started to resemble the earlier narrative biogeography of the early to mid-20th century. Crisp e*t al.* (1999), possibly underwhelmed by the cladistic biogeographical approach and its failure to uncover a general pattern, had returned to biomes and elements. The Gondwanan hypothesis of an ancient Australian biota, which evolved *in situ* with fragments in Australia, New Zealand, South America, India and Africa, became intertwined with the notion of historical general patterns. The lack of general patterns effectively neutered the Gondwanan hypothesis.

Biome hypothesis: Australian biotic areas as biomes

The development of geographical information systems (GIS), particularly in Australia, has led the way for digitised bioregionalisations, such as the Interim Biogeographic Regionalisation for Australia (IBRA; see Ebach 2012), and concepts such as phylogenetic endemism and diversity. Together bioregionalisation has acquired its own unique set of numerical methods that manipulate distributional data. Unlike the endemic areas proposed by historical biogeographers, geospatial software can draw highly detailed distributional maps based on species distributions, climate, soils, and so on. However, these methods are limited. Although they can propose areas of endemism and compare areas on taxic, climatic or soil similarity, they are unable to test biogeographical hypotheses. Seemingly abandoning tracks and Cracraft's areas, botanist and biogeographer Mike Crisp used geospatial software 'to detect centres of vascular plant endemism by analysis of specimen-based distributional data', and falsely dismissed Cracraft's areas as having been derived from the phytogeographic map of Burbidge (1960), 'which was an intuitive classification based largely on climatic zonation' (Crisp *et al.* 2001, p. 184). Cracraft's areas were generated using a parsimony analysis of endemicity (PAE; Rosen 1988), an approach similar to that used in Crisp *et al.* (2001). One wonders why Crisp would undermine his own legacy (Crisp *et al.* 1995, 1999). The 1999 areas, published in the introduction to the second edition of the *Flora of Australia*, served as the standard for botanical research. But looking back at Crisp *et al.* (1995) we understand why – their analysis found a different pattern to that of Cracraft (1991): one that grouped the areas into larger regions (Fig. 2.1),

> 'Areas with monsoonal to arid tropical climates form a clade (Monsoon), whereas the wet tropical area (Atherton) is at the base of a separate clade (East/south coast), which shows successive differentiation along the east and southeast coasts' (Crisp *et al.* 1995, p. 467).

Monsoon? Wet tropical area? Had Crisp *et al.* (1995) found biomes? Or has the same mistake that Tate (1889) made by confusing biomes with taxic distributional areas been repeated?

> 'Here, we recognize five major biomes within Australia … based on previous maps that used climate, vegetation structure and endemism as criteria (Burbidge 1960; Schodde 1989; Crisp *et al.* 2001) … Biomes, in general, are not fixed in space or time but evolve continuously as landscapes and climates change' (Crisp *et al.* 2004, p. 1551).

It is hard to understand why historical biogeographers would use phylogenetically uninformative biomes to understand the history of endemic areas. Crisp *et al.* (2004), however, argue it this way,

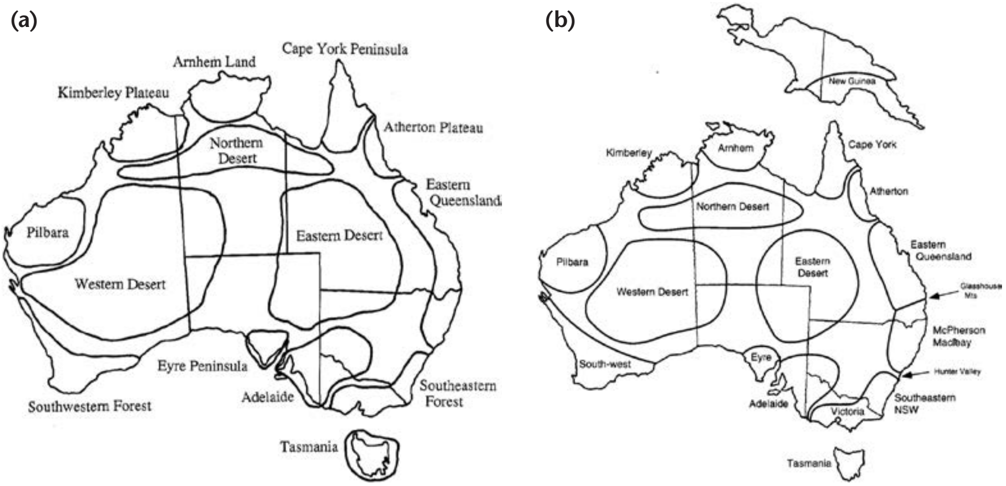


Fig. 2.1. A comparison of the original zoological areas of (a) Cracraft (1991, p. 213, Fig. 1) with the botanical areas of (b) Crisp *et al.* (1999, p. 337, Fig. 76). The gaps represent 'minor areas of endemism'.

> '… taxa occurring in the same biomes appear to have exhibited similar macro-evolutionary patterns, and these have differed among biomes. However, this commonality of response may have been limited to the periods of major climatic change' (Crisp *et al.* 2004, p. 1566).

This assumption immediately assumes that biomes are representative of general patterns based on phylogenies. If so, then, like Tate (1889), Crisp *et al.* (2004) make the mistake of assuming that congruent patterns detect climatically derived areas (e.g. vegetations), something that is again highlighted by Crisp (2006):

> 'Narrowly, a "biome" is a recognizable area of endemism containing a "biota". In one viewpoint, biomes are analogous to organismal lineages, responding as a whole to events in earth history and, in the extreme view, classifiable like organisms' (Crisp 2006, p. 1332).

By reinventing biomes (ecological biogeography) and treating them as analogous to biotic areas (historical biogeography), Crisp (2006) has muddied the waters of Australian biogeographical classification. This so-called integration combines incompatible ecological and historical hypotheses and classifications. Biomes are by definition young, because they are based on current climatic trends and vegetation types. Biomes would not form historical patterns that can be found by cladistic biogeography. What is interesting is how the concept of elements has made its way back into biome thinking. Crisp *et al.* (2004) refer to 'immigrants', which are a part of a biota that has its origins elsewhere (namely elements), which are 'defined by hypothesised origin' (Crisp *et al.* 1999, p. 345). In fact, Crisp (2006) brings the whole biome concept back,

> 'A biome might contain any combination of both kinds of elements' (Crisp 2006, p. 1332).

Biomes are based on climate and vegetation types: a classification system that harks back to the 19th century Humboldtians. Elements are necessary to describe the taxonomic or phylogenetic components of a biome. But all this is ecological, not historical, biogeography.

If we return to Ball (1975), who states that historical biogeography combines the narrative and analytical phase, then why attempt an ecological biogeography – one that gives up the search for general patterns? Even Crisp *et al.* (1999) acknowledge this error,

> '… is it possible to find general patterns with common cause, or should every taxon be considered to have its own unique history, incongruent with any other? Some would believe that the search for congruent patterns is delusive … If this conclusion is true, then biogeography cannot progress beyond the narrative stage' (Crisp *et al.* 1999, p. 332).

Five years later, Crisp *et al.* (2004) abandoned Ball's analytical phase, namely geographical congruence, in favour of biomes, and integrated two opposing classification systems – biomes and biota. Other biogeographers, thankfully, have not given up the search for congruence, but the tradition is slowly fading in Australia. One indicator is the lack of a common classification system; that is, a single set of area classifications. For example, the studies by Ladiges *et al.* (2005) and Ladiges *et al.* (2011) overlap geographically, but each has its own area classification (Fig. 2.2). Is geographical congruence possible in light of these studies? The simple answer is no, which returns us to the question 'it is possible to find general patterns with a common historical cause?' In studies of equally complex biogeographic regions, biogeographers have managed to find geographical congruence between vastly different plant and animal groups (e.g. Turner *et al.* 2001; Escalante *et al.* 2007; Parenti and Ebach 2009). Why are Australian biogeographers reluctant to find such congruence and test the validity of their areas?

My own belief is that Australian biogeographers, particularly phytogeographers, have a strong ecological background. Before the adoption of Cracraft's areas, there were few phytogeographical regionalisations that discounted climate and vegetation both in Australia and internationally. Tate's biomes, modified by Burbidge, served the phytogeographical community right up until Crisp *et al.* (1995). Internationally, the world regionalisation of Ronald Good (1974), Miklos Udvardy (1975) and Armen Takhtajan (1986) was based on ecological biomes rather than on Candolle–Wallacian regions. Those who did use Australian regions that were based on actual taxon distributions were mostly zoogeographers such as Charles Hedley, Thomas Sloane, Tom Iredale and Gilbert Whitley. Besides, Australia has few geographical features, such as mountain ranges or inland seas, which would emphasise biotic areas, rather than ecological formations. Late 20th century biogeographers have been seduced by labour-saving computational or numerical implementations. Off-the-shelf software is far easier to use and doesn't include the complicated matter of finding phylogenies with overlapping distributions. Finding geographical congruence, it seems, is simply too hard. Why waste months searching for monophyletic areas, when an off-the-shelf program can generate a quantified narrative in far less time? Easy-to-use biogeographical models helped biogeographers pursue the old chestnut of biogeographical origins, by either finding

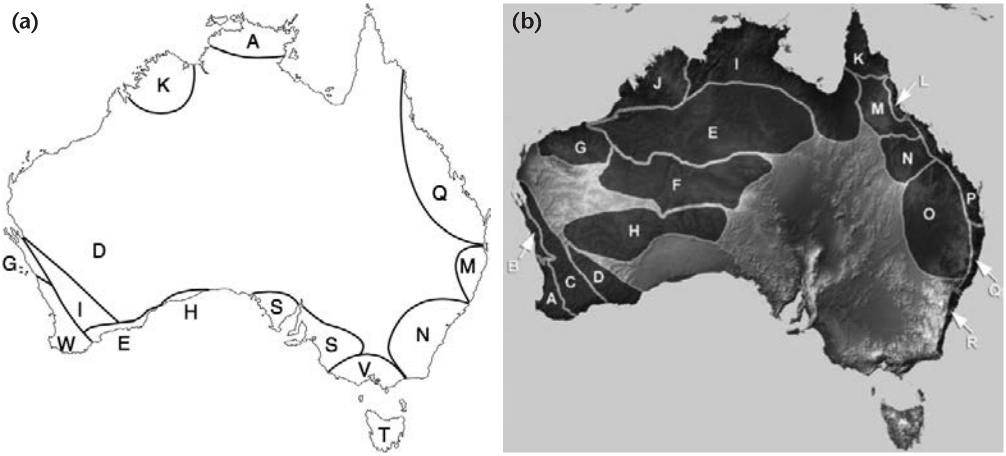


Fig. 2.2. A comparison of (a) Rhamnaceae areas of Ladiges *et al.* (2005, p. 1912, Fig. 3), which are modified from Cracraft (1991) and Crisp *et al.* (1995), with (b) the eucalypt areas of Ladiges *et al.* (2011, p. 32, Fig. 2).

correlations between taxic distribution, endemism and climate (e.g. Byrne *et al.* 2008; Bowman *et al.* 2010) or modelling historical events, such as dispersal, vicariance and extinction, onto existing phylogenetic trees or as graphs (e.g. Cook and Crisp 2005a,b; de Bruyn *et al.* 2012). These approaches, however, are not designed to find geographical congruence, and test for geographical congruence (area monophyly), meaning that 'biogeography cannot progress beyond the narrative stage'. In 2016, for instance, phytogeographers are still unaware whether their plant regions are real or not. The Eremaean, for example, is still used as a valid area when biogeographical analyses consistently (and unwittingly) show it to be an artificial; that is, a non-monophyletic area (see Ebach and Parenti 2015). Without area monophyly, biogeographers are stuck using areas that may be artificial and uninformative. Given that many recent biogeographical methods are model simulations (e.g. Ree *et al.* 2005), using artificial areas is another case of garbage-in-garbage-out. Australian biogeography has returned to the ways of the early 20th century, in proposing numerous bioregionalisations and endlessly debating what it all could mean. A way forward is to propose biogeographical hypotheses based on a natural area classification.

The need for testable hypotheses

Since Cracraft (1991) and Crisp *et al.* (1995), Australian biogeographers have produced numerous equally valid bioregionalisations, none of which have been tested for area monophyly. Rather than find geographical congruence, there has been a tendency to return to biomes (*sensu* Burbidge 1960), especially within phytogeography. The result, it seems, are agreed climatic regions, such as the Eremaean or Monsoonal or Wet Tropics biome (Yeates *et al.* 2002; Byrne *et al.* 2008; Bowman *et al.* 2010). But biomes are ecological regions, that are traditionally defined as 'the plant and animal community of a major climatic region or type of habitat' (OED 2015b) and not as 'recognizable area of endemism containing a "biota"' that are 'are analogous to organismal lineages' (Crisp 2006, p. 1332). Doing so has created a trend in Australian biogeography to confuse biomes as endemic areas and therefore somehow phylogenetically informative,

> '… there has been a revolution in phylogenetics: rigorous phylogenies and phylogeographies are now routinely produced using molecular genetic data, often using divergence time dating techniques. These data sets are critical to tests of biome origin and assembly' (Byrne *et al.* 2008, p. 4399).

Comparing biomes to phylogenetic informative biotic areas is a trend occurring among phylogeneticists such as Crisp *et al.* (2004) who 'use biome in a geographically restricted sense (sub-biomes and ecoregions as defined above), which allows better incorporation of phylogenetic and taxonomic information' (Pennington *et al.* 2004, pp. 1456–1457). This has created a hybrid similar to that of Tate's regions, especially,

> 'If the main emphasis is on vegetation structure, ecophysiology, and climate, then biomes can be seen to be the reactions of the living world to these conditions, and the "same" biome can be found in different continents. If, instead, the emphasis is on the taxonomic or phylogenetic aspect of its plant components, then the biomes become regional, as in Takhtajan's "floristic regions". On the whole, the word, "biome" is best used in the former, non taxonomic sense' (Cox and Moore 2010, p. 22).

Biomes are often made up of unrelated biogeographical elements, which means they are by and large not congruent (non-monophyletic). Redefining biomes as biotic areas only complicates matters, particularly when testing biogeographical hypotheses, especially when 'research questions are framed as hypotheses, biogeographical scenarios become testable' (Crisp *et al.* 2011, p. 66).

Crisp *et al.* (2011) over-simplify the notion that, once proposed, hypotheses can simply be tested. Many hypotheses are immune to testing, particularly those that fail to acknowledge natural classification. In systematics, for instance, our classifications are hypotheses of natural taxa. If we propose a taxon and not test it for monophyly, our hypotheses about the taxon may be immune to testing. Take, for example, an artificial group, let's call them 'spiny-critters', which are made up of a tenrec, echidna, porcupine and a cactus. This proposed group is artificial because its members share closer relationships to other taxa than they do to each other. But if we take our group for granted and propose hypotheses about character evolution, we will end up with a model that is baseless. In biogeography, the same is true for biotic areas or biomes. Consider the aim of a recent biogeographic study: 'We compare the patterns in the Australian arid zone [i.e. Eremaean biome] with those emerging from other biomes, and use these spatio-temporal patterns to generate questions and testable hypotheses to direct future research on the history and conservation of the Australian arid zone' (Byrne *et al.* 2008, p. 4399). What if we discover that the Eremaean biome is non-monophyletic, merely an artificial man-made construct? Then the hypothesis of Byrne *et al.* (2008) is clearly immune to testing. Without area monophyly, our hypotheses are simply meaningless. But biomes are informative as ecological units, because they can be generated when species distributions and climate overlap in geospatial analyses (González-Orozco *et al.* 2014). The problem is that they are not necessarily phylogenetically informative. If this is the case, why on Earth (deliberately) confuse the two? Again, this may be a result of no known definitive geographical barriers in the Australian mainland. If biomes act as geographical barriers, why not use them as such? Tate made this same mistake, because biomes are based solely on climate and can change rapidly over time. In contrast, a lineage may stick around and adapt to the new climatic regime. The marsupial mole (*Notoryctes*) is adapted to the Eremaean biome. The nearest relatives of *Notoryctes*, the Miocene fossil (*Naraboryctes philcreaseri*) is also found in the present day Eremaean biome, but it inhabited a tropical rainforest. The rainforest biome had moved on, but the biota had stayed behind. What this means for biogeography is that *Notoryctes* is a remnant of an older biotic area. What that biotic area is, biogeographers have yet to discover.

Biomes are valid ecological driven regions that may or may not have a significant impact on historical biogeography. The only way to understand whether they do is to treat biota as separate historical and phylogenetic relevant areas. Without monophyletic areas, our hypotheses are moot and our bioregionalisations are unrestrained. Australasian biogeographers have spent over a century attempting to find a natural classification – one that would encompass a large taxonomic group of organisms, like that of Wallace (1876) or Udvardy (1975). Although this has been a success in some parts of the world, Australasian biogeographers have struggled since Tate (1889) to find a robust classification that works for multiple taxonomic groups.

Chapter 3

Carving up Australasia: the quest for natural biogeographic regions

Most systematists will squirm at inferences derived from a non-monophyletic or artificial taxon. The importance of monophyly is critical to understanding the natural world and drawing inferences about past processes and events. Since the early 19th century, plant and animal geographers have also been concerned about correctly identifying natural areas. Plant geographer and taxonomist Augustin de Candolle tried to propose natural laws when proposing natural areas and failed. Humboldt abandoned natural classification and assigned vegetable forms, thereby creating a useful classification, which was unfortunately artificial. For early 19th century Australasian biogeographers, the concept of cladistic biogeography and area monophyly was decades away, while the importance of finding natural areas was immediate. Natural areas allowed the biogeographer to make inferences about the biotic evolution of a region such as Australia or New Zealand. Discovering the relationships between natural areas would allow for better inferences about dispersal pathways and evolutionary connections between continental floras and faunas, rather than proposing ephemeral land-bridges or sunken continents. Still, after 150 years of searching, biogeographers puzzle over the natural regions of Australasia. Why natural regions? As in biological systematics, artificial taxa represent a pastiche of distantly related taxa (think of the term 'insectivores', which would include all insect eating animals, such as funnel-web spiders, bee-eaters and echidnas). Artificial taxa are more closely related to other taxa than they are to themselves. The same is true for biogeography – artificial areas, such as 'Australia', are composites that are more closely related to other areas than they are to themselves. Natural areas, like natural taxa, are essential to understand the history and evolution of biotic areas. The goal of finding natural areas has been hampered by conflicting patterns of distributions and the desire for accurate and uncomplicated maps leading to new, and often conflicting, bioregionalisations (area classifications) being published on a regular basis. Charles Hedley understood this too well and warned,

> 'for I have no sympathy with writers who plot out different areas for different groups of animals and plants with a view to the reconstruction of past continental land. Where the evidence of one group conflicts with that of another, either the testimony or the application is at fault' (Hedley 1899, p. 405).

The background to this lack of consensus is in the lack of an analytical test. For instance, how do we know if our regions and sub-regions are real? Rather than pursue and answer the question, biogeographers have engaged in a debate over 'testimonies' and 'applications' in order to find an agreed meta-narrative of the origins of the Australasian flora and fauna. The

Charles Hedley (1862–1926)

Charles Hedley, a British-born and self-taught naturalist, had travelled through much of Australasia. Travel experience, and a formidable knowledge of botany, malacology and ethnology, made Hedley an outstanding biogeographer. Unlike Hooker, Huxley and Hutton, Hedley rejected land-bridges or sunken continents as potential explanations for present-day distributions of plants and animals between Australia and New Zealand. Rather, Hedley proposed that much of the Australasian fauna and flora arrived to Australia and New Zealand via Papua and Melanesia and Antarctica in two separate waves, accounting for a similar biota in both countries.

Charles Hedley. © Australian Museum: http://australianmuseum.net.au/charles-hedley-conchologist.

debate over what is a real area (as opposed to how you would go about finding one) has dominated Australasian biogeography from the outset. The result is a cycle of reinvention: new bioregionalisations are debated until another is proposed, leading some to reinvent the same areas over and over again. The cyclic nature of debate in Australasian biogeography continues today, with biogeographers still ignoring Hedley's early warning.

Is New Zealand a zoological region?

The early 19th century lumping together of New Zealand and Australia in a single biogeographic region, based on their geographical proximity, was later dismissed by Hooker,

> '... under whatever I regard the Flora of Australia and New Zealand, I find all attempts to theorize on the causes of their community of feature frustrated by anomalies in distribution such as I believe no two other similarly situated countries in the globe present' (Hooker 1859, p. lxxxviii).

Hooker's observation was shared by Wallace, who insisted that while the 'extreme peculiarities of New Zealand ... have induced several naturalists to suggest that it ought justly to form a Zoological region by itself', based on birds alone, New Zealand genera ‘belong to Australian genera, and where the genera are peculiar they are most nearly related to Australian types’ (Wallace 1876, p. 77). Wallace doesn’t point out who the ‘several naturalists’ were or why they would object to such a classification. After all, Wallace is using Sclater’s 1858 regions, which were based on bird distributions alone. Why shouldn’t New Zealand be grouped with Australia? The main opponent to Hooker’s and Wallace’s view of a close relationship between New Zealand and Australia was Charles Hedley,

> ‘That the flora of New Zealand should present so many features akin to that of Australia, and yet entirely want the distinctive botanical characters of its nearest continent, is a problem to which Hooker first drew attention. No solution was attempted by that writer, who limited his discussion of the question to a clear statement of the facts in a passage [Hooker 1859, pp. lxxxviii – lxxxix] so frequently quoted that it need not be here repeated’ (Hedley 1893b, p. 187).

Hedley, a naturalist and newly appointed to the Australian Museum in Sydney in 1891, locked horns with the establishment,

> ‘I have not asserted, as you say, an absolute land-connection between Australia & New Zealand, but only a very much closer approach … I have endeavoured to show the fallacy of such assumptions both in my “Geog[raphical] Dist[ribution] of Animals” & in my “Island Life”; and you are only drawing conclusions similar to those which I have again & again shown to be invalid’ (Wallace (1892) writing to Hedley on 7 July 1892).

It was not the first time that Wallace’s bioregionalisation was challenged. He had already defended his classification a decade earlier in 1883 as he did battle in the pages of the prestigious journal *Nature*. North American zoogeographers such as Alfred Newton, Joel Asaph Allen and Angelo Heilprin thought that the Nearctic and Palaearctic regions, proposed by both Sclater and Wallace, should be combined into a single Northern region called the Holarctic (Ebach 2015). Hedley, however, was persistent and, also writing in *Nature*, demanded the opposite, that New Zealand be separated from the Australasian Region,

> ‘… the New Zealand fauna is *not* most closely allied to that of North-east Australia (Queensland). It is significant that those writers who advocate the alliance of New Zealand to Queensland have not seen either country, while those who deny such relationship have studied or travelled in both or either areas’ (Hedley 1900, p. 589, original italics).

Hedley was responding in part to a letter sent in by New Zealand naturalist H. Farquhar and to Wallace. Farquhar was certain that ‘had Mr. Sclater [Sclater 1858] considered what is natural rather than what is convenient, he would have divided his Notogœa into two regions separating the New Zealand area from that of Australia, for these two areas are essentially distinct from one another in all their great fundamental zoological characteristics’. For Sclater it seemed absurd to give a small group of islands with barely any mammals the rank of region. Second it was one of ‘practical convenience’. But, it is ‘to Mr. Sclater’s third reason that I have more especially to take exception', namely the assumption that the whole New Zealand fauna is derived from Australia (Farquhar 1900, p. 246). Wallace was having none of it,

> 'Throughout the whole argument there is an assumption which vitiates it, namely, that the amount of resemblance of the New Zealand fauna to that of *Australia* is what alone determines its resemblance to that of the *Australian Region*' (Wallace 1900, p. 273, original italics).

Wallace makes the point that by removing New Zealand as a sub-region of Australia, it causes a domino effect: 'And if Australia by itself is to become a "Zoological Region", New Guinea and its surrounding islands must also be a "Region", the Central Pacific Islands another, and the Sandwich Islands [Hawai'i] yet another!' (Wallace 1900, p. 273). For Wallace, the Australian region was 'more natural than any subdivision can make it'. But isn't Wallace invoking Sclater's 'practical convenience', what Hedley calls 'the inconvenience of an opposite view'? What if we have a classification in which oceanic islands form regions? Later practitioners such as Mayr (1944) suggested the same (see Chapter 6). The problem is one of relationship. If New Zealand is not part of the Australian region, then what is it part of? If Notogœa is separated into two regions, as Farquhar suggests, then New Zealand will still be more closely related to Australia than to any other area. This I believe is Wallace's point – the fact that New Zealand, no matter how classified, will always be related to another area. Hedley is less generous of Wallace's reply: 'that an error is convenient is no good reason for its maintenance'. Hedley (1895) already had offered a solution: a Melanesian sub-region made up of 'New Zealand, New Caledonia and neighbouring groups (inclusive certainly of the Solomons, perhaps New Guinea)' that fall within Wallace's Oriental region or a yet undescribed Malayan region (Hedley 1900, p. 590). Consider Hedley's classification in context to the Wallace Line or in fact any of the proposed lines separating the Oriental region from that of Australasia. In Hedley's classification, the region between Wallace's and Weber's Lines (i.e. Wallacea) would be Australian and the areas to the west Oriental or Malayan. To a modern-day biogeographer, Hedley's classification looks decidedly modern (see Solem 1968).

Hedley's view that New Zealand should be a separate region had support mostly from zoogeographers. For example, both Alfred Newton and Richard Bowdler Sharpe included Lord Howe and Norfolk Islands into a New Zealand region (or sub-region) based on bird distributions (Newton 1893; Sharpe 1893). Huxley (1868) divided Australia and New Zealand into two primary divisions, along with Austro-Columbia and Arctogaea also based on bird distributions. American ichthyologist Theodore Gill (1883) proposed nine primary divisions on the distribution of animals, two of which are the Australian and the Ornithogaean (New Zealand). The debate of whether New Zealand is a separate zoogeographical region, or not, has had little impact on 20th and 21st century zoogeography bioregionalisation (see Chapter 6). The carving up of Australia into distinct east–west or north–south areas has, however, been the mainstay for much of late 19th and 20th century bioregionalisation.

Australian phytogeographers have been key in driving Australian terrestrial bioregionalisation. The freshwater and marine bioregionalisation, however, were the domain

Julian Edmund Tenison-Woods (1832–1889)

British-born Julian Tenison-Woods was a priest, polymath and early Australian naturalist who had made significant contributions to Australian geology, palaeontology and zoology. Tenison-Woods was the first person to propose zoogeographic regions of Australia in a little known booklet published in 1882: *On the Natural History of New South Wales: an Essay* (Tenison-Woods 1882).

Julian Edmund Tenison-Woods. National Library of Australia nla.pic-an23530162, http://nla.gov.au/nla.pic-an23530162.

of land and seashell specialists, such as Julian E. Tenison-Woods, Charles Hedley and later Tom Iredale, Don F. McMichael and Brian J. Smith who together named the first freshwater and marine areas of Australia.[17] These bioregionalisations formed two independent classifications that still exist today. But these two systems of classifying Australia's biotic regions had a turbulent history, particularly when it came to the origins or elements within the Australasian biota.

Are Australia's regions artificial?

Since Hooker (1859), there never was a consensus on the origins of Australian flora and fauna. Hedley had a bone to pick with the dominant view of Australia's biotic origins, stemming mostly from Wallace,

> 'The explanation offered by Wallace in "Island Life," and generally accepted, is: (1) commencing the biological history of Australia with the Cretaceous era, that Eastern and Western Australia were then totally severed; (2) that Eastern Australia was at that time quite devoid of a typical Australian terrestrial fauna and flora, which was then confined to Western Australia; (3) that a large area of what is now the floor of the Tasman Sea was upheaved, and nearly, or quite, connected New Zealand with Australia, whereby the flora and fauna, then existing in Eastern Australia, were enabled to colonise New Zealand; (4) that

> this hypothetical bridge then sank, isolating the New Zealand colonists, and afterwards dry land appeared between Eastern and Western Australia, upon which the characteristic Australian forms first crossed from west to east' (Hedley 1893b, p. 187).

Hedley saw this division of 'the fauna and flora as falling into a temperate and a tropical division, which again subdivide into eastern and western sections … to be quite artificial' (Hedley 1893b, p. 189). Indeed, are these subdivisions real or artificial? None seems to tackle this single fundamental point. Rather, biogeographers are more interested in telling stories about migrations or elements. Australian botanist and ornithologist, Richard Schodde, called these 'a comfortable theory': one that vertebrate zoogeographers 'found little to question and were content to leave the running to dispersalists such as Mayr, Darlington and their disciple Allen Keast' (Schodde 1989, p. 5). But, as I will show, this 'comfortable theory' has its origins in phytogeography, and over time it has failed to answer Hedley's point: whether the east–west division of Australia's biota is real at all?

The key element in this debate is the notion that the south-west of Western Australia holds the oldest endemic biota, commonly referred to in late 19th and early 20th century literature as the Autochthonian region – a term coined by botanist Ralph Tate, and later dismissed by Ludwig Diels as attaching 'itself to certain genetic concepts, which I am unable to make myself'. What Diels is referring to is the notion that the term 'Autochthonian' refers to 'the oldest component of the whole Australian Flora. Originating on the continent, the autochthonous element separated during the Cretaceous, establishing itself in the southeast, in which Eremaea became heavily modified, while the southwest remained unchanged' (Diels 1906, p. 375, my translation). Diels wanted to rid the term of its underlying concept and introduced 'southwest Australia' instead. But the origins of an Autochthonian element or region lie not with Tate but with Hooker's claim that 'the peculiar features of the Australian Flora in the west, unmixed there with Polynesian, Antarctic, or New Zealand genera, is an argument for regarding southwestern Australia as the centrum of Australian vegetation, whence a migration proceeded eastward; and the eastern genera and species must in such a case be regarded as the derivative forms' (Hooker 1859, p. liv). The older endemic Australian element isolated from the eastern areas is wholly phytogeographic – one that did not sit well with Australian zoogeographers such as Spencer: 'We find no great Autochthonian region occupying the western and south-western part of the continent ... there is no evidence pointing to the fact that in the case of the most important groups of Australian animals – the Monotremes and Marsupials – the old western part of the continent has any claim to the title Autochthonian' (Spencer 1896, pp. 176–177).

Spencer's 1896 *Report on the Work of the Horn Expedition* was the most influential work on Australian zoogeography, as much as Tate's 1889 *On the Influence of Physiographic Changes in the Distribution of Life* was to phytogeographers. The problem was that both works offered two different classification systems and biogeographic theories. Tate thought that the Autochthonian was an older element, which explained an east–west division, whereas Spencer rejected the claim wholesale. Regardless, Tate's Autochthonian region did strike a chord with early 20th century zoogeographers, such as the coleopterist Thomas Sloane,

> 'At present I can only feel confident of Tate's Autochthonian Region being a surely defined faunal district' (Sloane 1915, p. 148).

Spencer rejected the Autochthonian because of mammal distributions, something which ironically Sloane listed as a central tenet of zoogeography, 'Wallace's view that the great faunal regions should be founded on the Mammalia ought to be adhered to' (Sloane 1915, p. 140). What is going on? The problem is that Tate's region may not be defined by mammals, but is well defined by other animal groups, particularly beetles. In fact, in his 1932 Presidential Address at the ANZAAS Congress, George E. Nicholls, a zoogeographer, surveyed the entire biogeographic literature in order to devise a common biogeographic classification for plants and animals: one that included the Autochthonian or, as he renamed it, the 'Hesperonotian'. Like Diels, Nicholls didn't subscribe to an older element, but more to a 'closed region'. However, unlike Diels, Nicholls believed that the 'isolated' south-west overlapped with the Eremaean. Many zoogeographers believed that the south-west shared elements from other regions. Herpetologists Main and colleagues speak of 'migrations of the Bassian and Eyrean faunal elements into western Australia' (Main *et al.* 1958, p. 233), as did ornithologists Serventy and Whittell (1951). Schodde's (1989) remarks were correct – dispersalists were in control. For zoogeographers, younger elements had dispersed into the south-western regions: the problem now was trying to identify which was truly Autochthonian.

Possibly the most important contribution to the development of the great east–west debate was made by Burbidge (1960). There the debate had moved from whether or not the south-west was truly autochthonous. For Burbidge,

> 'The Province is not regarded as the "cradle" of the autochthonous elements of the Australian flora though it is apparently an asylum for many relict forms' (Burbidge 1960, p. 76).

Rather it was about establishing dispersal routes for Australia's three floristic elements – the Tropical, Antarctic and Autochthonous elements (Fig. 3.1),

> 'At the generic level many of the taxa have western and eastern groups of species and these indicate a period when the flora of southern Australia may have been virtually continuous, in a floristic sense, and there was free interchange' (Burbidge 1960, p. 202).

The south-west, it seems, is presently 'far from any well-marked migration route', indicating that historical processes were at play (Fig. 3.2). What is curious is the lack of a distinct east–west migration route in Burbidge (1960, Fig. 4). Ironically, the dispersal or migration routes from Papua partially match those of Hedley (1899), rather than those proposed by Hooker and Wallace. Had Burbidge moved on? Perhaps. If we return to Hedley's criticism of Wallace, we find two points of contention concerning the biota of Australia: (i) south-west Australia is representative of the oldest Australian biota and may be regarded as a centre of origin or diversification; (ii) eastern Australia consists of migrations from the north and another from South America via an Antarctic land-bridge. Burbidge (1960) added in the

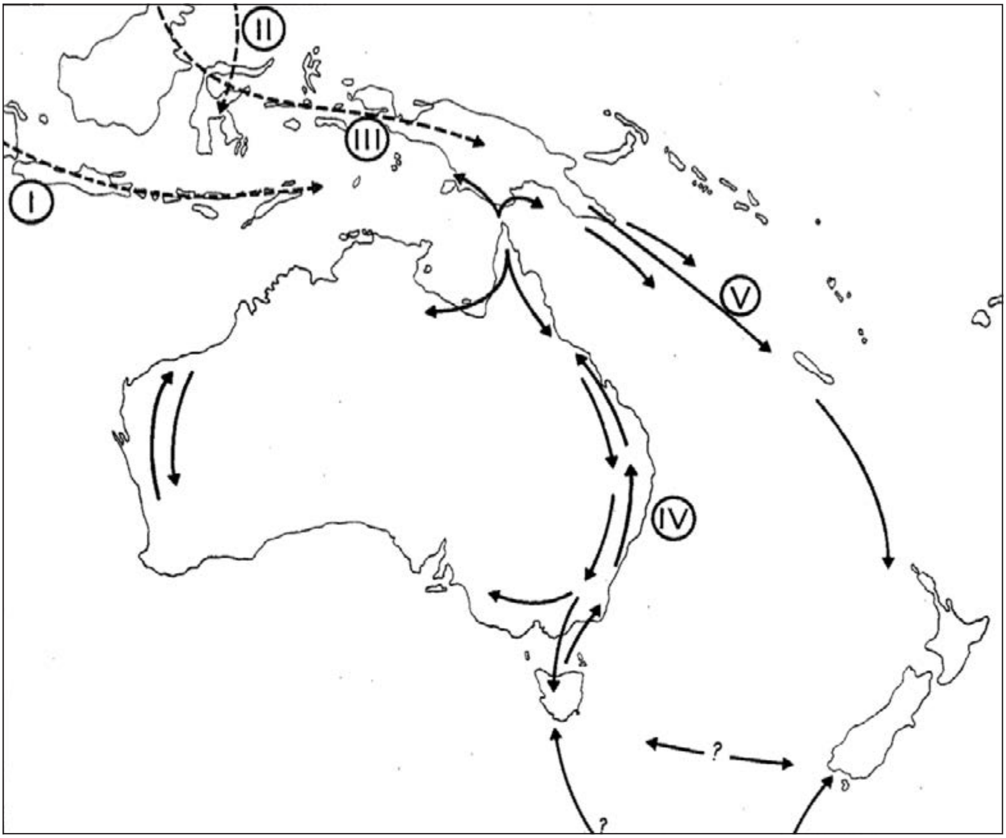


Fig. 3.1. 'Migration tracks affecting the Australian Region. (I) Sumatra track; (II) Luzon track; (III) New Guinea track; (IV) Eastern Australia track; (V), New Zealand track … Movement within the Australian Region has undoubtedly been in more than one direction and there has been interchange with New Guinea' (Burbidge 1960, p. 142, Fig. 4). Burbidge's migration tracks are similar to the molluscan migration routes of Hedley (1899, Fig. 6.1 herein).

idea that central Australia was inundated by marine incursions, but rejected the idea of an Antarctic land-bridge. Was this a significant move forwards?

Burbidge did not fully accept continental drift as a driving factor in the evolution of the Australian flora. She did consider other geographical approaches that would be considered tectonic today (e.g. geosynclines). But notions of drift – of continents being fused together or broken apart – were not favoured by biologists at the time. What drift did do was stymie any further debate about land-bridges and sunken continents. What was left of biogeographic theory was incorporated into post-tectonic meta-narrative such as the fusion of Hedley and Burbidge – one that is still with us today. For example, compare Burbidge's conclusions with those of modern-day botanists,

> 'Analysis of examples of extant flora and fauna that are distributed across the continent reveal lineages that first diverged in the southwest during the Paleogene, as Australia rifted from Antarctica and as environments differentiated

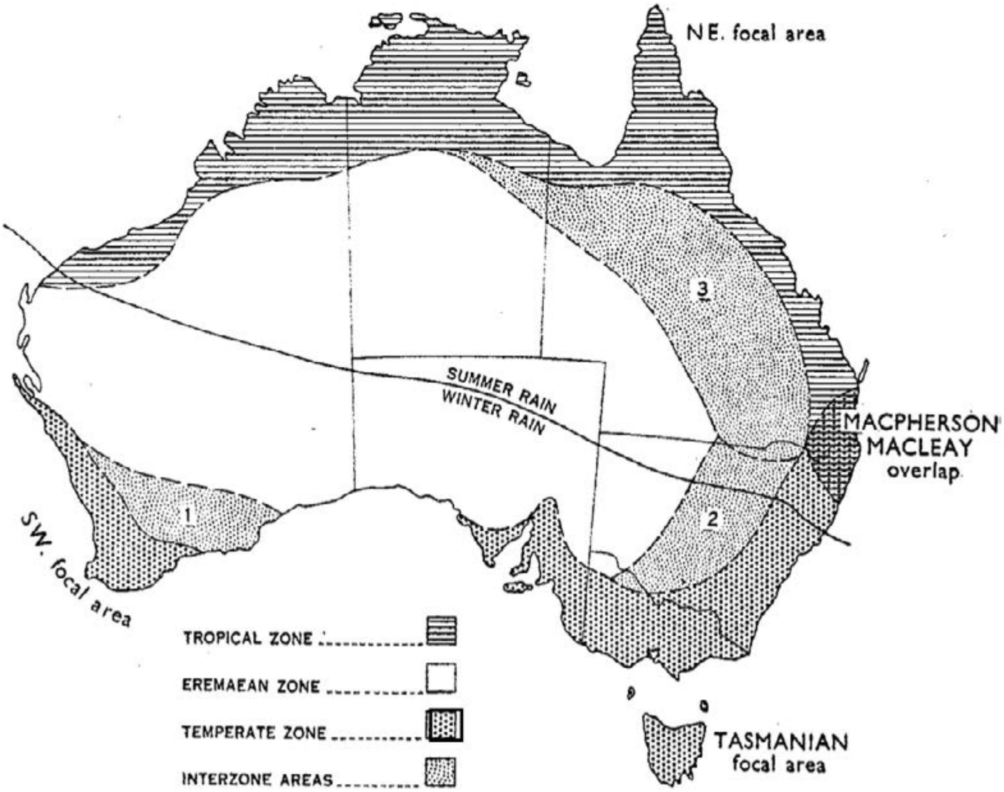


Fig. 3.2. 'The principal floristic zones of the Australian Region' (Burbidge 1960, p. 79, Fig. 1).

> earlier than in the more humid eastern part of Australia. The southwest later became isolated by marine inundations and periods of climatic cooling – vicariant processes that led to the isolation and differentiation of clades from west to east' (Ladiges *et al.* 2012, p. 707).
>
> 'There is a long-standing question as to whether there was an early vicariance event between the southeastern and southwestern temperate biomes followed by endemic radiations in each biome … Marine intrusion from the Great Australian Bight ca. 30 Myr ago, and perhaps aridification inland, isolated the southwest … Subsequently, uplift of the Nullarbor limestone plateau replaced the marine barrier with an edaphic barrier and more recently, an aridity barrier' (Crisp *et al.* 2004, p. 1565).

Not even the use of molecular data, as in the studies above, has helped resolve what is truly autochthonous. Rather it has only confirmed past meta-narratives of a continent drying out, marine inundations, successive migrations and a centre or origin hidden in the south-west corner. Past prejudices of Australia as an island continent that was colonised by northern taxa, seemingly confirmed by modern paradigm shifts in geology and molecular systematics, has done more to keep Australian biogeography in the 1880s. Australian biogeography really hasn't moved on and shown whether this subdivision is real or not. Is Schodde's observation true? Have biogeographers 'found little to question and were content to leave the running to dispersalists'? I think it goes deeper than just blaming it on one type of narrative. What is missing from Australian biogeography is a solid biogeographic fact, and one that Hedley alluded to over 120 years ago: are the biogeographic regions of Australia and New Zealand real or artificial?

Reinvention thesis and bioregionalisation

In the 2006 meeting summary, *A Remarkable Moment in Australian Biogeography*, David Bowman and David Yeates make an important observation,

> 'The challenge for Australian biogeography is to move beyond these broad-brush generalisations by uncovering regional and continental phytogeographical patterns; assessing the phylogenic congruence among different taxa, particularly plant and animals; and integrate these data to make a coherent whole' (Bowman and Yeates 2006, p. 212).

But what about Australia's biotic areas? 'At the broader scale, we need to move from phylogenies of individual lineages to phylogenies that encompass lineages characteristic of entire biomes, thereby riding the gap between historical and ecological approaches to biogeography' (Bowman and Yeates 2006, p. 212).

'Lineages characteristic of biomes' again do not allow us to test to see if these biomes are in fact natural. This is one of the many problems with combining two conflicting classification systems: namely biomes (vegetation) and biotic areas (taxic distributions). Although in some cases they may overlap, they are mostly historically incongruent. A plant form is not the same as a species, in the same way a vegetation is not the same as a taxon. Biomes are not synonymous with biotic areas – they are based on two entirely different theoretical premises and function in different ways. Biomes tell us about the effect of climate on a vegetation or fauna, while a biotic area tells us about endemism. Again, why deliberately confuse the two?

Australian biogeography has been in a 150-year cycle of reinventing the same areas. For example, take the first zoogeographical areas proposed by Tenison-Woods in 1882,

> 'A. the Neo-cambrian, or the south-eastern, including none of the south-coast; B, the Tasmanian, including Victoria; C, the Adelaidean, including the coast and watersheds of the colony of South Australia; D, the western, from the boundary of South Australia to Perth; E, the north-western, and taking in the western half of the north coast; F, the north-eastern, comprising the eastern half of the north coast and the northern half of the east coast [; G,] The Central, comprising all the inland waters and central regions' (Tenison-Woods 1882, pp. 48–49).[18]

Six of these seven areas overlap perfectly with those of Brian J. Smith proposed 102 years later (Fig. 3.3).[19] We may celebrate this discovery as confirmation that these areas really exist. Alternatively, it may confirm a 102-year cycle of reinvention. Are the regions of Tenison-

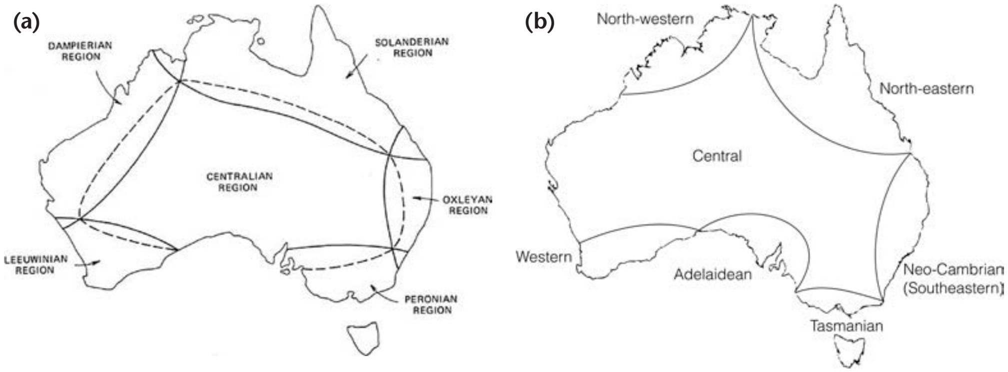


Fig. 3.3. A comparison of (a) 'The six faunal regions of Australia for the native land mollusc fauna' (Smith 1984, p. 179, Fig. 1) with (b) the seven zoogeographical areas proposed by Tenison-Woods (1882, pp. 48–49), here drawn for the first time. Tenison-Woods did not assign an area to the central part of Western Australia, 'I do not deal with the Western fauna, for I know so little of it, that my remarks would possess no value' (Tenison-Woods 1878, p. 147).

Woods real or not? Smith (1984) did not test his areas. We have to go back to Hedley who considered them 'neither natural nor well-defined' and also noted that they 'were overlooked by Tate, Spencer and other writers of Australian zoogeography' (Hedley 1904, p. 880, footnote*). The same criticism could be made of Smith's areas. Are they natural or artificial? Smith tells us that the 'elucidation of the exact positions of the borders of these regions will have to be to await further revisionary and population distribution studies. Each region contains a large number of endemic species and its own characteristic groups' (Smith 1984, p. 178). Smith's areas reveal something interesting, and perhaps an answer to why Australian biogeography is stuck in a rut.

Smith, like many biogeographers, relies on identifying possible areas of endemism. The idea is that areas of endemism are identifiable by counting which endemic species occur there. The result, usually a table with the numbers of each taxon in each area (Table 3.1), is a tally of endemism. Statistical biogeography – namely the practice of tallying species or taxa – stems back to de Candolle and early 19th century phytogeography. Even early Australian zoogeographers such as Tenison-Woods, Spencer and Sloane tallied their organisms against what is characteristic of a region. What makes this practice problematic is the lack of a historical record. Organisms go extinct, particularly in a continent that has dried out over a long period of time. The Tasmanian tiger (*Thylacine canis*), for example, occurred through mainland Australia, so did the Tasmanian devil (*Sarcophilus harrisii*). 'Identifying' an area on the recent distributions of either species would be erroneous. But there is a way to identify an area based on other characteristics. The appeal of biomes, such as those proposed by Tate, is that they are defined by climate, such as rainfall, soil moisture, temperature, and so on. Today, identifying biomes using sophisticated geospatial software is easy given the large volumes of climatic data. What is more, plants and animals have adapted to present-day biomes, making them even more identifiable. But the problem of taxic distribution doesn't go away. The Nullarbor Plain, part of the Eremaean biome, contains the recent remains of

Table 3.1. 'The number of described species in each family of native land molluscs in each final region of Australia'.

Redrawn from Smith 1984, p. 180, Table 1.

Family	Damperian	Leeuwinian	Centralian	Solanderian	Oxleyan	Peronian	Total
Helicinidae	1	–	–	4	1	–	4
Hydrocenidae	1	–	–	1	1	–	1
Cyclophoridae	–	–	–	2	–	–	2
Pupinidae	–	–	–	12	2	–	12
Diplommatinidae	–	–	–	1	3	–	3
Veronivellidae	2	–	–	2	2	–	2
Rathouisiidae	–	–	–	1	1	–	1
Succineidae	1	1	1	1	1	–	1
Athoracophoridae	–	–	–	1	1	–	1
Achatinellidae	1	–	–	2	1	1	4
Vertiginidae	2	–	1	3	2	–	6
Chondrinidae	1	2	7	2	2	2	8
Pupillidae	1	1	5	3	2	–	9
Enidae	1	–	–	2	–	–	2
Megaspiridae	–	–	–	1	–	–	1
Subulinidae	1	–	1	2	1	–	3
Rhytididae	–	1	1	7	7	12	23
Caryodidae	–	–	–	1	6	4	11
Bulimulidae	–	16	4	–	–	1	21
Punctidae	–	6	7	–	8	19	30
Charopidae	3	6	7	9	23	57	85
Helicodiscidae	1	–	1	1	–	–	1
Cystopeltidae	–	–	–	–	1	2	2
Helicarionidae	2	1	3	12	21	14	42
Camaenidae	96	5	50	64	16	6	229
Total for each region	114	39	88	134	102	121	504

Tasmanian tigers – an animal characteristic of the cooler temperate regions of the Bassian. Even Burbidge (1960) found tropical elements 'in the Temperate Zone', which she believed may have been 'descendants of early migrants'. Biomes may be easy to identify and quantify using the latest computer software, but like biotic areas, they are problematic in that they contain endemics (read 'elements') from elsewhere. A biome with elements originating elsewhere is by definition an artificial or non-monophyletic area.

Could a large-scale area such as a biotic region be a true indicator of a natural region? Surely smaller endemic areas would be better suited to biogeographic analysis? In his introduction to the edited volume *Austral Biogeography*, Norman Platnick noted that gross level regions are largely artefactual – an artificial assemblage of endemic areas that are 'unlikely to provide an accurate picture of the complex history of most biotas' (Platnick 1991, p. iv). If we are able to identify the smaller endemic areas, the sub-regions or provinces, could these be used to test for area monopoly at the gross level? If so, can biogeographers find a reliable way to identify endemic areas?

The endemic area concept

As the basic units of biogeography, endemic areas, like species, are based on several concepts. The concepts help to explain what an endemic area is and how it can be identified. Unfortunately, like species concepts, there are many definitions each with its own specific parameters (Table 3.2). Older concepts are general, such as an area or region to which an organism is native. More recent definitions are far more specific: 'The smallest area with significantly congruent distributions recognized as significantly different from all other areas at a particular level …' (Deo and DeSalle 2006, p. 1512). Congruence is key to understanding and identifying an area of endemism, rather than the usual 19th century approach of assuming the place to which a taxon is native. First and foremost the taxon needs to be monophyletic. If we closely examine Smith's gastropod families, we find that the Camaenidae occurs 229 times in over six regions, making it the most abundant taxon. Given this, the Camaenidae may be responsible for the endemicity Smith (1984) observed. The problem is that the Camaenidae were found to be non-monophyletic over a decade later by Scott (1996). Already Smith's regions are in need of revision.

The second criterion is minimal endemism, 'defined by the congruent distributional limits of two or more species. Obviously "congruent" in this context does not demand complete agreement on those limits' (Platnick 1991, p. iii). Regardless, minimal endemism can be problematic, particularly when the actual distribution of a taxon over time is not known. We would require fossil data as well as accurate distributional data from extant specimens. Typically our best guesstimate is to use general distributions, such as continents or islands such as Australia or Tasmania. Make the area any smaller and the biogeographer returns to regional climatic regions or vegetations – a practice common in Australian herpetogeography (Pianka 1969; Cogger and Heatwole 1981; Bowman *et al.* 2010).

With overlapping distributions, however, we have independent evidence for known distributions, such as sightings in a bird count or collections data. This is what makes the second criterion so important: overlapping distributions of monophyletic taxa are part of natural distributions. Again we run into problems. Although overlapping distributions are independent, they are never complete, meaning that the edges of the endemic area are either

Table 3.2. 'Select definitions of endemic area'.

Redrawn from Parenti and Ebach 2009, p. 58, Table 3.1, p. 60, Table 3.2.

Author	Definition
Clements (1905)	Region to which an organism is particular
Nelson and Platnick (1981)	Area delimited by coincident distributions of taxa that occur nowhere else
Hinz (1989)	Delimited or restricted distribution of a single taxon
Platnick (1991)	Congruent distributional limits of two or more species
Humphries and Parenti (1986)	Region occupied by a monophyletic group of organisms or a species found only there
Harold and Mooi (1994)	'Area of occurrence': biogeographic region occupied by a monophyletic group of organisms or a species
Crisp *et al.* (2001)	A taxon (e.g. a species) is considered endemic to a particular area if it occurs only in that area
Hausdorf (2002)	Area delimited by geographical barriers
Ebach and Humphries (2002)	Geographical distribution of a taxon within its physical range and ecological boundary
Laffan and Crisp (2003)	Recognised by the coincident restriction of two or more taxa
Szumik and Goloboff (2004)	An area in which numerous species are endemic
Domínguez *et al.* (2006)	An area containing species not living elsewhere
Deo and DeSalle (2006)	The smallest area with significantly congruent distributions recognised as significantly different from all other areas at a particular level in nested clade analysis (NCA)
Rosen (1978)	Regions where populations evolved in isolation
Cracraft (1985)	Areas that demonstrate distributional congruence of constituent taxa
Axelius (1991)	Area occupied by two taxa, with overlapping area identified as a separate area
Griswold (1991)	Smallest coincident ranges of two species and the geographic extent of forest islands
Platnick (1991)	Area defined by the congruent distributional limits of two or more species
Harold and Mooi (1994)	Area recognised on the basis of distributions of two or more species
Morrone (1994)	Smaller generalised tracks
Mast and Nyffeler (2003)	Extensive co-occurrence of biotic elements (*sensu* Hausdorf 2002)
Quijano-Abril *et al.* (2006)	Areas where the distributions of at least two taxa overlap

sketchy or completely unknown. Using geographic, climatic or vegetative features may very well be a better alternative, given the nature of the distributions. In short, the two criteria for identifying endemic areas are hard to apply in many cases. Like taxonomists, who, having few but well-preserved specimens, are still able to name their species, so too are biogeographers able to identify an endemic area, based not only on the distribution of their potentially monophyletic taxon, but also on the abiotic factors, such as soils and geography. Adhering to an endemic area concept may be an ideal way to do biogeography; it is, however, not always possible. What is possible is to test whether the larger regions are monophyletic.

Breaking the cycle: the search for natural areas

'A symposium entitled "Austral Biogeography" was held as part of the IXth annual meeting of the Willi Hennig Society in Canberra, Australia on 24–27 August 1990. The goal of the symposium was to bring together different schools of biogeographers … to seek common ground' (Ladiges and Humphries 1991, p. ii). The symposium was the first time monophyly was discussed in terms of finding biogeographical congruence; that is, the relationships between endemic areas – or natural biotic regions. The foreword to the conference proceedings *Austral Biogeography* (Ladiges *et al.* 1991), written by Norm Platnick, was titled 'On areas of endemism' where Platnick criticised biogeographic analyses at the time, 'At one extreme, even smaller areas may be defined – on a purely geographical basis (e.g. different river basins) – and treated as separate areas, even though no taxa in the analysis are endemic to them. This can only be interpreted as the triumph of hope over reason' (Platnick 1991, pp. iii–iv). Looking at the analyses attempted during this time, you see why Platnick makes the point he does, '… this study is based on only a single *Acropora* species-group …' (Wallace *et al.* 1991, p. 207). Using large non-endemic areas was not the problem *per se*, rather it was using arbitrary areas in single taxon studies, as in the case of Wallace *et al.* (1991). A study using a single monophyletic taxon (i.e. a relationship) and *ad hoc* areas will not find a geographical pattern. Non-endemic areas are more closely related to other areas than they are to themselves, meaning that any multiple taxon biogeographic study will only result in conflicting area relationships and no pattern. The *Austral Biogeography* volume is testament to the triumph of monophyly and minimal endemism over arbitrary areas. Half of the chapters had shown that geographical congruence is possible, in both plant and animal groups, over regional, continental and inter-continental regions. Surely the *Austral Biogeography* volume had shown that biogeography, with its trove of methods, was ready and set to go?

Platnick's 'triumph of hope over reason' was a larger problem than he imagined. Yes, geographical congruence was possible, but most biogeographers were more concerned about the geographical history of their own taxon, not that of many different taxa. In short, the practice of using *ad hoc* areas did not go away. It simply got worse. Biogeographers continued to use single taxon biogeographic relationships in order to create evolutionary scenarios for their taxa. The result was an ever increasing number of arbitrary areas and bioregionalisation schemes. The goal had somewhat changed. Could there be a way to test for endemism for people not interested in geographical congruence? For instance, endemic areas proposed by Cracraft (1991), in the same volume as Platnick, had used phenetic similarity in order to define minimal endemism in Australian vertebrates. Cracraft's areas have been popular ever since – even forming the basis for the phytogeographic regions of Crisp *et al.* (1999) in the *Flora of Australia* introductory volume. Rather than test for area monophyly, Australian biogeographers had established ways to test for endemism in single taxon studies. With the development of GIS and geospatial software, more sophisticated methods of determining minimal endemism appeared, such as 'phylogenetic endemism' (Faith 1992; Rosauer *et al.*

2009; Rosauer and Jetz 2015), 'species richness' and 'spatial autocorrelation analysis' (Crisp *et al.* 2001). A new cycle of bioregionalisation started at the turn of the millennium as Cracraft's areas were abandoned in favour of areas recovered by geospatial techniques. The upshot was tailor-made endemic areas for each taxon based on distributions. The downside was sets of disposable areas, useful for a single analysis and forever being replaced by newer analyses. In short, Australian biogeographers were back to generating endless bioregionalisations and hypotheses about area relationship and not testing them. Why did Australian biogeographers abandon the brief analytical phase of Ball in the 1990s?

The first step to stopping the cycle of reinvention is by looking at overlapping distributions. Take the analysis of marine algae by New Zealander Jonathan Waters,

> 'Our detailed biogeographic analyses of 1487 macroalgal taxa provide clear support for the three traditionally recognized broad marine biogeographic provinces in southern Australia' (Waters *et al.* 2010, p. 990).

'Specifically' the analyses of Waters *et al.* (2010) 'validate Bennett and Pope's (1953, 1960) classic descriptions of Peronian (east), Flindersian (west) and Maugean (south-east) provinces (see also Womersley and Edmonds 1958), qualitative patterns identified on the basis of a relatively small number of coastal taxa', areas that are still in use in marine bioregionalisation. But does this 'validate' these existing regions? Not necessarily. Waters *et al.* (2010) assembled 'a custom-built data matrix … based on all marine temperate macroalgal species (Chlorophyta, Phaeophyta and Rhodophyta)'. The final data matrix 'was composed of 1487 species and 21 IMCRA bioregions' (Waters *et al.* 2010, p. 989). Compare this with the approach of Bennett and Pope by taking 'into account the distributions of as many groups of intertidal animals and plants as possible in delineating geographical provinces … The data come partly from the two detailed surveys of over 2,000 miles of coast made by the authors, and partly from the other modern sources' (Bennett and Pope 1953, pp. 140–141). Both methods simply surveyed the presence of taxa across an area and ended up with a similar quantitative result that identifies possible biogeographic regions. Although this is a bold first step in proposing areas based on overlapping distributions, it falls short of testing and discovering whether these regions are natural areas or not.

Another step towards testing for natural areas is in identifying conflicting area relationships. If a larger area is natural, it will share a closer relationship to itself than it does to any other area. Take the analyses in Crisp *et al.* (2004), for example. Therein the authors show the distribution of biomes in *Eucalyptus* (*Symphyomyrtus*) and *Eucalyptus* (*Eudesmia*) (Fig. 3.4a,b). What becomes apparent is that the Eremaean shares a closer relationship with every other biome than it does with itself. Confirmation of this can be found in an analysis of *Eucalyptus* (*Corymbia*) + *Eucalyptus* (*Eudesmia*) by Ladiges *et al.* (2011). By combining two monophyletic taxa, Ladiges and colleagues had evidence in the form of geographical congruence that the Eremaean is an artificial area (Fig. 3.4c). Unfortunately, by ignoring the Eremaean region or biome as artificial, the cycle of reinvention continues.

Breaking the cycle of reinvention is not easy when areas are not seen as the key component to an analysis. This last clue is perhaps the most perplexing. If areas and their relationship

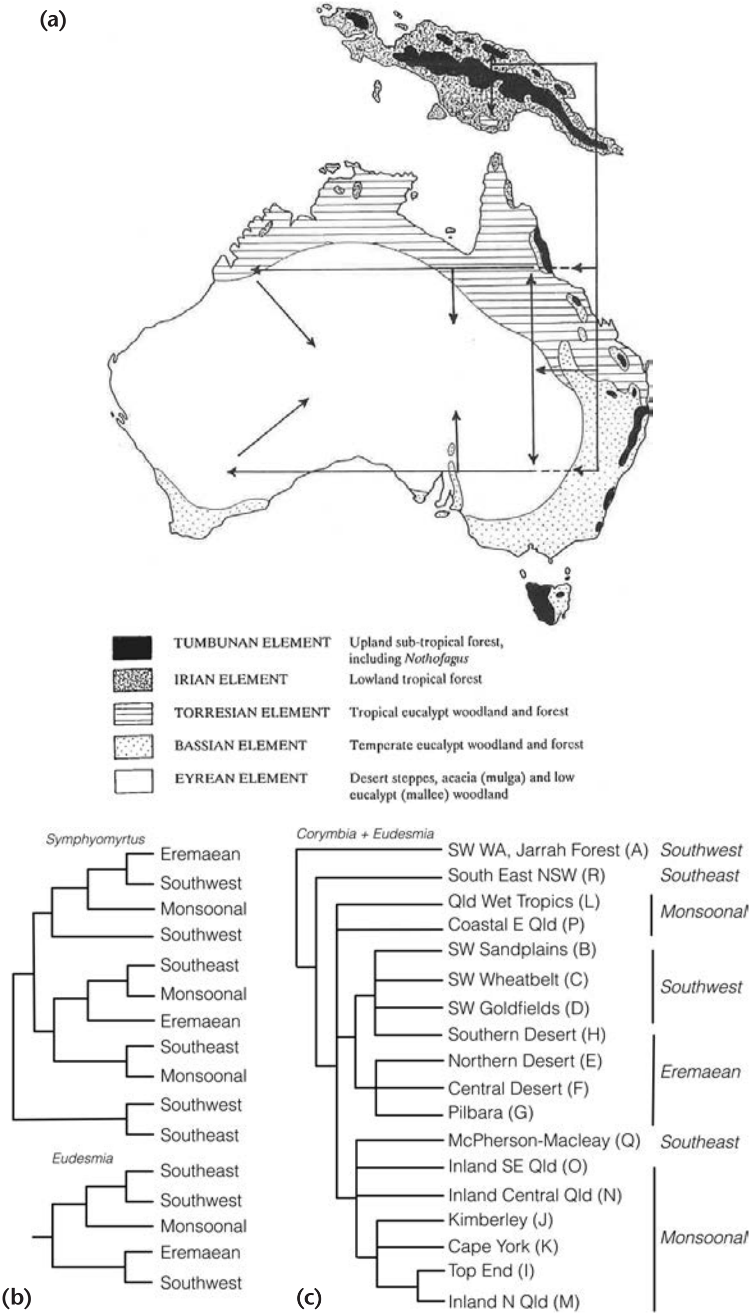


Fig. 3.4. (a) The areas of Crisp *et al.* (2004, p. 1552, Fig. 1), which, incidentally, is a reproduction of the 'Australian biotic regions' of Schodde (1989, p. 10, Fig. 1), with only the names replaced (i.e. Eyrean = Eremaean; Bassian = south-western temperate/south-eastern temperate; Tumbunan = aseasonal-wet; Torresian = monsoonal tropics). The map of Schodde (1989) is shown here; (b) the reduced areagram of *Eucalyptus (Symphyomyrtus)* and *Eucalyptus (Eudesmia)* (Crisp *et al.* 2004, p. 1556, Fig. 3); (c) the general areagram of *Eucalyptus (Corymbia)* + *Eucalyptus (Eudesmia)* (Ladiges *et al.* 2011, pp. 37, Fig. 5).

are not important to biogeography, then why use them? Take this example from Ree *et al.* (2005) where the authors introduce a new method for 'inferring the evolution of geographic ranges on phylogenetic trees'. The new method is part of 'a pioneering series of papers [that] shifted the focus of historical biogeography back toward inferring the geographic history of lineages (hereafter, ''lineage geohistory''), emphasizing the reconstruction of their ancestral ranges' (Ree *et al.* 2005, p. 2299). The approach is derived from ancestral area analysis – pioneered by Swedish botanist Kåre Bremer (Bremer 1992). The idea is to use the tree topography in order to infer ancestral ranges of taxa through time. The method proposed by Ree *et al.* (2005) builds the approach further, but the underlying principle remains the same: 'inferring the evolution of geographic ranges on phylogenetic trees'. I have chosen this method because it is currently a popular approach with biogeographers using single taxa or clades. Where the method fails is in the way it ignores areas as 'a discrete geographic unit that is assumed to maintain its identity over the duration of interest … the model may often correspond to areas of endemism, the use of rigorous methods to define such areas will not generally be necessary for our purposes. Instead, areas should be circumscribed according to the particular aspects of geographic history that are motivating the analysis: for example, if the history of dispersal between continents is of primary interest then continents may be specified as areas in the model' (Ree *et al.* 2005, p. 2300). Treated in this way, an area is nothing more than an *ad hoc* or arbitrary unit that may obscure or ultimately skew the result. Why then encourage biogeographers to avoid using informative data, particularly when approaches such as these are heavily reliant on areas? The answer may lie in similar methods such as molecular divergence dating.

In an analysis of South-East Asia by Stelbrink *et al.* (2012), molecular divergence dating analyses were used 'to test the compatibility of divergence time estimates with dispersal and vicariance hypotheses'. The analysis included 20 taxa in 27 areagrams that occur in four areas: Sulawesi, Asia, South-East Asia (Philippines, Moluccas, and Lesser Sunda Islands east of Bali) and Australia (including New Guinea). In a reexamination of the data, Parenti and Ebach (2013) found 15 of 27 areagrams contained no informative area relationship (Table 3.3). Moreover, the areas in the study contain two well-known composite (artificial) areas, namely Sulawesi and the Philippines (Michaux 2010), which together created a high degree of conflict in the data. Unfazed by their largely uninformative data, the authors conclude,

> 'Dispersal seems the primary mechanism of bringing taxa to the island and a standardized molecular clock approach has led to the falsification of vicariance hypotheses for some Sulawesi taxa of Asian origin' (Stelbrink *et al.* 2012, p. 2268).

It is surprising that any conclusions could be reached, given the conflicting state of the data, but therein lies a clue – something that has been haunting Australasian biogeography for quite some time,

> 'Sulawesi has a fauna of mixed geographic and temporal origin' (Stelbrink *et al.* 2012, p. 2268).

Table 3.3. 'The eight informative three-area statements'.

Redrawn from Parenti and Ebach 2013, p. 818, Table 2.

Sulawesi (Asia, Australia)
Sulawesi (Asia, South-East Asia)
Australia (Sulawesi, Asia)
Asia (Sulawesi, Australia)
Asia (Sulawesi, South-East Asia)
South-east Asia (Sulawesi, Asia)
Sulawesi (Australia, South-East Asia)
Asia (Australia, South-East Asia)

Clearly, Sulawesi is not a natural area, rather it is artificial or composite, like many of the regions in Melanesia and Indonesia,

> 'New Guinea reprints a zoogeographer's puzzle. It certainly represents a fauna of mixed origins, but there's a great disparity in the manner in which various zoologists have explained the situation' (Gressitt 1982, p. 897).

Treat an artificial composite area as natural and you will find mixed origins. The problem isn't to explain why the origins are mixed, but rather to identify and test for the natural areas within New Guinea and Sulawesi.

The so-called problem of mixed origins returns us to the dreaded biotic element: the progenitor taxa that dispersed between present-day Australasian biotic areas. Are elements, the ancestors in biogeography, the single cause for the lack of a stable Australasian bioregionalisation?

It's elementary! Origins are a problem for a stable Australasian bioregionalisation

Australasian bioregionalisation has come full circle in the form of digitalised area bioregionalisations, biomes and taxic elements. The ability to identify the three parts to a cycle – namely, the repetition, conflict and disregard of biogeographic monophyly; that is, natural areas – and the ability to test for natural areas, will prevent future cycles.

The foremost problem is that of elements or origins in biogeography. Area classifications are based not on narratives, but on patterns of area relationships, like monophyly in biological systematics. Once our patterns are established, we are able to engage in the narrative phase of dispersal, vicariance and extinction. Before all this can happen, we need to propose our areas first and that means engaging in the narrative phase. Furthermore, there needs to be some understanding that the narrative phase is the final phase in biogeography. Consider Australia's regions and subregions, starting with the descriptive phase. Tate and Spencer never proposed an area hierarchy other than the three sub-regions of the Australian region. If we borrow from Wallace (1876) and employ a third level, say a realm, we could place Australia into a realm or sub-realm, the Eremaean, Euronotian and South-western into regions and the areas in Crisp *et al.* (1995) into sub-regions (Fig. 3.5). The area taxonomy

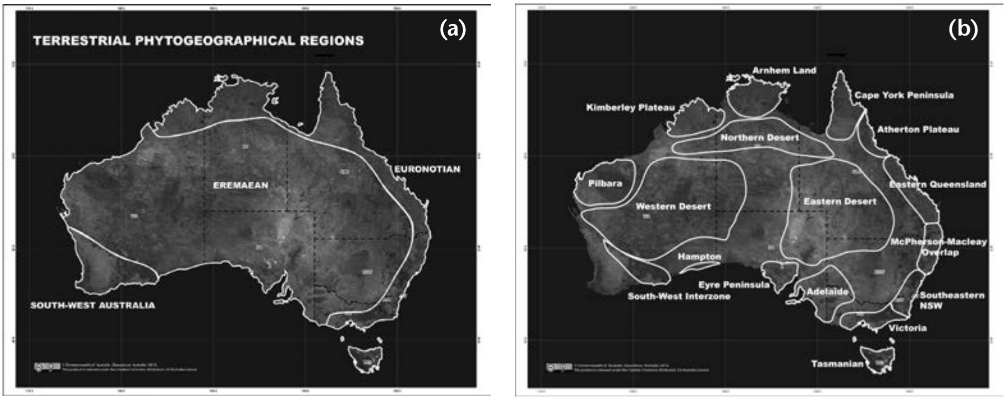


Fig. 3.5. (a) Phytogeographical regions of Australia (excluding New Guinea) (Ebach *et al.* 2013, p. 319, Fig. 1); (b) phytogeographical sub-regions of Australia (excluding New Guinea) (Ebach *et al.* 2013, p. 320, Fig. 2). Images available under Creative Commons Attribution CC BY Licence.

would accurately reflect what is being used universally within phytogeography. If we switch from the descriptive to the analytical phase, we would test these regions by using the sub-regions in an attempt to find geographical congruence – namely the biogeographic patterns across many plant groups within the regions. Two ideal groups to use, as Barlow points out, are *Eucalyptus* and *Acacia* because they 'dominate much of Australia's vegetation and contribute greatly to its character. The history of the Australian flora is in large measure the history of these two genera' (Barlow 1981, p. 58). Once congruence is (or isn't) established, the regions can be revised in light of the new evidence. We may find that certain sub-regions form clades, thereby forming a new region. Once the original regions are revised and reclassified, we can engage in the narrative phase. That crucial analytical phase is currently missing in Australasian biogeography and many biogeographers simply propose areas within the descriptive phase and skip into Ball's narrative phase.

Identification and testing alone will not help Australian biogeography move on, unless biogeographers understand that the cycle of reinvention is a problem. The solutions are all there. Identifying the three parts to the cycle and the approach to discover general congruence are all well known and understood. What is needed is an awareness of the history of Australian biogeography and the problems previous workers have faced. A good way to tackle this is to highlight the problem of elements. There was an overwhelming belief that Australia and New Zealand were at one stage 'a biotic vacuum, a bottomless cup waiting to be filled with everything that Eurasia could pour into it' (Schodde 1989, p. 5). Swedish botanist Carl Skottsberg made a similar observation,

> 'It even may be worthwhile to ask why we always assume that everything there is in the Pacific must have come from some distant place. Nobody asks where the Chinese, or Malayan or Brazilian floras come from. We are quite satisfied to believe that they develop right where they are, that their early history goes back so far that it is useless, for the present at least, to ask any but general questions as to their origin' (Skottsberg 1928, p. 914, also in Craw 1978).

I do not wish to enter into a discussion on the post-structuralist history of science and blame colonialism for the way Australasian scientists do biogeography. But it is hard to forget that it was during colonial times that European naturalists such as Hooker, Wallace and Diels seeded the literature with the concept of elements. Given that both Australia and New Zealand do have highly endemic floras and faunas, it seems odd that elements are considered at all.

The problem isn't elements *per se*, but the need for centres of origin; that is, the need for biogeographic mechanisms to explain our distributions. The most popular by far is dispersal, which by its definition requires an element or point of origin. Without centres of origin, our biota are truly endemic. What can be said of dispersal then? Very little indeed. Our desire to tell the tale of the geographical history of the 'lineage geohistory' for a single taxon is interfering with our ability to find a natural biotic classification or bioregionalisation. Only once we have discovered natural classifications, is it possible to understand the processes involved in the evolution of our biota, regardless of what those processes are – dispersal, vicariance, extinction, and so on.

There is also no point in confusing classification with biogeographic processes, such as dispersal or vicariance. As in biological systematics, natural classifications are predictive, whereas ancestor–descendant narratives are just that: stories. These stories are manufactured through our belief that molecular divergence dating models are somehow real or are hard evidence for timing divergence. A similar approach, called stratophenetics (Gingerich 1979), dates hypothesised lineages up and down stratigraphic columns as though they represent real divergences in phyletic lineages. These narratives have no place in area classification and retard any hope of finding natural areas. The curse of early 20th century elements has shown that areas with two or more elements are essentially polyphyletic and artificial, yet we want our biomes and biotic areas to consist of them, as if it helps us tell a story. But the real story lies in natural areas, their evolution and geographic history. This is not to say elements do not exist. Many taxa are cosmopolitan and are found in many different areas and may be endemic to a large region or realm. But widespread taxa are not what area classifications are built on, in the same way that the classification of mammals is not built on characteristics such as the presence of a vertebral column or the presence of forelimbs. Not all taxa will fit into an area classification scheme in the same way that not all characteristics found in vertebrates will fit into the Mammalia. A large majority of taxa, however, will fit into an area classification; otherwise we wouldn't have the repetition of areas as in the case of Waters *et al.* (2010) and Bennett and Pope (1953) or more significantly in Tenison-Woods (1882) and Smith (1984). But what has this all achieved? Is there really a universal Australian biogeography as Nicholls (1933) had imagined or are there separate plant, animal, freshwater or marine classifications – one for each taxon (e.g. Ebach *et al.* 2013)? If for argument's sake we were to put Australasian biogeography in the dock, what is one thing we can say in favour of Australasian bioregionalisation?

For a field that has been in existence for over 150 years, since the first regions of von Mueller (1858), there is little we can say in favour of Australasian bioregionalisation. We have no evidence for natural regions. The South-west region may very well be a natural region. The

Eremaean, by its definition of multiple elements, is highly likely to be artificial. The same is true for the Monsoonal biome. We may also say that there is a climatic east–west division and north–south division as Burbidge (1960) had imagined. But whether this is biogeographically informative still remains to be seen (see Ladiges *et al.* 2011). What we can say with a degree of confidence is that Australia and New Zealand do have biogeographic regions that are based on smaller endemic areas. Just because biogeographers have come up with similar bioregionalisations time and time again, does not mean these regions are natural. The only way to determine natural regions is to discover whether they are monophyletic.

The discovery of Australasia's natural regions lies in the monophyly of both taxa and areas. The method for finding taxic monophyly, cladistics, has its own unique and controversial history. Cladists had battled it out with evolutionary and numerical taxonomists in the Natural History Museum in London and the American Museum of Natural History in New York. Far away in Australia, news of these battles trickled in and some Australian systematists even dabbled in it. But it wasn't until the early 1980s that cladistics had finally come to the 'Land of Oz'.

Chapter 4

The spectre of cladism: cladistics in the Land of Oz

Australian biogeography has benefited greatly from the adoption of cladistics in the early 1980s, particularly because it helped some biogeographers move into the analytical phase. Rather than make speculative hypotheses about potentially artificial taxa, cladistics ensured that our taxa were natural and that our phylogenies were supported by evidence. Moreover it told us about the relationships between taxa; something that was genuinely vital for biogeographers – taxic relationship translates to area relationships and towards more robust biogeographical hypotheses. But the parties of cladistics had started late in Australasia. As cladists were reforming palaeontology in the 1960s and 1970s, it remained largely unchanged in Australasia. Although it was taught and discussed in universities, museums and herbaria, cladistics became established in Australasian biology in the 1980s and later in palaeontology in the 1990s.

The cladistics war

German entomologist, Willi Hennig, introduced phylogenetic systematics as a way to determine natural (i.e. monophyletic) taxa; that is, taxa that are more closely related to each other than they are to another taxon. Monophyletic taxa share a common ancestor, which to all intents and purposes is unknown. What makes Hennig's method unique is that *any* taxon can be used, providing it has recognisable characteristics. Hennig's ideas made little impact when they first appeared in the 1950s. Few commentaries tried to make sense of a theoretical approach that treated all taxa as equal. In the mid-20th century, fossils were the key to determining evolutionary (i.e. monophyletic) taxa. If your taxon had a fossil record, then you could find its ancestors and be assured that it was monophyletic. At the time, monophyly was determined by finding direct lineages between living and fossil taxa. However, Hennig's theory defied the palaeontologists: the monophyly of any taxon could be determined whether or not it had a fossil record. What made Hennig even harder to decipher (other than it was written in dense German), was that he used branching diagrams to signify these relationships.

Hennig's phylogenetic trees posed more problems than they solved. First they *looked* like evolutionary trees, but they contained no ancestors at the nodes. Next they depicted characters at the nodes that are *shared* and not unique to a single taxon. The most significant problem is that by the 1950s numerical taxonomy was the most dominant methodology in systematics, and this too used branching diagrams called phenograms, which were built using metrics of similarity. Between these two well-established schools of thought, the phyletic trees (ancestor–descendant trees) of evolutionary taxonomy and the phenograms of numerical taxonomy, Hennig's ideas had to fit somehow. The evolutionary taxonomists, mostly dominated by palaeontologists who lacked any systematic method, disapproved of

Hennig's theory. The seemingly theory-free numerical taxonomists or pheneticists, steeped in statistical method and implementation, tutted at the apparent mathematical simplicity of Hennig's method. By the 1960s, Hennig had a handful of followers: most were taxonomists implementing his method by hand, and few had dared to champion his theory in a field dominated by palaeontologists. Not until Swedish entomologist Lars Brundin published his monograph, *Transantarctic Relationships and their Significance, as Evidenced by Chironomid Midges* (Brundin 1966), were Hennig's ideas accessible to English speakers. An English translation of Hennig did appear in the same year as Brundin (1966), but the Swede was easier to understand and provided excellent examples, unlike those in Hennig's English edition. The impact of Brundin's work revolutionised systematics and reformed palaeontology, mostly through a young generation of taxonomists based in Europe and the US. Independent of Brundin and his followers, there were the original Hennigians. Some followed Hennig directly, implementing his methods as outlined in his 1950 and 1966 works. Others, steeped in the statistical implementations of the pheneticists, attempted to find suitable numerical approaches to implement Hennig's method, namely numerical cladistics,

> 'The methodology of numerical cladistics … used herein aims to produce cladograms depicting taxa linked by the shortest branching network whose nodes represent the emergence of unique derived characters' (Hopper and Burgmann 1983, p. 36).

A statistical approach to Hennig would after all make it interesting to phylogeneticists who, at the time, were doing phenetics and engaged in debates about best-fit trees and tree metrics. Phylogeneticists too wanted to be able to implement cladistics. Since phenetics also produced trees, just like those of Hennig, phenetic programs such as CLADON and CLAX could be used to find cladograms. Effectively the first practitioners of cladistics were phylogeneticists using phenetics computer software.

By the 1970s and 1980s, Brundin's followers were deeply embroiled in theoretical debates, mostly about the nature of monophyly and homology in taxonomy and less about phylogenetics. These cladists defined their field as *transformed cladistics*, namely '[a] method of cladistics that determines the nodes of cladograms on the basis of character distributions rather than appeals to ancestors' (Ladiges and Humphries 1983, p. 132).

Transformed cladists adopted the algorithmic implementations of the numerical cladists and used them to do battle with evolutionary taxonomists, challenging the notion of ancestors and non-monophyletic taxa. Together with the phylogeneticists, or *numerical cladists*, transformed cladists attacked phenetic approaches such as overall similarity. The 1970s and 1980s was a time when numerical and transformed cladistics existed side-by-side in relative peace: numerical cladists were busily stamping out other forms of phenetics, while at the same time transformed cladists were challenging the non-monophyletic taxa of evolutionary taxonomists. While at peace, these two forms of cladistics had a shaky relationship, particularly when it came to methodology and the concept of a transformation series – the transformation of primitive and derived parts modelled onto a phylogenetic tree. By late 1989 and the early 1990s, several of the transformed cladists and numerical cladistics clashed.

The cladistics war appeared to be over methodology. By the 1980s, numerical and transformed cladists had established parsimony as the only form of cladistic implementation. Parsimony is a term given to a series of statistical procedures in which the shortest tree represents the best solution according to Occam's Razor. Character-states are then mapped onto the shortest tree and treated as an ordered transformation series, in which some states can 'reverse'. Parsimony was one of many cladistic implementations that existed, but it was the very methodology that was championed by James S. Farris and Arnold Kluge and members of the then newly founded Willi Hennig Society. Effectively, Farris succeeded in establishing an official methodology for cladistics. Any other method was not cladistic and therefore phenetic or, worse, 'not evolutionary'. Several practitioners saw several major flaws in parsimony. For example, mapping character-states and treating them as ancestor–descendant lineages smacked of evolutionary taxonomy. Moreover, 'reversals', where a primitive character-state reappears in a transformation series, were nothing more than non-homology. The numerical cladists defended their position by returning to Hennig's example of the loss of wings in fleas. Given that fleas are not primitive, the secondary appearance of a character-state signifying an 'absence of wings', may represent a 'vestigial wing'. If character-state 0 represents the absence of wings and character-state 1 represents their presence, then a reversal is represented by the following transformation: 0 → 1 → 0. Hennig's example, however, does not support this argument. In fact, Hennig never spoke of secondary appearances. Rather he gave the example that wing loss in fleas was nothing more than a reversal of the transformation, from 0 → 1 to 1 → 0. More important still is what was the secondary appearance of a character-state doing on the tree anyway? If the same character-state supports two different nodes, it is non-homologous. If so, why call it a reversal? The genius of Farris' parsimony method is that it turned a non-homology (i.e. uninformative character-state) into an evolutionary process (i.e. a 'reversal'). But Farris had a trick up his sleeve – one that entrapped those who opposed his method with a simple rhetoric – deny reversals and you deny transformation. Deny transformation and you deny evolution wholesale. Cladists opposed to Farris were singled out as *pattern cladists* and demonised for opposing evolution. The rhetoric of the numerical cladistics was infamously unfair,

> 'No one but a creationist could think it realistic to exclude transformational considerations from the process of grouping' (Kluge and Farris 1999, p. 208).

Unfortunately for the pattern cladists, a vast majority had adopted Farris' parsimony implementation by the early 1990s and few were willing to change. The main journal of the research program, *Cladistics,* refused to publish non-parsimony papers or papers that were critical of Farris' implementation. The battle that ensued was odd. The numerical cladists, in hoping to defend Farris' parsimony implementation, turned the pattern cladists' argument about a numerical implementation into one about deep theoretical principles. What makes this odd is that the criticism of a faulty method had been converted into an outright attack on evolution. Pattern cladists, it was claimed, were denying the existence of reversals and were therefore rejecting evolution. Pattern cladists, such as Gary Nelson and Norm Platnick, were ridiculed at meetings and in print as 'creationists' who were unwilling to accept evolution. Philosopher of science, David Hull, famously wrote about the cladistic war in his philosophical and sociological book *Science as a Process* (Hull 1988). Hull sided with Farris and the numerical cladists – his own view was expressed in the title. The term 'pattern' was associated with so-called 'theory-free' or 'non-evolutionary' thinking. Pattern cladistics was effectively banned.

The cladistic war of the 1980s and 1990s had been mainly fought in the universities, museums and herbaria in Europe and North America. A famous émigré to Australia was Gary Nelson who in the late 1990s, from his new home in Melbourne, contributed several important papers to both cladistics and biogeography. But the story of cladistics in Australia and New Zealand is a little more complicated than one would expect, given the limited number of practitioners.

Phylogenetics, a well-established field by the early 20th century, had already made it to Australasia via the work of T. Jerry Parker, who in 1883 presented the first phylogenetic table [tree] of the crayfish *Palinurus* to the Otago Institute in Dunedin (Parker 1883, p. 303; see Craw 1992a, p. 81). In Australia, entomologist Robert John Tillyard, who also published phylogenetic trees as well as introducing the data matrix, inspired a generation of Australasian systematists including New Zealand entomologist John Golding Myers. Craw (1992a) suggests that Tillyard (1921) had 'anticipated' Hennig's phylogenetic systematics in his creation of fundamental 'cladistic' concepts such as a data matrix and the notion of primitive and derived characteristics. These seemingly 'cladistic' ideas were part-and-parcel of early 20th century systematics and phylogenetics: two fields that before Hennig's time had existed independently of each other. Therefore it is not surprising that early systematists living in Australasia had adopted these concepts.

Early Australasian practitioners and critics of numerical cladistics

> A SPECTRE is haunting palaeontology – the spectre of cladism (Campbell 1975, p. 87).

A spectre was indeed haunting palaeontology, but not the same spectre that Karl Marx and Friedrich Engels declared was haunting Europe. What Australian palaeontologist Ken Campbell is referring to is a new movement of young biologists. The likes of Gary Nelson and Donn Rosen were determined to topple the dominance of palaeontology from systematics and phylogenetics, replacing it with a new world order. Campbell, however, in choosing to borrow Marx's phrase, places himself in the position of the establishment – the 'Pope and Tsar, Metternich and Guizot, French Radicals and German police-spies' of Marx – in trying to rid palaeontology of cladism. By 1975, however, Campbell was in the majority, along with Ernst Mayr, George Gaylord Simpson and other established scientists attempting to resist the popular appeal of Hennig's phylogenetic systematists to a new generation of biologists and palaeontologists wanting to reform systematics. The establishment insisted that ancestors – that is, fossils and the fossil record – were essential to understanding evolutionary relationships, meaning systematics was essentially a palaeontological pursuit. Hennig showed that you can find meaningful relationships and monophyly without the need for fossils (i.e. ancestors). In fact, fossils belonged up on the tips of the branches alongside extant taxa and not as evidence at the nodes. Cladistics reformed systematics by making it a level playing field in which characteristics of taxa were used as evidence, and not spurious assumptions of ancestry.

The reform of systematics in palaeontology and biology came to Australia in the 1980s and had established itself firmly through the work of Gavin Young and Michael Archer in palaeontology and through the work of biologists Pauline Ladiges, Chris Humphries (on sabbatical from the British Museum, Natural History), and Peter Weston. These represent different histories and reflect the varied influences at the time. Before the reform came, cladistics was not lauded as a movement or a theoretical makeover of the modern synthesis. Rather it was regarded to be another implementation within phylogenetics – one that was pitched against phenetics (numerical taxonomy), the reigning methodology of the 1970s. What followed was a war of methods, of overall similarity versus homology, of dendrograms versus cladograms and of black boxes piled upon black boxes.

Australian systematics and biogeography during the 1960s and 1970s was little affected by Hennig's phylogenetic systematics or cladistics. Australasian phylogenetic systematics was largely confined to entomology, mostly published in short papers comparing Hennig's system to phenetics and evolutionary taxonomy (Mackerras 1964) and various critiques and suggested phylogenies or species relationships (e.g. Dumbleton 1963; Marks 1968). Until the 1970s, no Australasian author had attempted a phylogenetic systematic or cladistic analysis.

While taught in some university departments during the 1970s and 1980s, cladistics was not widely practised in Australia or New Zealand. Peer-reviewed scientific articles would refer to cladistics or its implementation indirectly as 'cladists would argue' (Sanson 1976, p. 23) or refer to Hennig's method in terms of 'phylogenetic relationships' (McDowall 1973, p. 196), but few implemented the method. Those who did, such as Lawrie Johnson and Peter Baverstock, altered existing numerical implementations to accommodate certain forms of cladistic methodology (i.e. parsimony, Wagner trees), but not necessarily the theory (i.e. monophyly) (Colless 1967; Johnson 1970; Penny 1976; Baverstock *et al.* 1979). These early adopters of numerical phylogenetic methods remained impartial to cladistic theory and the underlying debate about monophyly and homology that was reforming systematics in the UK, Europe and North and South America. In New Zealand, the numerical phylogeneticists such as David Penny and Mike Hendy chose to ignore the cladistic debate:

> 'Cladists they were preachin, Mike n Dave just did not hear' (Lockhardt *et al.* 2009, p. 54).

Australian ornithologist and biogeographer J. Alan Keast summarises 'the cladistic approach to biogeography' in a chapter on mammal and bird zoogeography and phylogeny given at the NATO Advanced Study Institute Major Patterns in Vertebrate Evolution meeting in 1976. While Keast's summary is neutral, it still confuses the role of fossils in cladistics,

> 'Cracraft's [1974] analysis of the phylogeny of the ratites may be reviewed here as an example of the application of the cladistic method to historical ornithogeography. It is a bold effort to develop an orderly history for this

> interesting group, but at the same time highlights, in almost 'classic' form, the difficulties of being limited to incomplete fossil material and of trying to fit limited geological and other facts into a framework' (Keast 1977, p. 287) ... Hennig (1966) stresses the great difficulty of trying to use the cladistic approach with fossils from which the critical parts are commonly absent. This handicap comes through in the present study' (Keast 1977, p. 289).

Compare this with,

> 'The placental radiations are so poorly documented by fossils that phylogenetic hypothesis rests solely on determination of the cladistic relationships of modern placentals' (Archer and Bartholomai 1978, p. 16).

Although extinction may pose problems in biogeographical theory, the absence of fossil data does not affect relationships within a cladogram (see below). Keast's summary is perhaps the longest written by an Australian in the 1970s (although at the time he was based overseas at Queens University in Kingston, Ontario, Canada). The debates in systematic theory flourished in North and South America and Europe, perhaps explaining why early cladists were mostly based overseas or were North American or European, rather than Australian or New Zealanders. One such European working on Australian biota was German entomologist Peter Zwick who published several cladograms in his revision of Australian flies (Blephariceridae) in the CSIRO journal *Australian Journal of Zoology* (Zwick 1977). However, the title of the first Australian cladist would have to go to Australian botanist Roger Carolin, who conducted the first numerical cladistic analysis on the native cornflower plant *Brunonia* (Carolin 1977; Morrison 2014; and see below).[20]

In rarer cases, cladistics came to Australia in the form of conference proceedings. For instance, cladistics was mentioned in the abstracts of the 16th International Ornithological Congress, held in Canberra in 1974. There, Joel Cracraft made a case for phylogenetic relationships as a 'prerequisite for reconstructing the historical biogeography of any taxon', dutifully citing Hennig (1966) and Brundin (1966) as well as the new generation of cladists, such as Gary Nelson and Donn Rosen. Cracraft continues,

> '... the lack of knowledge about the interrelationships of the higher taxa of birds is the main reason why biogeographic hypotheses ... must remain tentative' (Cracraft 1976, p. 40).

In the discussion that follows, Australian botanist and ornithologist Richard Schodde claims 'that it is impossible to understand the relationships and patterns of radiation in Australian birds without knowing where equivalent forms in New Guinea stand' (Schodde 1976, p. 99). Cladistics would provide an answer without knowledge of 'where equivalent forms in New Guinea stand', something that Cracraft's chapter did not emphasise. The usefulness of cladistics in general is somewhat muddied in the chapter by Walter Bock, who wishes not to 'delve into the controversy between these [phenetic and cladistic] approaches or why I advocate classical evolutionary classification' (Bock 1976, p. 177). Bock was not the only critic of cladistics. By the early 1970s, Ernst Mayr had a long track record of battle with cladists and, during the 1974 Ornithological Congress, he visited Wellington, New Zealand,

> 'One of his purposes in doing so was to visit Charles Fleming, who was both FRS and FRSNZ, and a Member of the United States Academy of Sciences (quite possibly nominated for the latter honour by Mayr himself). Mayr had been keen for Fleming to spend time at the MCZ [Museum of Comparative Zoology, Harvard], but this never eventuated, much to Fleming's disappointment, as he once told me. But Fleming had a photo of Mayr in his office, which reflected something of their mutual respect. As far as I am aware, I was the only New Zealander to have studied at the MCZ during Mayr's term as Director, though it would have been Mayr who invited New Zealand echinoderm taxonomist H. B. Fell (also FRSNZ) to take up a position as Curator of Marine Invertebrates in the early 1960s (which is how I became a graduate student there)' (McDowall 2005).

McDowall, a student at the time, invited Mayr to attend an informal discussion group in the Zoology Department,

> 'Later in the day, a group of about 30–40 people gathered in a room in the Zoology Department at Victoria University, sitting in an informal circle. Mayr was introduced, probably by Fleming, and questions invited … There followed another question about cladistics and the role of the ideas of German taxonomist Willi Hennig in modern taxonomy. Mayr, a little defensively I thought, discussed this question, again at some length, and about the role of derived (apomorphic) characters in determining phylogenetic relationships' (McDowall 2005).

One can't help wondering if Mayr had influenced those students attending the 'informal circle' at Victoria University in 1974, particularly his view on 'the ideas of German taxonomist Willi Hennig in modern taxonomy'.

For Australian systematics, cladistic critiques were mainly derived from pheneticists such as Don Colless, who were concerned with statistical implementation of Hennig's methods, which he thought are 'methodologically equivalent to phenetic methods, but deficient in the statistical rigour demanded by empirical science' (Colless 1969a, p. 143, see also Yeates and Cranston 2013). Colless, however, is supportive of Hennig's underlying philosophy, in regards to 'his views on *classification*, I am on his side, e.g. on the vexed question of paraphyletic [non-monophyletic] taxa' (Colless 1969a, p. 142, original emphasis). Compare this with Australian botanist Lawrie Johnson,

> 'The philosophy underlying our approach, which is broadly phyletic but not strictly cladistic ("Hennigian"), is discussed at length by Johnson (1970). A similar approach is defended by Mayr (1974) in his cogent criticism of the use of cladistics as the sole basis for classification. Grades [non-monophyletic taxa], when sufficiently well characterized and presumably monophyletic, are

> recognized as taxa, and the practical impossibility as well as the theoretical difficulties of pure cladism are acknowledged' (Johnson and Briggs 1975, p. 88).

By the late 1970s, numerical cladistic implementation had been dismissed by a leading entomologist (Colless 1967, 1969a,b, 1972), its underlying theory rejected (and subsequently remodelled) by a renowned botanist (Johnson 1970) and adopted by a few (e.g. Carolin 1977). Cladistics, however, was taught at Australian and New Zealand universities during the 1970s, most notably by Roger Carolin and Trevor Whiffin (in Australia) and Bastow Wilson (in New Zealand) (Morrison 2014; Heads *pers. comm.* 2014). Cladistics in Australia remained numerical and grounded in evolutionary taxonomic theory until the 1980s when the ideas of a new generation of reformists, the transformed cladists, made it to the Land of Oz.

Transformed cladistics in the Land of Oz

> 'Clearly, in Australia, cladistics is viewed as a viable and lasting classificatory method' (Raven 1985, p. 96).
>
> 'Even if the Australian environment is in a parlous state, cladistics here is not' (Cranston 1991, p. 79).

In May 1984, the Cladistics, Systematics and Phylogeny Symposium was held at CSIRO in Canberra and 'hosted by the Canberra chapter of the Australian Systematic Botany Society [now the Australasian Systematic Botany Society] in conjunction with the Australian and New Zealand Association for the Advancement of Science (ANZAAS) Congress' (Raven 1985, p. 95). In his review for the journal *Cladistics*, Australian arachnologist Robert Raven heralded it as 'Australia's first multidisciplinary symposium on systematics', but 'much of the energy was directed at cladistics despite several critics' (Raven 1985, p. 96). Critics such as Lawrie Johnson and Barbara Briggs took 'several glancing blows at "transformed" cladistics and other illusory objects' (Raven 1985, p. 95). The reactions were very terse,

> 'I find it very hard to distinguish transformed cladism from phenetics … its practitioners seem to insist that taxa should be "monophyletic" on the cladogram' (Colless 1984, p. 11).
>
> '… we regard transformed cladistics as a sterile aberration' (Johnson and Briggs 1984, p. 20).

Why was the reaction to transformed cladistics so negative? Australian phylogeneticists such as Johnson, Carolin and Colless remodelled cladistics to accept non-monophyletic groups, something that Hennig considered to be problematic (Hennig 1965). Second, was the rejection of 'expert' opinion – namely the labelling of some groups or taxa as ancestral by those working on them – based on hunches rather than evidence? These views were being debated in the cladistic literature by a new breed of systematist – transformed cladists – who worked in the old bastions of taxonomy, such as the Muséum National d'Histoire Naturelle in Paris, the American Museum of Natural History in New York and the then British

Museum (Natural History) (BM[NH]) in London. The transformed cladists, however, had arrived in Australia, mostly through the influence of British botanist Christopher J. Humphries who had taken a sabbatical to work with Australian botanist Pauline Ladiges at the University of Melbourne in 1981 (Williams *et al.* 2010). Humphries was based at the BM(NH), which at the time hosted several cladists, such as ichthyologists Roger Miles, Colin Patterson, Peter Forey and Humphry Greenwood (see Williams and Ebach 2008; Gee 1999). Intrigued by Humphries' version of cladistics, Ladiges subsequently took a sabbatical at the BM(NH) to learn from the transformed cladists, including US ichthyologist Lynne Parenti, who was there on a postdoctoral fellowship.

By 1984, Australia had two types of cladists: the numerical cladists who had focused strongly on phylogenetics (Kluge and Farris 1969; Farris 1983), and transformed cladists who were immersed in taxonomic procedures (Platnick 1979; Patterson 1982). Both groups used the same parsimony method and were supporters of each other's approach. The new transformed cladists, including Ladiges and Humphries, did not take long to stir up the taxonomic establishment. For instance, the strongly held belief that some groups cannot be resolved phenetically or cladistically, due to reticulation, was firmly in the minds of established botanists such as Johnson and Briggs,

> 'For many years I have worked with the large genus (or group of genera) *Eucalyptus*, which presents a maze of anastomosing situations of this kind, though not including alloploidy. It has long been clear to me that no single "best" classification, phenetic or "biological", is possible in such genera' (Johnson and Briggs 1975, p. 231).

The cladistic study of Ladiges and Humphries (1983) shows that the genus *Eucalyptus* is monophyletic, with *Angophora* as a sister taxon in defiance of Pryor and Johnson (1981) who considered *Eucalyptus* to be divided into three assumed monophyletic clades or 'suballiances' (*Angophora*, *Symphyomyrtus* and *Monocalyptus*). The result of Ladiges and Humphries (1983) led to an exchange of blows within the *Australian Systematic Botany Society Newsletter*:

> 'A recent paper by Ladiges and Humphries [1983] may be brought up in some discussions. This purports to show that *Angophora* departed early from a common ancestor of the rest of the eucalypts. We have indicated at the Myrtaceae symposium in Perth in May 1983 that this study is erroneous as to some data, incomplete and unbalanced in the character-sets used, and have shown that its conclusions are not sustainable when these deficiencies are corrected. More detailed comment on this will be published [Johnson and Briggs 1984]' (Johnson 1984, p. 27).

The publication, later to become Johnson and Briggs (1984), was 'in press for some time' (Ladiges *pers. comm.* 2014). Johnson presented his study separately at the Myrtales Symposium chaired by Weston during the 1981 XIII International Botanical Congress in Sydney, which was published as a special issue in the *Annals of the Missouri Botanical Garden* in 1984. Ladiges was in attendance and managed to publish both her co-authored revisions in 1983 based on

Johnson's presentation and the publication of Pryor and Johnson (1981). Without any knowledge of what Johnson and Briggs' forthcoming publication contained, Ladiges was forced to reply to Johnson's 'sweeping dismissal' of Ladiges and Humphries (1983),

> 'It is unfortunate that at this stage the paper of Johnson and Briggs, which analyses the Myrtaceae in depth, is still in press. It makes it difficult for all to judge the basis of Johnson's final phylogenetic interpretation of the eucalypts (and hence the proposed taxonomic revision) and to judge the differences in our data sets and methodology. Nonetheless, given that we have exchanged and discussed (our in particular) draft manuscripts, and that he utilised some of our data matrix in his latest numerical analysis to present a result different from that which he presented at the Botanical Congress (1981), I am disappointed that he describes our work as 'erroneous, incomplete and unbalanced' (Ladiges 1984, p. 29).

The phenetic analysis of Johnson and Briggs (1984) found a similar result to Ladiges and Humphries (1983), namely that *Arillastrum* is not part of the *Angophora* sub-alliance. Where the results differ is that Johnson and Briggs (1984) recovered what they believed to be a polyphyletic *Eucalyptus* – one in need of revision, possibly into multiple genera. Johnson and Briggs realised the failure of the eucalypt subfamilies,

> 'It is doubtful that any new taxa at the level of subfamily will be satisfactory, and we strongly advocate the abandonment of the subfamilies hitherto recognized on the grounds that continued reference to them is misleading in setting a phylogenetic context and is phytogeographically irrelevant' (Johnson and Briggs 1984, p. 752).

Johnson and Briggs did not believe that *Eucalyptus* was a stable classification.[21] For example, Pryor and Johnson (1971) proposed the genus *Corymbia*, which Ladiges *et al.* (1995) showed is non-monophyletic, with only one part of it, the bloodwoods, forming a monophyletic clade with *Angophora* based on a previous molecular analysis of Udovicic *et al.* (1995).[22] In an ironic twist, however, Hill and Johnson (1995) also undertook a cladistic analysis and revised *Corymbia* by including the ghost gums (*Blakearia*) with the bloodwoods. Hearing of Ladiges *et al.* (1995) while their manuscript was in press, Hill and Johnson managed to squeeze in a pre-production footnote,

> 'Its conclusions are similar to ours in most respects, but are based on considerably smaller taxon and character sets. The study of Ladiges *et al.* in fact strongly supports the concept of *Corymbia* as defined in the present paper' (Hill and Johnson 1995, p. 189, footnote 1).

Although the revision of *Eucalyptus* appears to be a comedy of errors, it merely reflects how taxonomy works. New groups are proposed and revised. Not until monophyly is established, as in Ladiges *et al.* (1995), Udovivic *et al.* (1995) and Hill and Johnson (1995), and genera revised, can a stable classification exist. In other words, finding monophyly within a cladogram or phylogenetic tree is only the beginning of a revision, not the end. What is more, classifications based on monophyletic taxa are predictive, meaning that any newly discovered bloodwood species would fit into the revised *Corymbia* without altering the classification or causing the taxon to become non-monophyletic. Given this, why do systematists such as Johnson declare the 'practical impossibility as well as the theoretical difficulties of pure cladism'?

> 'Nature does not comply with our classificatory desires' (Johnson and Briggs 1984, p. 752).

Many evolutionary taxonomists fail to understand how cladistics works. Cladograms, regardless of whether they are based on morphological or molecular data, are silent about actual ancestor–descendant lineages and ancestors: a fact that transformed cladists have been advocating. Nonetheless, comments such as these pepper the literature of the 1980s,

> 'Cladistics (ignoring meaningless "transformed cladistics") assumes divergent evolution and, usually, that best estimates of phylogeny are obtained by parsimony principles, both questionable assumptions at times' (Johnson 1989, p. 95).
>
> '…[cladograms] must show only dichotomous branching [cladogenesis]' (Cogger 1987, p. 276).

As transformed cladists had shown, a cladogram represents both divergent (cladogenetic) evolution and non-branching (anagenetic) evolution. For example, a cladogram represented by parentheses: (A,(B,C)) states that B and C are more closely related to each other than they are to A. This relationship may be explained by anagenesis, namely species A evolves into species B and species B evolves into species C or A evolves into species C and species C evolves into species B. The same cladogram may also represent cladogenesis, namely A evolves into B and C. The problem is that evolutionary taxonomists and cladists both use the same branching diagram to represent three different evolutionary scenarios. If an evolutionary taxonomist such as Johnson assumed that a branching diagram represents cladogenesis, then surely it must also be true for cladists. Therein lies the confusion – although in conflict, all three scenarios are equally valid. Why, then, hadn't anyone pointed this out?

Cladistics had lacked a basic introductory text for students. The majority of texts that were available during the 1980s and 1990s were written for academics or were written as supplements to existing graduate courses in cladistics that were held at the AMNH, University of Columbia, CUNY and University of Michigan (Eldredge and Cracraft 1980; Nelson and Platnick 1981; Wiley 1981) and at the Natural History Museum, London (Forey *et al.* 1992; Kitching *et al.* 1998). Other texts such as the *Compleat Cladist* (Wiley *et al.* 1991) and *PAUP* (Swofford 1989) were written as a supplement to a computer program. Another problem was that cladists and evolutionary taxonomists used the same terms for very different ideas. For example, the term monophyly, a fundamental concept in cladistics, has five different definitions (Vanderlaan *et al.* 2013). Those being taught cladistics in Australia were aware of these ideas, but many of the established commentators, such as Johnson, were effectively untrained in the foundational concepts in cladistics. For example, in his chapter in the first edition of the introduction to the *Flora of Australia* (George 1981), the bible of Australian botany, Andrew Kanis mistook several fundamental ideas in cladistics. The first is that cladistic classifications are constructed from phyletic lineages,

> 'If one adopts the model of a phylogenetic tree, it is only justifiable to regard it as buried by the sands of time, with the living species just visible as extremities of the finest twigs' (Kandis 1981, p. 81).

Cladograms (or phylogenetic trees) do not depict actual phyletic lineages, nor are ancestors or fossils located at the nodes of a cladogram. All known taxa, whether they be extinct or extant, are represented at the 'twigs'. The second misinterpretation that classification is blind to convergent evolution,

> '… however, once the sand is removed, since twigs of different branches may have grown towards each other and may have become closer than twigs of any single branch developing either divergently or in parallel' (Kandis 1981, p. 82).

Kandis believed that cladistics deals with reordering the 'tips of the branches' of actual phyletic lineages. Cladograms relate taxa based on character-states: namely the parts or homologues of a taxon. It is the character-states that reside at the nodes. If convergence occurs, namely the 'twigs of different branches may have grown towards each other' in a phyletic tree, then those characters will be highlighted as non-homologous. Many common misunderstandings of cladistic theory, then and now, are based on how characters are represented and how cladograms are read. Regardless, these mistakes were never challenged in print and allowed critics of cladistics to reject the philosophy out of hand and without debate. The difference between those taught cladistics and having understood it via the literature resulted in conflicting views of cladistics, particularly in the 1980s and 1990s.

These conflicting views resulted in three forms of cladistics (numerical, transformed and pattern). Before any constructive debate had resolved these issues, new data and methods appeared. The availability of molecular DNA led to an explosion of new analyses and methods. Rather than question the role of molecular data – what is molecular homology? – molecular systematists simply applied existing numerical implementations without worrying about the consequences. At the same time, cladists were battling it out in the pages of *Cladistics,* seemingly unaware that molecular systematics and new statistical software was dominating systematics. By the end of the 1980s, cladistics had finally become synonymous with method, namely parsimony. By the time the Willi Hennig Society finally came to Canberra for their annual meeting, any theoretical considerations about foundational issues such as the nature of monophyly and homology were seemingly forgotten.

The IX Willi Hennig Society Meeting was held in conjunction with the Australian Systematic Botany Society (ASBS) in Canberra in 1990. By the late 1980s, cladistics had many followers, a journal (called *Cladistics*), annual cladistics meetings, computer programs (Hennig86, PAUP) and what seemed to all, methodological unity. Parsimony was the choice implementation, given that Farris and the numerical cladists had sidelined other approaches such as George Estabrook's compatibility analysis. Cladists triumphant in toppling the evolutionary taxonomists had themselves become the establishment. Australian botanist David Morrison recalls the 1990 Hennig meeting,

> 'The image that my mind has retained is of Steve Farris sitting in an armchair with a group of acolytes sitting at his feet (literally!). Chris's [Humphries] place was made quite clear – he was also sitting in a chair but slightly to one side. Steve and Chris were both smoking cigars, which even at that time was becoming a no-no indoors in public. This looked very much like a deliberately and unnecessarily aggressive performance by the pair of them – a point was being made and it was not a welcoming one' (Morrison 2010, p. 42).

The scene Morrison describes brings to mind an older story: that of Mayr's circle in New Zealand, discussing the work of Hennig. The tables had turned and it was the cladists discussing the value of Mayr. In any case, the quick rise of cladistic methodology and computer algorithms meant that much of the theoretical debate was left unfinished. For example, the 1991 appearance of Nelson and Platnick's 'Three-taxon statements: a more precise use of parsimony' in *Cladistics*, caused an uproar between cladists. Nelson and Platnick (1991) had worked out that homology was a hierarchical topographical relationship and not a linear transformation of homologues (i.e. character-state reversals). The numerical cladists were outraged. Nelson and Platnick had not only challenged established numerical implementations (i.e. Hennig86, PAUP, NONA), but also their overall philosophy.

Needless to say, the philosophical premises of the pattern cladists were ridiculed at the level of trivial statistical implementation. Nelson and Platnick's theoretical concept of homology was unfairly dismissed as an incorrect statistical procedure. Those cladists associated with Nelson and Platnick's methods were outed as 'pattern' cladists, even by transformed cladists.[23] In 1995, a damning reply to Nelson and Platnick's paper appeared in *Cladistics,* titled 'Explanation' and authored by 30 cladists, all members of the Willi Hennig Society (Farris *et al.* 1995). The reply, later known as the 'Gang of 30 paper', was simply an eviction notice – pattern cladistics no longer had a place in the Willi Hennig Society. One key player was Humphries, who, ironically, co-authored the 'Gang of 30 paper' and the subsequent reply (Platnick *et al.* 1996). While Humphries promoted the methods of Farris, he also was close with the pattern cladists. The dispute, which had been about methodology, had turned into a witch-hunt. Those who did not adopt Farris' parsimony method wholeheartedly were effectively barred from the committee of the Willi Hennig Society, unfairly reviewed or criticised in its journal *Cladistics* and shunned by a larger part of the cladistic community. Farris' method had become cladistics. Humphries, desperate for recognition within a society he co-founded, tried to play both sides and failed. At risk of losing his close friends, Humphries begrudgingly joined the pattern cladists in a last reply (Platnick *et al.* 1996).[24] Sadly for Humphries, the reply was the last time he published in a journal he co-founded with Norm Platnick 11 years earlier.

Farris and Humphries were no longer to sit side-by-side. By 1996, they never really spoke again – the split between numerical and transformed cladistics was final. The solidarity at the IX Willi Hennig Meeting was followed by an ostracism of pattern cladistics from the society. Pattern cladists made their final appearance at the 1999 meeting in Göttingen in Germany (Williams *pers. comm.* 2016). While the war started in press and in the corridors of the AMNH and BM(NH), Australian cladists enthusiastically read the debate. More importantly, they formed discussion groups.

Coopers and cladistics: Australians debate the debate

In his 1991 report of the Hennig meeting, Cranston acknowledged the 'Canberran "Coopers and Cladists" discussion group for reviewing this report' (Cranston 1991, p. 79). Even before the Hennig Society arrived in Canberra, Australian cladists had already organised their own discussion groups in the late 1980s. At the CSIRO Christmas party in 1987, three entomologists – Pete Cranston, Gerry Cassis and Chris Reid – considered the idea of a cladistics discussion group. The idea was to spread the word of cladistics through a journal discussion group, but without the formality of US journal clubs, such as having a presenter and audience confined to a lecture theatre. Moreover, holding the discussion group in the neutral territory of the Australian National University campus after hours would mean a less formal group with plenty of social lubricant – namely Coopers, an Australian brand of beer (Cranston *pers. comm.* 2014).

In January 1988, Coopers and Cladistics was founded in Canberra and has been held fortnightly since 1988.[25] Early members were Cranston, Reid and Cassis as well as Don Colless (entomologist), Colin Groves (mammalogist), Dan Faith (ecologist), Ebbe Nielsen (entomologist), Penny Gullan (entomologist) and Gavin Young (palaeo-ichthyologist). A year later, in 1989, the Sydney branch of Coopers and Cladistics was set up by Australian Museum researchers Tony Gill (ichthyology), Dan Bickel (entomologist), Jim Lowry (marine invertebrates) and Gerry Cassis (Australian Museum 1990, p. 43; Gill *pers. comm.* 2014). Together with cladists George 'Buz' Wilson (marine invertebrates) and Greg Edgecombe (palaeontologist), the Australian Museum was later to become a hub of Australian cladistics.

The first meeting of the Sydney branch was held in the East Sydney Hotel on Crown Street in Woolloomooloo in 1989, because it had a back room away from the hustle and bustle of pub traffic (Fig. 4.1). More importantly, it had the Australian ale, Coopers on tap. In attendance were Gill, Cassis and Peter Weston, among others. Meetings involved discussion of methodological and theoretical articles hot off the press from journals such as *Cladistics* and *Systematic Zoology*[26] or dissecting draft manuscripts. Students and researchers alike attended meetings, some to vigorously debate new ideas or to defend existing paradigms, while others came to watch the heated debates. The Sydney chapter remained strong until the late 1990s, but started to die off by the early 2000s. Factors such as research staff redundancies at the Australian Museum, as well as museum politics, effectively killed-off the Sydney chapter[27] (Edgecombe *pers. comm.* 2014).

Coopers and Cladistics had an impact on many students and seasoned researchers alike. Acknowledgements of the Canberra branch of Coopers and Cladistics pepper the 1990s literature, some thanking members for reviewing draft manuscripts for publication and others for helping in arguing out ideas (e.g. West and Faith 1990, p. 18; Young 1995, p. 17).

Fig. 4.1. The East Sydney Hotel, Woolloomooloo (corner of Crown and Cathedral Streets, Sydney). The Sydney branch of Coopers and Cladistics was held in a private room in the Hotel during the 1990s and early 2000s. Photo taken by Melinda L. Tursky (29 September 2015).

Cladistics and biogeography

While Coopers and Cladistics was engaging Australian cladists and those interested in cladistics, the IX Willi Hennig Meeting would help spread the word a little further. The conference had a mixture of international, as well as Australasian, systematists and taxonomists: Ladiges, Morrison, Cassis, Weston, Crisp, Jennifer Chappill (botany), Mark Harvey (arachnology), Kevin Thiele (botany), Steve Van Dyck (mammalogy) and Robert Raven (invertebrates). There were also several contributions from Australasian molecular biologists, such as Peter Baverstock, Andy Austin, Adrian Daniell, David J. Miller, Adam H. Porter and Craig Moritz. The contributions by these seemingly 'molecular pheneticists' seem out of place in a cladistics conference, but yet there they were. Numerical cladistics, focused on algorithmic applications, attracted debates in methods, less so in theory. For instance, compare the Hennig meeting of 1990 with that of the 12th ASBS meeting, 'Plant systematics in the age of Molecular Biology', held a year earlier. There was very little mention of cladistics, perhaps indicating that molecular biologists had other plans; after all, established researchers such as Baverstock and Penny had their own methods, which were developed in the 1970s and were continuing to be developed. Moreover, 'gel-jockies' also had their own version of

Farris, namely, Joe Felsenstein, who retreated from the cladistics-phenetic wars and refined numerical methods. Cladistics had won among taxonomists, who primarily used morphological data. In molecular systematics it was another matter. DNA analysis was compatible with, and often compared to, phenetic or model-based methods. *Australian Systematic Botany* published the proceedings of the Plant Systematics in the Age of Molecular Biology and Gondwanan Elements in the Australian Flora ASBS Symposium, which was held at the University of Sydney. The symposium contained only five out of 15 papers that compared the results from cladistic (morphological) and phenetic (molecular) methods (West and Faith 1990; Moran *et al.* 1990; Coates and Hnatiuk 1990; Doyle *et al.* 1990; Colgan 1990).

The Nancy T. Burbidge Memorial Lecture by ornithologist and botanist Richard Schodde on the 'Origins, radiations and sifting in the Australasian biota – changing concepts from new data and old' (Schodde 1989), leaves the reader wondering what happened to cladistics. Schodde ignores Australian cladistics and the work by Ladiges or Weston in favour of the phenetic work done through electrophoresis and DNA-DNA hybridisation. While it was befitting for the symposium to focus on molecular studies, it raises the question why several of the talks by cladists were not mentioned. Consider this remark,

> 'In the absence of a complete fossil record, finer tuning of these anomalies in birds is only possible through a finer tuning of phylogenetic links, something that comparative morphology has not been able to achieve after 200 years of research in this the most studied group of organisms in the world … New sets of characters were needed. No doubt you have all heard at this meeting of how molecular genetics has become the new whizzbang technology for systematic biology … Today there is a wide and growing range of molecular and biochemical techniques – all good and with different values and virtues – for attacking different kinds of taxonomic and phylogenetic problems' (Schodde 1989, p. 8).

Schodde's candour is somewhat revealing. Has he caught a glimpse of the future, in which molecular data (and molecular biologists) replace the old, redundant and problematic morphological data (and taxonomists)? Molecular data in 1990 was revolutionary and it did add to our ever increasingly larger and larger datasets. But what does it tell us of theory, or the role of ancestors and centres of origin? Seemingly little,

> 'From all this data – old morphological and new palaeontological and molecular – a broad new picture emerges of the origin and radiation of Australasia's phanerogam flora and vertebrate fauna. Australia and New Zealand inherited from Gondwana a prevailing cool temperate to subtropical rainforest biota … Breaking away first, New Zealand may have missed out on monotremes and marsupials; and being small and at times broken, it had much less space for diversification than Australia. Its biota was probably never particularly rich, but it probably also changed rather little under a moderately constant climate on its northward drift through the Tertiary' (Schodde 1989, p. 9).

With new data and whizzbang technology, old stories can be told anew, without any change to theoretical foundations. Transformed cladists, who challenged narrative over evidence, may as well not have bothered.

To his credit, Schodde does acknowledge 'cladism and its biogeographic sister, vicariance' (Schodde 1989, p. 5). By 1989, little cladistic biogeography had been done on Australia's biota for it to feature prominently in any talk on Australian biogeography. Interestingly, Schodde did provide an updated area classification: one that moved on from Tate and Spencer, and included new regions (or 'elements') such as the Irian and Tumbunan.[28] Regardless, these areas were not mentioned in the following ASBS symposium on Austral biogeography, held in conjunction with the 1990 XI Hennig meeting.

Much of early Australasian biogeography was missing from the 1990 ASBS Austral Biogeography Symposium held in conjunction with the XI Hennig meeting in Canberra. Had cladistic biogeography and 'its biogeographic sister, vicariance' removed all mention of Tate and Spencer's regions and much of Schodde's history of the Australian biota? And what was cladistic biogeography anyway? By 1990, few articles existed on Australasian cladistic biogeography, and those that did left Australian biogeographers perplexed. Dispersal, the default explanation in biogeography, played a small role. How could biogeographers even discount the notion of dispersal in determining the history of the Australian biota? That was Keast's criticism,

> 'On the debit side there continue many of the shortcomings of much vicariance writing, supporting the thesis by chosen examples, rather than analyzing a biota to determine what proportion of distribution patterns can best be explained by vicariance relative to dispersal or other means' (Keast 1987, p. 188).

The distinction between vicariance and dispersal was not clear in the 1980s, and only a few evolutionary taxonomists such as Lawrie Johnson picked up on the analogy between non-monophyly (e.g. polyphyly) (gradism) and dispersalism,

> 'It may be extreme, methodologically obsessed, and may infuriate by putting down those who get labelled pejoratively as 'dispersalists', just as cladists pejoratively use 'gradist', a term I have been assailed with, but repudiate for its implication of support for polyphyletic taxa … Humphries and Parenti (1986) could pay much more respect to the intelligent synthetic approach of such as Raven and Axelrod [1974, 1975]' (Johnson 1989, p. 103).

In defence of Humphries and Parenti (1986, 1999), cladistic biogeography looked for patterns and not for lineage geohistory of single taxa. Patterns are best explained by vicariance and not dispersal. Cladistic biogeography is a method for finding area classifications that are explained as resulting from vicariance. In doing so, cladistic biogeography doesn't discount the existence of dispersal, only its inability to form historical patterns. Perhaps it was this distinction that was confused? The Austral Biogeography Symposium papers, later published in *Australian Systematic Botany* (Ladiges *et al.* 1991),[29] are a mixture of cladistic biogeography, single taxon histories and phenetics. Although a jumble of different approaches, it was a first step at looking at the Australasian biota through area relationships. What this new generation of cladists had discovered is that many earlier biogeographical hypotheses were fraught with problems.

The problem was time. Earlier hypotheses stated that much of the Australian biota have many recent elements. Discoveries of Miocene fossils of the same taxonomic groups in places such as Riversleigh led to questioning of these hypotheses. Moreover, Pleistocene radiations from Asia and New Guinea did not explain why some taxa in Australia had closer relationships to South America than they did to New Zealand. Brundin discovered this in his trans-Antarctic relationships of non-biting midges (Brundin 1966, 1981); now the same relationships were being discovered in many different organisms. Australia was not only non-monophyletic, it had trans-oceanic relationships spanning the Southern Hemisphere.

The combination of a lack of cladograms and the fact that many Australian taxa were part of an Austral biota, possibly created the conceptual break between early Australian biogeography and the 'disciples of Darlington' such as Keast (Schodde 1989), and that of the new plate tectonics and cladistics-influenced biogeography of the late 1980s and early 1990s. The old phytogeographical regions were replaced with new endemic areas. The old dispersal routes from New Guinea were discarded in favour of plate tectonic induced trans-oceanic connections between Africa, Australia and South America. In his 1989 Burbidge Memorial lecture, Schodde warned of these new beginnings,

> 'The concept of dispersal routes, as it is being used today in Australasian biogeography, is all too often misused, confusing the difference between vicariance and dispersal at continental level, and the different contributions that both – and I stress both – have made to shaping the distribution patterns of plants and animals in the world today' (Schodde 1989, p. 6).

Schodde's warning mostly reflects the view of the practitioners rather than the theory. The confusion between vicariance and dispersal is still very much prevalent in 21st century biogeography (see Chapter 6). In the 1980s, it was hotly debated in international conferences and fought out in prestigious journals, such as *Systematic Zoology*. When the joint XI Hennig and ASBS Meeting brought the debate to Canberra, one would have thought that it would feature in the ASBS Nancy Burbidge Memorial Lecture, particularly one that is presented by an early Australian cladist. Instead, Roger Carolin chose to present a lecture on plant classification since the ancient Greek Democritus. Why ignore Austral biogeography after a symposium on the topic in a memorial lecture dedicated to a prominent Australian biogeographer? We may never know, but for Carolin, cladistics may have moved beyond its remit of finding stable classification. In the case of Schodde, fossils were undermining established biogeographical theories of Australasia,

> 'While the fossil record may provide good clues to the origin and radiation of Australasia's biota, it can never, on its own, provide final answers. It is too patchy stratigraphically, too limited geographically and too biased against the less easily preserved organisms '(Schodde 1989, p. 7).

Nevertheless, it didn't stop Australasian palaeontologists challenging the established idea that marsupials radiated separately in the Northern Hemisphere to Australia and South America,

> '… additions to the available fossil record substantially to an interpretation of the biogeographic theory of marsupials … Recent discoveries strongly indicate that the "Sherwin–Williams effect" probably accurately describes the origin of the group in the Northern Hemisphere and its dispersal into South America, but not Australia. Dispersal of marsupials, but not their eutherian contemporaries, across Antarctica to Australia, a possibility rejected by W.D. Matthew, probably occurred very late in the Mesozoic or early Cainozoic' (Clemens 1991, p. ii).

Australian palaeontology, unlike biology, took up cladistics at a much later date. The reasons varied: fossils had too few characters, or cladistic theory made no sense within biostratigraphy. Most important was the role of ancestors. Biological cladists were challenging the role of ancestors in classification, whereas palaeontologists such as Ken Campbell, steeped in evolutionary taxonomy, were resisting the spectre 'haunting palaeontology'.

Cladistics in Australian palaeontology

In his 1975 'spectre of cladism' article, Campbell explains his reasoning:

> 'As with the original spectre there may be something to be said in its favour, from a theoretical point of view at least, and no doubt it will be in the haunting business for many years to come. Whether it is allowed to take up a permanent post of spirit-in-residence, however, will depend not so much on the frequency of its visitations or the sophistication of the guises it adopts, as on the benefits we derive from having it around the ancestral home.
>
> What would we as palaeontologists accept as benefits? In the first place we would expect a strengthening of the basic fabric of the palaeontological structure, understanding the evolutionary relationships between organisms, thus providing a basis for stable classification. Then, in the second place, we would hope that it would enable us, using the insights thus obtained, to order geological phenomena in more satisfactory ways than we can at present, and increase the geological explanatory power of palaeontological data ... So before taking this particular spirit on permanently it would do well to look not only at what it plans to do, but also at the effects of its previous manifestations' (Campbell 1975, p. 87).

Campbell was grappling with the relentless creep of the cladistic reform of palaeontology: one that removed the need for ancestors in favour of treating fossils on par with extant taxa. For Campbell this was unacceptable. Cladistics had gone too far in treating fossils as sets of homologues, like extant taxa. Fossils as taxa, rather than as ancestors, undermine 'the geological explanatory power of palaeontological data'.

Campbell's paper was published in the first issue of *Alcheringa*, the journal of the Association of Australasian Palaeontologists. The first editor, Bruce Runnegar, appealed to readers that *Alcheringa* sought 'articles of wide appeal that draw conclusions, integrate knowledge from different fields or sources, or point to areas for further exploration' (Runnegar 1975, p. 1). Given that cladistics had reformed palaeontology and evolutionary taxonomy worldwide, did Campbell's anti-cladistic article, 'Cladism and phacopid trilobites', published in the same volume delay the adoption and effectively delay the development of cladistics and cladistic biogeography in Australasian palaeontology?

Cladistics finally entered the pages of *Alcheringa* in 1981 in the form of a paper on the 'Biogeography of Devonian vertebrates' by palaeontologist Gavin Young, which included a cladistic biogeographic analysis (Young 1981). Three years later this was followed by an in-depth cladistic biogeographic analysis in *Proceedings of the Linnean Society of New South Wales* (Young 1984). During this time, the cladistic literature had published the first major text on cladistics (Eldredge and Cracraft 1980; Nelson and Platnick 1981; Wiley 1981). Cladistics was reforming Australasian palaeontology, but slowly.

While Campbell thought that 'from a palaeontological point of view, cladism is long on theory and short on rigorously worked out examples' (Campbell 1975, p. 88), he dismisses any such examples by stating a common misconception held by palaeontologists at the time, namely that 'vertebrate fossils lend themselves more readily to cladistic analysis than do invertebrates' (Campbell 1975, p. 89). In fact, a rigorous cladistic study of phacopid trilobites appeared in 1991, but not in a paleontological journal. *Cladistics*, the journal of the Willi Hennig Society, published the first large-scale analysis of invertebrate fossils using cladistic software. The paper titled 'The phylogeny and evolution of some phacopid trilobites' by Ramsköld and Werdelin (1991), dismissed Campbell's argument. Monophyletic taxa, Ramsköld and Werdelin correctly argued, are 'the only taxa that have a biological and paleontological reality' (Ramsköld and Werdelin 1991, p. 30). What makes this paper so remarkable was that it showed that fossil invertebrates (phacopid trilobites) do lend themselves to cladistic analysis – a claim that is not lost on 21st century palaeontologists,

> 'Eldredge (1977) represented the first call to arms to reconstruct trilobite evolution using cladistic methods, and it is clear that that call to arms was effective in stimulating additional research' (Lieberman and Karim 2010, p. 121).

The additional research came later with the availability of computer software; however, earlier 'pen and paper' approaches of Hennig's method in trilobite systematics were unsuccessful (Hahn and Hahn 1967; Lauterbach 1983).

Australasian palaeontologists did not adopt cladistic methodology until the early 1980s, although it was taught in palaeontology courses in various Australian universities (Archer *pers. comm*. 2015). Other than the pioneering work by New Zealand biologist Bernard Michaux on fossil ancillinid gastropods in 1989 in *Alcheringa*, cladistic analyses remained largely absent in the paleontological literature in Australasian journals (Michaux 1989). Perhaps this is a legacy of Campbell, or of a general discontent with cladistics in Australasia. Australians did, however, publish cladistic treatments in international journals. Invertebrate cladistics, however, remained in a hiatus until the arrival of Canadian palaeontologist Gregory D. Edgecombe at the Australian Museum in 1991. Edgecombe, a student of Niles Eldredge, was trained in New York at the AMNH, where Ladiges had spent time a decade before. Unlike Ladiges, who had a largely open-minded botanical community to interact with, many of Edgecombe's Australian invertebrate (and some vertebrate) palaeontological peers were staunchly anti-cladistic.[30]

The anti-cladistic sentiment in Campbell's work extended also to fossil fishes. At the same time, Archer and Clayton's book hit the shelves in 1984, Charles Marshall was the only palaeontologist to present a talk at the Cladistics Symposium held in Canberra. The topic concerned a cladistic study of Roger Miles on fossil lungfishes, which Marshall likened to an analysis by Campbell and Barwick (1983) of dipnoan dentitions which 'renders Miles' parsimony [cladistic] argument invalid' (Marshall 1984, p. 23). Marshall restates this claim in a larger paper in a special issue published in the *Journal of Morphology* titled 'The biology and evolution of Lungfishes' (Marshall 1987). There, Marshall compares a cladogram 'based on Campbell and Barwick's ('83, '84) study of early dipnoan dentitions' to the cladogram of Miles (1977), which shows that the 'phylogenetic conclusions [of Barwick and Campbell] are based on a richer empirical base and are more consistent with observed functional trends' (Marshall 1987, p. 151). Although Marshall pointed out that 'it is important to realize that they did not employ cladistic techniques to arrive at these conclusions', he nevertheless favoured 'the phylogeny based on the dental characters of Campbell and Barwick's study ('83, '84, this volume) … even though it is less parsimonious' (Marshall 1987, p. 161). Why would Marshall favour what is essentially an authoritarian 'expert' account over an empirical approach? Authority lies in the hands of the experts, who in turn believe they are immune to criticism. Rather than an empirical approach, Marshall prefers the 'morphological, functional and stratigraphical evidence' of Campbell and Barwick (1983). Functional 'evidence' is highly prone to analogy (i.e. analogous non-homologous characters) and stratigraphy denotes an expert 'seeing' ancestry, with the latter being a bugbear of cladists. In the same volume, British palaeontologist Peter Forey bemoaned the use of ancestors,

> 'There are, however, various problems surrounding the recognition of ancestors (the nature of primitive characters, introduction of hypotheses of process, paraphyletic [non-monophyletic] status, etc.) that conspire to render any hypothesis of ancestry an authoritative statement rather than a theory capable of being criticized … Many of these problems have now been acknowledged and new attempts are being made using cladistic analysis, in which the emphasis has shifted away from searching for ancestors toward a preference for searching for sister-groups' (Forey 1987, p. 88).

Cladistics started with the reform of palaeontology – the dismissal of authoritarian expert opinions as 'evidence' on topics such as ancestry (Williams and Ebach 2008). Some palaeontologists, such as Barwick and Campbell, seemingly will never give up that authority,

> 'Rather than attempting to discover relationships between the various groups using cladistic methods which we consider to be misleading, we consider that

> studying the functional structures that newly appeared at that time and then try to give an integrated study in functional terms, would give a better understanding of the course of evolution' (Campbell and Barwick 2006, p. 375).

Cladistics attempted to reform palaeontology, yet palaeontologists still search for ancestors and centres of origin, something that seems to have infatuated molecular systematists. In fact, Nelson has gone so far to suggest that the,

> 'palaeontology of the past is revived in molecular systematics of the present, in the search for ancestors and centres of origin' (Nelson 2004, p. 127).

One wonders, has the cladistic reform of palaeontology failed? Perhaps not, depending who you read (e.g. Williams and Ebach 2008 versus Felsenstein 2003). But Australasia played host to a reform of both New Zealand biogeography and biogeography worldwide – possibly the most controversial topic in 20th century biogeography – called panbiogeography.

Chapter 5

A new biogeography: the panbiogeography revolt in New Zealand

Possibly the greatest challenge to the cycle of reinvention was the revolutionary new approach to biogeography called panbiogeography. Emerging as a quasi-student revolt in the otherwise quiet setting of 1980s New Zealand, panbiogeographers did more to stop the cycle of reinvention in New Zealand than any other group of scientists before or since.

Panbiogeography is an oft-misunderstood scientific endeavour, prone to knee-jerk reactions by its detractors and considered methodologically neutral by its supporters. Its history has been shaped by vitriol, confusion and contradiction, and it has had a global impact in historical science, and in the history and philosophy of biology. Remarkably, this history was played out in New Zealand in the 1980s and 1990s and has caused great national shame or international legacy, depending on whom you ask.

What most biologists and historians of biology fail to realise is that panbiogeography is an evolutionary synthesis: one that rivals the modern synthesis in all respects. Panbiogeography has its own evolutionary, developmental and distributional theory. It has a unique epistemology that may be implemented in several ways, both qualitatively and quantitatively. It has its own unique history rooted in foundational concepts separate to those of the modern synthesis. With all this in mind, it is surprising why anyone would confuse it as a mere biogeographical method.

Panbiogeography: Earth and life evolving together

Panbiogeography is founded on the idea that evolutionary theory is derived from geographical distribution in the same way that Darwin and Wallace's evolutionary theory was given credence by 19th century biogeographical research. The modern synthesis, a legacy of Darwin, places greater emphasis on dynamic populations and historical lineages than on distribution in explaining evolution. Panbiogeography, however, does the opposite: it primarily focuses on the spatial or geographical dimension as key to understanding evolution. Panbiogeography focuses on distribution, the geography and geographical processes as primary subjects, while foremost in the modern synthesis are the physiological processes, morphology/molecules and population structure or organisms. The difference between the two syntheses is the underlying theories of evolution. Panbiogeography is based upon orthogenesis – namely that evolution is driven in part by external (e.g. geography) and intrinsic (e.g. mutation) processes. In fact, 'Evolution = Space + Time + Form; geographic distribution is not the same as dispersal; dispersal forever repeats; adaptation only works on a background of orthogeny … earth and life evolved together' (Croizat 1964, p. ii). Unlike the modern synthesis, panbiogeography treats distribution in the same way taxonomists treat a taxon: a conceptual type that contains the sum of the parts. Within a taxon's distribution, individuals disperse. If the distribution is broken up due to geographical events, the distribution is vicariant. Distribution effectively defines the organism. The opposite is true for modern synthesists. Organisms are individual histories over space and time. The organism defines the distribution that is dynamic, shifting from day to day, and not static 'areas' or fixed distributions. The modern synthesis version of distribution is solely defined by what the organism does, which is mostly disperse (e.g. migrate, founder effects) or on rare occasions find themselves cut off from their progenitor population (i.e. vicariance). These two radically different ways of viewing the world give rise to two very different syntheses, one in which geography is the driving force behind distribution, which in turn drives evolution, and the other where physiological processes (morphology, genetics and behaviour) drive distribution independently of geography. In the former, an active mountain range can shape a new distribution and cause new species to arise (i.e. Earth and life evolve together); in the latter geographical events are simply processes with which organisms may or may not interact (i.e. life evolves independently of Earth). But is there more to it?

The panbiogeographic literature, including the weighty tomes of Croizat's *Panbiogeography I* and *II* (Croizat 1958) and *Space, Form, Time* (Croizat 1964), contains more about practice than about how its foundations were developed. Like taxonomy, panbiogeography is defined by its practice: drawing lines that link 'the different localities or distribution areas of a particular taxon or group of taxa' (tracks); tracks overlapping 'a specific geographic or landscape feature' (the baseline); identifying where they intersect (nodes) and 'the greatest concentration of biological diversity with the geographic range of a taxon' (main massing) (Craw *et al.* 1999, pp. 20–21). Quite simply, panbiogeography includes a method about identifying and mapping distributions and the elements found within them. The rest is generating biogeographic models based on the correlation between geomorphology and taxic distributions. The appeal is that it looks directly at distributions and distributional mechanisms (i.e. Earth processes). Where biogeographers get confused is in its explanation of physiological distribution mechanisms. If panbiogeography is treated as a method within the modern synthesis, one cannot help thinking that it ignores dispersal, sympatry and allopatry – the distributional drivers and causations of Darwinian biogeography. If panbiogeography is seen as a synthesis on its own, then dispersal, like vicariance, is subsumed by distribution rather than being primary evolutionary or physiological drivers. The problem is that most biogeographers think within the paradigm of the modern synthesis.

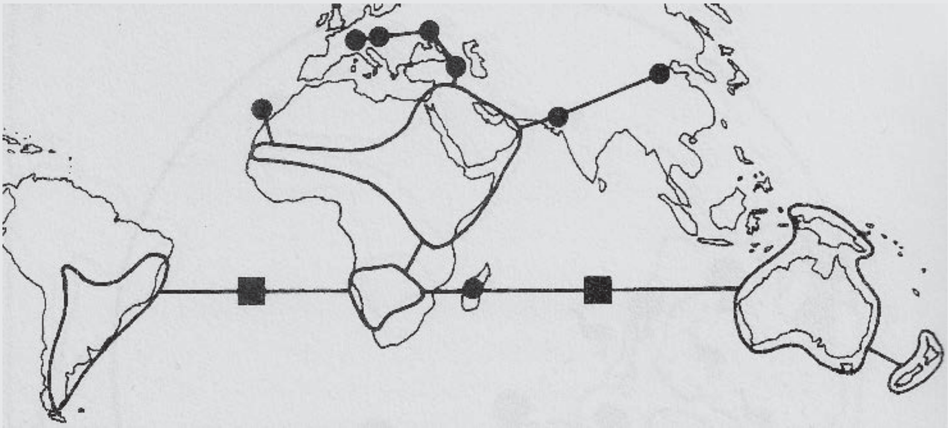
Understanding these fundamental differences is key to accepting panbiogeography as its own synthesis (Fig. 5.1). However, panbiogeographers have not explicitly helped other biogeographers see beyond the modern synthesis. In fact, the foundations of panbiogeography are rarely discussed. This has led to a misguided belief that panbiogeography rejects dispersal, which has caused the greater controversy, particularly within the New Zealand and Australian biogeographical communities (Waters *et al.* 2013; Heads 2015; McGlone 2016). The history of the sudden rise of panbiogeography in New Zealand, its dramatic fall and present day ostracism, is a story about this misunderstanding as well as whimsical bandwagons, false associations, methodological meddling and parochial politics.

Dispersal, tracks and areagrams

Tracks are lines on a graph indicating the route of dispersal in the same way lines on a map depict routes of transit in a road atlas. The routes of dispersal differ from those in traditional biogeography, which have a point of origin and the direction of dispersal of individual taxa. Rather tracks represent older corridors of distribution that formed via geological or geographical events over time.

The nodes of tracks indicate the area in which two taxa or populations overlap. Giving that tracks are drawn based on proximal geographical distance (two main massings are connected geographically by the shortest distance), tracks may be drawn as geograms, because they contain no phylogenetic information.

The problem arises when a panbiogeographic track drawn as a geogram conflicts with an areagram that is derived from a cladogram. Panbiogeographers would consider the track geogram to be the most informative, because the areagram is not *geographically* informative. Given this, how do tracks and areagram reconcile when they conflict?

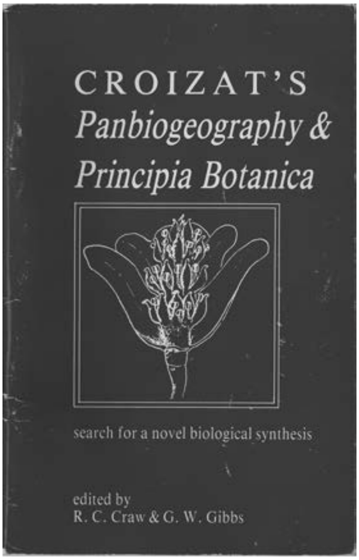


An example of a track (lines that connect filled dots or squares), a baseline (black square), and a main massing (polygon) using ratite bird distributions (from Craw *et al.* 1999, p. 26, Fig. 1–9a).

The development of panbiogeography in New Zealand (1978–1989)

In 1988 a symposium on the Panbiogeography of New Zealand was held at the National Museum in Wellington, later published as *Special Issue on Panbiogeography* (Matthews 1989) in the *New Zealand Journal of Zoology*. A review of the symposium heralded it a success in which 'we now have an emerging and competing third paradigm … that … is producing new ideas. That is exciting and constructive whether they ultimately turn out to be right or wrong. One does not need to be baptised and confirmed to appreciate that, whether or not the formative metaphors are appropriate, the methods can sometimes produce interesting and valid insights' (Caughley 1991, p. 191). However, Caughley makes an interesting note,

> 'Incongruously these ideas took firmest root in New Zealand. An entire school of panbiogeography arose there and set about adapting and extending Croizat's



CROIZAT'S
Panbiogeography &
Principia Botanica

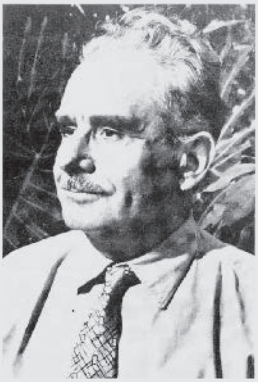
search for a novel biological synthesis

edited by
R. C. Craw & G. W. Gibbs

Fig. 5.1. The cover of the 1984 memorial edition of *Tuatara* (Vol. 27, No. 1) edited by Robin C. Craw and George W. Gibbs marking the passing of Léon Croizat (1894–1982). Note the title: 'Croizat's *Panbiogeography & Principia Botanica: search for a novel biological synthesis*'. Panbiogeography from the outset was more about achieving a workable *synthesis* than promoting a biogeographical method (Image: Victoria University, Wellington, New Zealand). The volume was unfavourably reviewed by Stoddart (1985) under the title 'Better never published'.

Léon Camille Marius Croizat (1894–1982)

A controversial figure in biogeography, Italian-born Léon Croizat inspired generations of biogeographers such as Nancy Burbidge, Lars Brundin, Gary Nelson and Robin Craw. Croizat offered a new biological synthesis called panbiogeography: one that challenged the modern synthesis of Mayr and Simpson. Croizat's work was also the basis for two very different approaches: vicariance biogeography and the panbiogeography of Craw. Croizat also coined the famous dictum Earth and life evolve together, much to the irritation of dispersal biogeographers such as Robert McDowall.



Léon Camille Marius Croizat. Image: John R. Grehan.

> models (and the cladistics of Willi Hennig) to the New Zealand region' (Caughley 1991, p. 190).

Caughley is referring to the attempts by Gary Nelson and Donn Rosen at the AMNH in New York to integrate panbiogeography into cladistics. Nelson and Rosen's attempt had already inspired the ire of Croizat, who felt his submitted paper to *Systematic Zoology* (Croizat *et al.* 1974) was hijacked by Nelson (Editor-in-Chief at the time) and Rosen to promote vicariance biogeography, rather than extol the virtues of panbiogeography. The exchange between Nelson and Croizat ended up with Croizat distancing himself from Nelson and Rosen, vicariance/cladistic biogeography as well as the co-authored 1974 paper (Croizat 1982). By the late 1970s, the cladists at the AMNH were *personae non gratae* with Croizat.[31] How then did panbiogeography grab the attention of non-cladists in New Zealand a decade later – a world away from the AMNH? Certainly palynologist and New Zealander Lucy M. Cranwell had contact with Croizat in 1960, years after she left New Zealand to work at the University of Arizona (see Grehan 1989), but would have contributed little to the panbiogeographical storm of the 1980s.

Panbiogeography had its first ardent supporter in New Zealand – Robin C. Craw, a PhD student at the Victoria University of Wellington.[32] In his 'Two biogeographical frameworks: implications for the biogeography of New Zealand. A review', Craw states:

> 'Vicariance biogeography, as developed by Leon Croizat, frees the biogeographer from adherence to particular geological models and presumed centres of origin. It allows the biogeographer to construct hypotheses using data of biotic distribution which can then be tested against a variety of geological hypotheses' (Craw 1978, p. 91).

Vicariance biogeography? Surely Craw means *panbiogeography* – a term he never used in his review. Given this, it is plausible that Craw was influenced by the debates between vicariance biogeographers and traditional biogeographers such as fellow New Zealander Robert M. McDowall, who had written a critique of Croizat in the same year (McDowall 1978). Could it be that Craw, like many traditional biogeographers, was confusing Rosen and Nelson's vicariance biogeography with Croizat's panbiogeography? Perhaps the shared dislike of the modern synthesis obscured the theoretical and methodological differences between the biogeographies of Croizat and Nelson? In referring to the 'two biogeographical frameworks', Craw (1978) is contrasting and older orthodox biogeography within a Darwinian pre-tectonic dispersalist framework and the newer vicariance biogeography, which exists in the Croizatian framework of tracks, main massing, and so on. Reading Craw (1978), one may wonder whether there are not two versions of vicariance biogeography: that of Nelson and Rosen and the panbiogeography of Croizat. Clearly it is semantics that had lumped vicariance biogeography and panbiogeography together as the same thing. Unfortunately, this oversight had already muddied the waters of biogeographical discourse:

> 'Those zoogeographers who work on continents, on the other hand are obsessed with the stability if not permanence of distributions and the ties that bind the

> fauna to an ancient landscape; they tend to be what are now called vicariance biogeographers' (Fleming in Grehan 1989, p. 516).
>
> 'An alternative to the divining of imaginary centers of origin and miraculous dispersal events practiced by Fleming and McDowall is offered by vicariance biogeography' (Craw 1979, p. 103).
>
> 'Few areas in systematic biology have undergone such major advances as has historical biogeography. The reason for this is two-fold: the introduction of cladistic theory and methodology (… and many subsequent papers) and then of vicariance biogeography (Croizat *et al.* 1974 …)' (Cracraft 1981, p. 460).
>
> 'Finally, some biogeographers have been inspired by the vicariance biogeography developed primarily by Leon Croizat in the fifties and sixties' (Frankel 1984, p. 161).

Not until 1982 was panbiogeography used separately to vicariance biogeography:

> 'I will, directly challenged this time by Brian Rosen from the British Museum under my name, deal separately in coming pages with my own (pan)biogeography, vicariance/vicariism, and alien "vicariance biogeography," in order that the reader may form, once for ever, *a solid understanding of these matters*, ready to detect for himself the countless falsehoods, misconstructions, etc., that now foul the history of their origin, growth etc.' (Croizat 1982, p. 292, original emphasis).
>
> 'As part of an ongoing study of the panbiogeography of New Zealand, based on the approach of Croizat' (Craw 1982, p. 304).

Nonetheless, panbiogeography (masquerading as 'vicariance biogeography') had entered the psyche of New Zealand biogeography. By the late 1970s and early 1980s, panbiogeography was in full swing in New Zealand. More important, not unlike cladistics in North America during the same period, its most ardent supporters were PhD students. Panbiogeography was reforming New Zealand biogeography and postgraduate students were steering the debate.

Compare this with the influence of panbiogeography in Australia. In 1984 the first meeting on cladistics was held at CSIRO in Canberra and panbiogeography had little coverage. Even in the 1990 Austral Biogeography Symposium, panbiogeography was notably absent, with the only two papers appearing in a special issue in *Australian Systematic Biology* (Grehan 1991; Henderson 1991). Panbiogeography truly was a New Zealand postgraduate phenomenon: one that had little currency in Australia.

Challenging the New Zealand establishment: a student uprising

Up until the 1970s, the ideas of Sir Charles Fleming dominated New Zealand biogeography. *The Geological History of New Zealand and its Life* was published in 1979 and draws on the work of New Zealand geologists, geographers and biogeographers at the time.

Reading Fleming (1975), one can't help wonder if plate tectonics had changed Fleming's views on biogeography by 1979. For Fleming, even Fell's (1962) west wind drift was still a valid mechanism and proved 'a more plausible hypothesis than a land connection' for Austral organisms with a South American–sub-Antarctic distribution. Although much of Fleming's book covers continental drift, it still uses the same pre-tectonic distribution mechanisms to explain much of New Zealand's distribution (see Chapter 2). In 1979, the biogeography of Darlington (1957, 1965) and Simpson (1961, 1977) was actively being challenged in North America (Platnick and Nelson 1978; Rosen 1978). For example, Fleming's book was an updated chapter that appeared in the edited volume *Biogeography and Ecology of New Zealand* by Kuschel (1975). In 1975, *Systematic Zoology* published a review, which pointed out that the book, solely authored by New Zealanders,[33] tends to favour dispersalist narratives even when vicariate ones are considered as equally plausible. Fleming noted the dualism of dispersal and vicariance in the preface to his 1979 volume,

> 'To attribute all to "dispersal" or all to "vicariance" would do violence to the principle of parsimony, since it would imply rejection of either the plate-tectonics timetable or the fossil record' (Fleming 1979a, p. 12).

A fair comment, but a challenge nonetheless.[34] In New Zealand, like Australia, Darlington and Simpson's biogeography still remained the dominant paradigm, remaining largely unscathed by plate tectonics, and with few detractors.[35] For a new generation of biogeographers, this may have seemed like an anathema. Where was the change that signalled a new era on a dynamic Earth? For the doyen of New Zealand biogeography, Fleming made his position very clear:

> 'I have consciously avoided adhering to any one master and have my reservations about the followers of W.D. Matthew and Leon Croizat alike' (Fleming 1979a, p. 12).

But what of the majority view – namely that of George Gaylord Simpson and Philip J. Darlington? Not even Fleming could afford to ignore their views.

Compare this to the overall sentiment of New Zealand biogeography:

> 'The New Zealand interest does not represent a "school" of thought, because the participants do not adhere to any one set of biogeographic principles or theories' (Grehan 1991, p. 333).

New Zealand biogeography, particularly between 1979 and 1991, was divided into three very distinct schools of thought: dispersal biogeography, vicariance biogeography and panbiogeography,

> 'Of the three recognized approaches – centers-of-origin/dispersalist, vicariance biogeography, and Croizat's panbiogeography – only the latter two are progressive scientific research programs …' (Craw and Weston 1984, p. 1).

These observations are remarkable for a country with a small population. Not even neighbouring Australia had all three branches of biogeography represented. But many of the established biogeographers were not happy with the anti-centre of origin views of the vicariance biogeographers and panbiogeographers. To add insult to injury, Ball (1975) had accused dispersal biogeographers of being stuck in the narrative phase of his three stages of biogeography, claiming chance dispersal to be untestable (Ball 1975, p. 420). Dispersalist biogeographers such as McDowall were staunchly Darlingtonian and were not going to entertain newcomers such as panbiogeography or vicariance biogeography – but the new generation of New Zealand biogeography students wanted change:

> 'Where in the New Zealand biogeographic literature is the critique one might expect of Fleming's work' (Craw 1980, p. 81).

Where indeed? Other than a single book review, little was forthcoming, with the exception of the pithy reviews by Robin Craw.[36]

Craw believed that many of the staff and students at Victoria University had a 'dogmatic adherence to canonical Darwinism and a particularly crude version of Baconian inductivism, combined with a general abhorrence of "theory" and "concepts"'. Craw's radicalism, which wanted to challenge 'canonical Darwinism' and overthrow the orthodox dispersalism of New Zealand biogeography, attracted few established New Zealand scientists. The only criticism of Fleming, the 1975 review of Kuschel's book, was written by none other than Gary Nelson – an older version of the young New Zealander who had made waves at the AMNH in New York. At the same time that Craw challenged the New Zealand establishment and Darwinism, Nelson was challenging palaeontology and its grip on systematics. Yet both saw themselves as champions of Léon Croizat's panbiogeography[37] – Craw formalised his own definitions (e.g. geographical homology) as well as wanting to quantify panbiogeography, while Nelson had combined Croizat's ideas with cladistics. Although amicable at first, the published discussions between panbiogeography and vicariance biogeography heated up as Craw's panbiogeography started to become more established in New Zealand, at first garnering the support of established biogeographers such as George Gibbs and young postgraduates and later when it had adopted a numerical method of its own.

By 1989, panbiogeography had over 18 practitioners, all studying or working in New Zealand; their output included special volumes of *Tuatara* (Craw and Gibbs 1984), *Rivista di Biologia* (Craw and Sermonti 1988)[38] and *New Zealand Journal of Zoology* (Matthews 1989; see Grehan 1991), a *Symposium on the Panbiogeography of New Zealand* (National Museum Wellington, 1988),[39] a plethora of papers in *Systematic Zoology* and *Journal of Biogeography,* and even a TV documentary.[40] Panbiogeography had established itself in New Zealand as a credible scientific research program in biogeography and conservation (Grehan 1989). But unlike Heads, Grehan and Climo, did Craw take his panbiogeography too far, isolating established Darwinian dispersalists such as Fleming and McDowall and blatantly attacking vicariance biogeography?

Picking a fight with vicariance biogeography

More has been written about 1980s New Zealand panbiogeography and the so-called 'anti-dispersalist' attack on the established views of Fleming and McDowall than has been written on the split between panbiogeography and vicariance biogeography (e.g. de Queiroz 2014; but see Hull 1988). Reading the literature of the panbiogeographers, one may see a methodological division on how to quantify tracks. For example,

> ‘Another approach to quantification of track analysis is known as cladistic biogeography’ (Craw 1989, p. 485).

Taken as such, much of the literature written by non-panbiogeographers and non-cladists has attempted to differentiate between the two fields on the basis of their methodology. Panbiogeography was about proposing geographical tracks based on geographical, geological and phylogenetic evidence, while vicariance biogeography just focused on endemic areas and phylogeny, something that McDowall (1978, p. 88) also agreed upon.

The panbiogeographic synthesis is unique in its use of geography (distribution of organisms) as the basis for making claims about the evolution of life on Earth. Geography and geological processes drive evolution (i.e. phylogeny), meaning that without abiotic factors, such as oceanic barriers, climate and tectonics, life would not evolve and form the patterns we see today. In this sense, panbiogeography favours Earth history equally to phylogeny. To a cladist like myself, this seems odd, because phylogenies are discovered by finding homologies in order to discover monophyletic groups. Homology and monophyly makes cladistics predictive. For example, any vertebrate with hair and locating glands will be related to all mammals. No equivalent method or theory exists in Earth science. For instance, orogeny (e.g. mountain building), rocks (i.e. agglomeration of minerals), and tectonic plates (i.e. accreted technostratigraphic terranes), lack this predictive nature. A sandstone found in New Zealand will be similar in composition to one found in the North American Appalachians, but it does not share a common history or parent rock. In this sense, Earth history is not equivalent to lineage history, meaning that phylogeny represents independent evidence, whereas Earth history does not. Take the ratites and the southern beeches (*Nothofagus*) as examples. Panbiogeography uses geomorphological, geological, tectonic and phylogenetic evidence to orient tracks and propose main massings. Tracks are derived from distributional information, and are oriented based on phylogeny and the shortest geographic distance (i.e. minimum distance criterion, Craw 1985, p. 7). Ratite phylogeny showed that African and southern South American taxa were more closely related to Australasian ratites (Sibley and Ahlqvist 1981; Sibley *et al.* 1988),[41] whereas the phylogeny of *Nothofagus* conversely showed a closer relationship between southern South America and Australia. Panbiogeographers formulated their hypotheses based on this information, as well as geological evidence – namely that Africa, Madagascar and South America were once connected, meaning the two main massings (Africa/Madagascar and South America) share a common baseline across the Atlantic Ocean. For panbiogeographers, this represents a biogeographic homology. The southern beeches, however, have a Pacific baseline – namely between Australasia and South America. The two biogeographic homologies do not match (Craw 1985). Although the phylogeny is independent evidence with predictive power (i.e. a newly discovered ratite will be more closely related to an existing ratite than to any other bird), the geological evidence is derived separately based on similarities in geography and geology. What if our phylogenetic relationships conflict with the geological evidence? Could the geological and distributional data trump cladistic evidence? Without a systematic method, geographical homology is *ad hoc* and the panbiogeographic method appears descriptive and its results irreproducible. By the 1980s, panbiogeography, like palaeontology, needed reform.

Panbiogeography and its reformation

Explanations in historical science are odd things. They are based on empirical observations and measurements, but few are in themselves empirical. Inferences are based on our own judgements, theories and models of evolution. One inference can be popular and universally agreed upon, like a static view of Earth, in which the continents are fixed. Regardless, the popularity of one view does not make it correct, *just like* the case of a dynamic view of Earth, with drifting continents. Historical science is not democratic nor is it autocratic in which one person's view prevails. Science is based on evidence, and evidence remains mostly silent about inferences, except in the rare cases such as plate tectonics mechanism (i.e. mid-oceanic spreading).

Biological syntheses such as the modern synthesis and panbiogeography are formed around certain evolutionary processes. As noted above, the foundation of panbiogeography is that the Earth and life evolve together. Although this is an appealing philosophy, it may not apply to all known organisms. For instance, some organisms, such as stretch spiders (*Tetragnatha*), have worldwide distributions and may have evolved independently of Earth structures, processes and events. But a great number of taxa are linked to Earth processes, climate and geography. Panbiogeographers, like neo-Darwinists, simply adapt their underlying theory to accommodate these ambiguities. Like Neurath's boat, syntheses are constantly restructuring themselves to best fit the empirical evidence. The restructuring helps syntheses incorporate two new paradigms, such as a dynamic Earth, in which continents drift. However, a biological synthesis may also change because of other newer theories and practices. But where does classification fit into these syntheses? For much of the 18th and 19th centuries, biological classification was practised independently of any synthesis. A 19th century evolutionist and 'creationist' would both come up with very similar classifications. In fact, they would probably practise classification in the same way. Natural classification does not need a synthesis, rather it is the foundation on which biological syntheses lie.

Biological syntheses are developed seemingly to enforce a worldview onto all aspects of biology, classification included. The modern synthesis attempts to undermine a natural classification by demanding that ancestors play a crucial role in formulating natural taxa via ancestor–descendant relationships. Panbiogeography similarly attempts to propose a natural classification by insisting hypotheses in Earth history play a significant role in shaping phylogeny. Each synthesis attempts to place the cart before the horse, namely by insisting that natural classification can only be determined through a particular theoretical medium: the modern synthesis demands ancestors and panbiogeography demands the inclusion of geography. By favouring narratives of ancestor–descendant lineages and Earth history over any contradictory evidence, we may distort our biogeographic hypotheses. What then is the evidence for a natural classification: one that relates taxa? One needs to look to the 19th century and the evidence for evolution, which ironically comes to us via the three-fold parallelism, an idea developed by the staunch anti-evolutionist Louis Agassiz.

The three-fold parallelism: space, time, form versus form, time, space

Evolution, defined broadly as change through time, is a conclusion made through examining empirical evidence such as form. For example, how do we relate humans, cats and dogs? The question should be read within the realm of 19th century concepts: namely that relationship means something that has an affinity to something else. Humans, dogs and cats share different manifestations of the same morphological structures throughout their development. A human forelimb is a manifestation of a cat's forelimb, and so on. Manifestation of form is often misread as similarity. A similarity is merely resemblance. The wings of birds and locusts may have a high degree of resemblance, but they do not share manifestations of the same form. Similarity and affinity are two different things.

The second parallelism is time. Human forelimbs, for example, appear in fossil forms that we know are older. A fossil record of these manifestations suggests that older forms now extinct share even closer relations to us than we do to living forms. Closely related manifestations of the same form tend to appear in close geographical proximity or space. Another aspect of time is ontogeny, or the development of an organism. Observed as embryos, closely related forms, such as humans and pigs, have the same type of development. Space is the third parallelism. Closely related taxa, such as species or genera, tend to be geographically closer together. Kangaroos, for instance, are found entirely within Australasia, where all their closest related forms also exist. Taken together, form, time and space serve as the foundations for vicariance biogeography. The three-fold parallelism can be used as evidence for a natural taxon: that is, the different manifestations of the same form are related because they share a common history. That common history is evidence for evolution – namely the existence of ancestors and ancestor–descendant lineages.

The notion of form, time, space, is itself part of an older evolutionary synthesis, namely, classical Darwinism. Although not as sophisticated as the modern synthesis, it does have certain principles:

1. A taxon has a single centre of origin.
2. A taxon is endemic to a single area.
3. An endemic area is defined by geographical boundaries of a taxon.

Although the above criteria seem rudimentary, they do assume that some intrinsic mechanism is involved – namely that taxa 'evolve' by means of a biological mechanism. Panbiogeography, however, has a set of very different criteria:

1. An organism has 'multiple' centres of origin, because the original geographical area is fragmented.
2. An organism is endemic to multiple geographical boundaries.
3. Distribution is defined by the distributional history of an organism and its underlying geology.

The differences tell of two very different syntheses. The first looks at taxa: that is, the named morphological parts of an organism that fit into a stable hierarchical classification system. An area is the known geographical distribution of a taxon that fits into a stable hierarchical area classification system. The second concerns the whole taxon, the geological areas in which it evolved and its historical and current distribution. The differences between form, time, space (vicariance/cladistic biogeography) and space, time, form (panbiogeography) are the duality of organisms and taxa, endemic areas and historical distributions, intrinsic and extrinsic modes of evolution.

Reforming and counter-reforming Croizat's panbiogeography

Vicariance (cladistic) biogeography is the result of the reformation of Croizat's panbiogeography.[42] Nelson and Rosen saw that the panbiogeographic synthesis could only work if form takes precedence – namely if phylogeny and fossils tell us something about distribution. Although this is contrary to Croizat's space, form, time, it still suggest that there is a reciprocality between Earth processes and evolution. If a cladogram converted to an areagram can tell us about the relationships of biotic areas, then it may also guide towards plausible geographical and geological processes involved in biotic divergence.

Panbiogeographic methods were reformed to relate directly to cladistic relationship. Croizat's tracks, which were essentially historical distributional pathways that are still operational today, were subsumed into areagrams. But not those area cladograms proposed by Hennig and defended by Brundin. Hennig's progression rule, in which the most basal areas in an areagram were considered to be ancestral and therefore determined dispersal direction, was also reformed. All areas were treated equally, regardless of where they sat in a cladogram. Baselines and main massing were effectively ignored. Croizat's panbiogeography was mostly about examples, and did not contain deep methodological or theoretical discussions that contained precise definitions or procedures in implementing the method. Rather, Croizat presented a way of looking at the distribution and evolution of life on Earth in a new synthetic way – life or the biosphere was the new geological layer in the study of our planet.

By the 1980s, panbiogeography reappeared with a carefully thought-out method, theory and well-developed concepts such as geographic homology and panbiogeographic area. These had little to do with Croizat's writings. Croizat, who was not fond of definitions, theories and methods, left modern panbiogeographers without an analytical method. However, by adding a theory (e.g. geographical homology, area classification), a methodology (e.g. spanning trees) and a numerical implementation, Craw effectively attempted to show how panbiogeography could enter Ball's analytical phase without fusing Croizat's ideas with those of Rosen and Nelson.

Craw's counter-reformation of Croizat's panbiogeography had resulted in a new form of panbiogeography, something that was clearly an attempt at bringing back tracks, main massing and baselines, as well as the dictum of space, time, and then form. Craw attributed all his ideas to Croizat, each apparently supported with an accompanying quote. For example, in his 1983 thesis Craw states,

> '… from the *very opening pages* of his first biogeographical book *Manual of Phytogeography*, all through his subsequent work, Croizat relentlessly and frenetically pursues the question: "What is the equivalent of a concept of homology in biogeography?"' (Craw 1984, p. 12, original emphasis).

However, looking at Croizat's works, the term 'homology' (in context to biogeography) appears twice, but no definition or context is given. 'Biogeographical' homology appears once in the index of *Manual of Phytogeography* as ‘homologies in dispersal’, but is not referred to in the text (Croizat 1952, p. 572), and briefly in Croizat (1968, pp. 109, 201; see Craw 1983, p. 432).[43] Did Croizat really ‘relentlessly and frenetically pursue’ an equivalent of homology in biogeography, or is it an idea Craw had come up with himself? Craw persists:

> ‘To Leon Croizat, a concept of homology for biogeography can only be developed as a consequence of the direct analysis of the geographic distribution patterns of animal and plants, which results in a spatiotemporal homology concept for biogeography: biogeographic homologies of taxa are ocean basins or sea basins’ (Craw 1984, p. 12).[44]

Why give someone credit for your own ideas? Perhaps Craw thought this would justify panbiogeography in its own right, rather than as a reformation of Croizat. As a young scientist fresh out of his PhD, Craw needed the support of a large body of work, such as Croizat’s, as something he could refer back to, as he often did.[45]

The concept of geographical homology was one that unfortunately backfired, particularly in relation to the ratites. Vicariance biogeographers had insisted that ratites and *Nothofagus* were both Gondwanan distributions: that is, deriving from an ancestral biota in Gondwana. Craw had denied this, showing instead the ratites to be Atlantic–Indian, based on the close phylogenetic relationship of *Struthio* and *Rhea,* the geological history of Africa and South America, as well as the minimum geographic distance between areas.

Bizarrely, evidence for an Australasian–South American connection was available, but was ignored, possibly in favour of a better fitting phylogeny (Prager *et al.* 1976, p. 287, Fig. 2). Regardless, vicariance biogeographers stuck to their guns – the age and distribution of *Nothofagus* and ratites alone suggest a Gondwanan distribution; otherwise each group would be the result of recent long-distance dispersal events.

The problem of spatial, or biogeographic, homologies was dividing both vicariance biogeography and panbiogeography,

> ‘Vicariance cladists group areas by the interrelationships of endemic taxa (i.e. on the basis of form homologies); panbiogeographers group areas by spatial homologies’ (Craw and Weston 1984, p. 5).

The concept of spatial or biogeographic homologies was becoming vague. Craw (1985) equated biogeographic sympatry to spatial homology, without any definition. Was spatial or biogeographic homology simply distance? If it included information about phylogeny, why contrast it with form homologies? If combined with the early analysis of Prager *et al.* (1976), both the ratite and *Nothofagus* relationships would overlap. What then of the minimum distance criterion? Effectively, at some point, phylogenetic, geographic distance and geological evidence conflict, but yet panbiogeographers rarely admitted that any conflict occurred. Regardless, the *Nothofagus*–ratite spatial homologies were used extensively by the New Zealand panbiogeographers as a case in point,

> ‘The congruence of cladograms reported for the ratites and *Nothofagus–Fagus* by Patterson (1981) and Humphries (1981) is spurious from the biogeographic aspect and certainly not indicative of a common history … So far vicariance

> cladistic theory has led to more general statements about these taxa than panbiogeographic analysis …' (Craw 1985, p. 8).

Unfortunately for Craw, later DNA analyses found a Rhea-Australasian clade (Sibley and Ahlquist 1990), which was subsequently ignored by Craw *et al.* (1999) almost a decade later:

> 'In panbiogeographic terms, the ratite birds can be described as having trans-Atlantic and trans-Indian tracks and baselines …' (Craw *et al.* 1999, p. 25).

Craw's concept of biogeographic homology was poorly thought out and seems an attempt to square panbiogeography with vicariance biogeography. Unfortunately for Craw, vicariance biogeography has its background in hundreds of years of theoretical debate, whereas biogeographic homology had a far shorter life that had endured absolutely no theoretical discussion at all. Panbiogeographers, armed with computing power and numerical methods, went on to quantify panbiogeography through the use of minimal spanning trees.

Quantifying panbiogeography

Reading the biogeographical and systematic literature of the 1980s and 1990s, one can't help paraphrasing Theodosius Dobzhansky: nothing, it seems, makes sense in biology except in the light of numerical methods. The plethora of methods in both systematics and biogeography that sprang up during this time outnumber the methods of today. Vicariance biogeography, mostly a collection of theories and methods with hypothetical examples (Rosen 1978; Nelson and Rosen 1981), was finally implemented through the use of numerical methods (e.g. Møller-Andersen 1991; Weston and Crisp 1994). Cladistic biogeography had been born – a biogeographical field that had a well-thought-out theory, methodology and numerical implementation (Humphries and Parenti 1986; Nelson and Ladiges 1993, 1996). As with most methods in the 1980s and 1990s, practitioners will not adopt them if there is no numerical implementation in the form of computer software. In fact, Craw (1989) goes so far as to list the lack of a numerical implementation as one of three major criticisms of panbiogeography,

> '(1) No serious attempt at a space/time panbiogeographic synthesis exists. (2) No quantitative or statistical basis for track analysis has been demonstrated. (3) Evidence for dispersal of taxa across barriers is dismissed apriori … A quantitative approach to panbiogeography does exist and this allows for statistical hypothesis testing of both area cladogram and track approaches' (Craw 1989, p. 541).

Craw is referring to the quantitative methods of his own panbiogeography, which were developed by Page (1987), but he still refers to Croizat's methods when criticising the methods of cladistic biogeographers:

> '… much of Croizat's work, and in particular *Panbiogeography*, is a critique of the traditional Wallace regions of zoogeography … Much vicariance phytozoogeography can then be seen to be little more than an attempt to interrelate Wallace's areas cladistically' (Craw 1982, pp. 309, 311, original emphasis).

and,

> ‘It does not matter how scientific or falsifiable a phylogenetic vicariance hypothesis is, if it is not constructed and tested against the novel, detailed and sophisticated approach to biogeography developed by Croizat’ (Craw 1982, p. 315).

These statements would confuse someone entering panbiogeography. Track analysis may also be implemented using modern numerical methods, but the way it was implemented was controversial. During the 1970s and 1980s, cladistics were engaged in a war against the pheneticists: a group of numerical taxonomists who believed that similarity, no matter the characteristics used, was in itself sufficient to reveal evolutionary relationships. The greater number of similarities, the more likely the pattern would reveal itself. Cladists were outraged at this approach. Phenetics offered no hypothesis-testing and no guarantee of finding homologous characteristics. It was simply churning out the greatest number of similarities in the hope of finding a pattern, regardless of the quality of that evidence. By the mid-1980s, cladistics had clearly won the debate. Although numerical approaches are in themselves valid, they can only reveal informative results – namely homology and monophyly – if there is a notion of hypothesis testing. The requirement was knowing your taxa and proposing possible character-state relationships before analysis. While this debate was taking place in cladistics, panbiogeographers adopted another phenetic implementation: minimal spanning trees.

Rod Page, a PhD student studying at the University of Auckland, developed a method to convert tracks into minimal spanning trees (Page 1987). The idea was to use putative monophyletic groups or existing phylogenies and simply connect the dots between the shortest geographical distances between main massings, resulting in minimal spanning trees. Multiple minimal spanning trees could also be converted into a binary matrix in order to find congruent (or generalised) tracks based on statistical similarities. Incongruent tracks were most likely a result of incorrect phylogenetic hypotheses or composite areas treated as single areas (Page 1987, p. 15). The numerical implementation of panbiogeography meant that it was easily comparable to other methods such as cladistics. Panbiogeography, in a way, had become transparent to other biogeographers,

> ‘It is not clear to us, however, that, lacking an independent analysis of characters, this possible truth is yet demonstrable as anything but a faith’ (Platnick and Nelson 1988, p. 417).

The numerical implementation of panbiogeography offers nothing more than phenetic similarity. More important, to cladists such as Platnick and Nelson, spanning tree analysis departed from Croizat:

> ‘Although they refer to their method as “panbiogeography”, after Croizat (1958), we prefer the more descriptive term “spanning-tree biogeography”’ (Platnick and Nelson 1988, p. 410).

Rather, Craw saw his own spanning-tree method and spatial homology as an implementation of Croizat’s panbiogeographic method,

> 'Croizat's track methodology (panbiogeographic method) was specifically developed to provide a means of analysing the geographic distributions of taxa in order to discover biogeographic homologies for those taxa' (Craw 1983, p. 431).

Panbiogeographers had no way of testing their hypotheses because they lacked a workable theory and independent systematic method. Without a coherent definition of biogeographic or spatial homology, and an independent way of discovering them, panbiogeography remained firmly rooted in Ball's narrative phase.

The legacy of New Zealand panbiogeography

Regardless, the search for biogeographical homology and panbiogeographic classification in New Zealand came to an end in 1990. Craw moved on, losing his position at Landcare, and with the panbiogeographic student revolt of the 1980s having turned into an exodus for the lack of employment.[46] Few panbiogeographers had adopted Craw's geographical homology. The 1989 Panbiogeography Symposium is perhaps testament to Grehan's statement that 'New Zealand interest does not represent a "school" of thought, because the participants do not adhere to any one set of biogeographic principles or theories' (Grehan 1991, p. 333). Neither did the panbiogeographers. During the infighting between Craw and the cladists, other panbiogeographers, using their own interpretation of Croizat, produced a large body of work. Michael Heads, Frank Climo and John Grehan continue to publish and discuss little in terms of panbiogeographical method.[47] Doing panbiogeography provides a far better indication of what panbiogeography is than attempts at its quantification. Like taxonomy, panbiogeography relies on the knowledge of organismal distributions, geology and geography in order to make an informed claim. However, within an age of methods and numerical implementations, critics of panbiogeography saw the schism between those 'who seek a methodological framework in panbiogeography and those who regard it as an all-embracing philosophy' (Holloway 1992, p. 234). Others saw phylogeny 'as the underpinning of any biogeographical analysis. Though the book [Craw *et al.* 1999] acknowledges phylogeny as important, examination of distribution patterns remains the central pillar of panbiogeography' (Cowie 1999, p. 766).

Another criticism was Craw's panbiogeographic area classification: namely the use of oceans as areas,

> '… the more recent modifications to his theory [panbiogeography], involving the use of a limited number of "ocean baselines", do not result in the identification of novel, valuable groupings of biogeographical phenomena that provide new insights into underlying regularities of nature, nor do the ocean basins themselves provide a system preferable to the Wallacean biogeographical regions' (Cox 1998, p. 826).

Craw developed panbiogeography beyond Croizat, towards a new panbiogeographic area classification: geographical homology and its numerical implementation. This new panbiogeography embraces Croizat's space and time over form, meaning that phylogenetic relationship is seen as secondary. Craw's seeming disdain for cladistics derives from the reformation of Croizat's panbiogeography by Nelson and Rosen during the 1970s and 1980s, in which cladistic principles of relationship have been added, thereby creating vicariance biogeography. Although both these approaches are valid, neither is truly faithful to the original panbiogeography of Croizat. While Craw acknowledges the general view that '… the ideas contained in the panbiogeographic methodology and synthesis of Croizat (1952–1964) have been "greatly extended" to result in the vicariance cladistic approach to the study of historical biogeography' (Craw 1983, p. 431), he denies vicariance biogeography the provenance of Croizat's panbiogeography.

The legacy of Craw's modifications to panbiogeography came undone with the introduction of concepts that were to rival cladistic biogeography: namely geographical homology and spanning trees. Craw did attempt to improve the panbiogeographic method, but did so in order to rival vicariance and later cladistic biogeography. In my own view, cladistics had reformed panbiogeography in using phylogenies as an independent test of area relationships. But the New Zealand panbiogeographers thought otherwise, particularly Craw.

All that Craw's panbiogeography has left the world is how one would quantify tracks independently of phylogenies. Latin American biogeographers have attempted this by linking panbiogeography to parsimony endemicity analysis (see Morrone 2014). Another legacy has been the multiple attempts to classify panbiogeography in the family of biogeographical methods. For example, former New Zealand botanist J. Bastow Wilson (former PhD supervisor to Heads) attempted summarising panbiogeographic methodology under 11 categories in order to compare it with traditional dispersal biogeography and vicariance biogeography. In fact, every biogeography textbook since the 1980s has invariably placed panbiogeography into multiple categories within biogeography (Cox *et al.* 1993; Morrone 2009; Parenti and Ebach 2009).

It did not take long for panbiogeography to fall in New Zealand. As students, panbiogeographers had the luxury of scholarships and an affiliation with a university, museum or herbarium. Come graduation, jobs were very difficult to find, particularly in a small nation such as New Zealand where the established biologists held the purse strings,

> 'During the 1970s and early 1980s, the only advocates of vicariance in New Zealand were PhD students (R. Craw, J. Grehan, I. Henderson and myself). In 1984, we were joined by a National Museum zoologist, F. Climo, who organised a symposium at the museum in 1989 [*sic* 1988] … Papers on vicariance were also contributed by two other PhD students, R. Gray and R. Page.
>
> Following the publication of the contributed papers (Matthews 1990), there was an immediate reaction from the establishment; the panbiogeographers employed in New Zealand lost their jobs (Craw[48] and Climo), whereas the graduating PhD students had to find work overseas (Grehan, Heads and Page), or they stayed in New Zealand but never wrote about vicariance again (Henderson and Gray). Following the 1989 conference, no funding proposal for vicariance research ever succeeded in New Zealand, and no vicariance work

> has been accepted for publication, in either the government or the Royal Society journals' (Heads 2014, p. 286).

By 1990, panbiogeography was effectively banned in the very country where it rose to international prominence.[49] Other than Craw, no other New Zealand panbiogeography PhD managed to attract employment. Those that had jobs, such as Gibbs and Henderson, stopped their panbiogeographic research altogether. With no more PhD students adopting the panbiogeographic approach and no jobs, it simply moved offshore.[50]

Panbiogeography did much to prevent the cycle of reinvention in New Zealand. The backlash against antics of people such as Craw, however, did not stop it completely. Fuelled with a vitriolic disdain for all things panbiogeography, many New Zealand biogeographers had rebelled. The rebellion, in the guise of neodispersalism, started the next cycle of reinvention. The vicariance hypotheses, tracks and main massings of the 1980s were swept away by the reinvention of sunken continents and dispersal hypotheses characteristic of the late 19th century.

Chapter 6

Goodbye Gondwana: the drowning of Zealandia and the rise of neodispersalism

Quite possibly, the most significant reinvention of late is the return to the early 20th century debate of the recent biotic invasion of New Zealand. The debate has given rise to a remarkable idea in biogeography – one that represents a set of beliefs or an ideology – namely neodispersalism. There have been attempts to document the history of neodispersalist thought (de Queiroz 2014; Heads 2014, 2015; Ebach and Williams 2016), in context to biogeography and New Zealand biota, but neither deals with a critical part of the argument – is New Zealand an isolated area or part of a larger region? If New Zealand is an isolated endemic area with unique taxa, then there is little reason to treat it as part of, say, a larger Gondwanan region. If, on the other hand, New Zealand was part of a larger region (Gondwanan or otherwise), with which it shares many biotic affinities, then we can assume it has become isolated recently or may still share taxa. A third variant could be that New Zealand is part of two or more different regions over time. In any case, every biotic area on Earth and through time, shares some relationship with other areas within a larger area classification. Seen from this perspective, speculative biogeographical explanations are not necessary. Either New Zealand still shares sub-regions with other regions in which there is regular genetic flow, or it is completely isolated both geographically and genetically. How that genetic flow or isolation is explained is another matter.

Using area classification (i.e. regionalisation) as a way to resolve the mystery of the New Zealand fauna and flora is a far more productive venture. However, biogeographers have dismissed the New Zealand sub-region as either being non-existent (Henderson 1991), too cryptic (Fleming 1962; Gaskin 1970), or part of a plate tectonic plot (Pole 1994). Regardless, biogeographers need biotic areas, and the taxic distributions that define them, in order to make biogeographical hypotheses; otherwise terms such as 'Gondwanan' or 'New Zealand' would make little sense.

New Zealand: archipelago, island continent or oceanic island?

The history of New Zealand biogeography is at odds with much of the world. Given its unique position – an island in the south-west Pacific – one would assume it to be a mill for dispersalist hypotheses (see Craw 1978). However, the first distribution mechanism offered was of a sunken Pacific continent with only the peaks of mountains showing on which life clung. A similar hypothesis was proposed by 19th century naturalist Philip Lutley Sclater. Moreover, his ideas and how they were received is a good metaphor for the development of 20th century New Zealand biogeography.

The uneasy relationship between classification and explanation

Many biogeographers in the 18th, 19th and early 20th centuries saw the Earth as fixed, with few global changes. Sea levels may have risen or dropped, ice ages may have come and gone, and mountains were uplifted and slowly eroded away. At best, land-bridges may have spanned continents as an ephemeral string of atolls, presently no longer visible, hidden by the surface of the ocean. Rarer still were suggestions that whole continents have sunk, leaving remnant floras and fauna stranded on either side of former continental margins. Sclater was possibly one of the first to propose such a sunken continent in 1864: one that spanned the coastlines between Africa and India. He called it Lemuria.

Sclater was intrigued by the distribution of mammals both in India and Africa. As a believer of a fixed Earth, like most scientists of his time, the distribution of similar species of large mammals in two unconnected continents made no sense. For Sclater 'Organic beings are not scattered broadcast over the earth's surface without regularity or arrangement, as the casual observer might suppose, nor are they distributed according to the variations of climate or of any other physical external agent, although the latter have, unquestionably, much influence in modifying their forms. But each species (or assemblage of similar individuals), whether of the animal or vegetable kingdom, is found to occupy a certain definite and continuous geographical area on the earth' (Sclater 1864, p. 213). Moreover, animals and plants stayed where they were created. The gap between Africa and India was to all intents and purposes a permanent barrier: one that African and Indian mammals could not, and did not, traverse. Each areas possessed 'special groups of animals and vegetables, and that, as a general rule, such tracts of land as are most nearly contiguous have their Faunæ and Floræ most nearly resembling one another; while, vice versâ, those that are farthest asunder are inhabited by most different forms of animal and vegetable life. When any similar forms, or two regions far apart exhibit similar forms, it is the task of the student of geographical distribution to give some reason why this has come about, and so to make the "exception prove the rule"' (Sclater 1864, p. 213).

A modern biogeographer may think Sclater had painted himself into a corner. The exception to the rule would naturally be that animals have dispersed between Africa and India. This would in all terms be the most economical or parsimonious explanation. But what of dispersal? Nineteenth century naturalists such as Darwin remind us of '… how ignorant we are with respect to the many curious means of occasional transport' (Darwin 1876). Like Sclater, Darwin is making a claim about evolution, namely how species disperse:

> '… if we bear in mind, and this is a very important consideration, how often a species may have ranged continuously over a wide area, and then have become extinct in the intermediate tracts' (Darwin 1876, p. 359).

The explanation offered by Darwin is economical and neat. It means that the same mammal once occupied the areas in between Africa and India. Why then go to the extreme lengths of hypothesising a sunken continent? Let us go back to the often-used phrase 'how ignorant we are with respect to the many curious means of occasional transport'. Most biogeographers suffer from an ignorance of historical events. Although there may be a curious number of dispersal events happening without our knowledge, there is at the same time an equally plausible number of dispersal events not happening. Just because something is possible in one instance does not mean it is possible or numerous in other instances. Take Sclater's own view that by introducing areas biogeographers would not have to trivialise taxic distributions by supposing the colonisation of Polynesia was made by 'stray pairs of Malays floating over the water like cocoa-nuts' (Sclater 1858, p. 131). However, evolutionary thinking, rather than biogeographical hypotheses, won in the end. Area classifications, such as that proposed by Sclater, were too tied up with polygenetist ideas. Darwin's idea of a single centre of creation with subsequent dispersal (i.e. distribution, isolation and evolution), removed the need for areas. But why were areas introduced to begin with?

The concept of areas was introduced as a way to deal with classifying natural distributions of taxa (rather than species, which are still a nebulous concept). If we had natural orders of organisms that occur in certain parts of the world, then surely there was some natural geographical order. The ways organisms moved around was no different in 1777 than it was in Darwin's or Wallace's day: there was a centre or origin and dispersion. In effect, the same mechanisms of distribution were present in the 18th, 19th and 20th centuries, only the concept of evolution was missing in earlier thought. The same is true for taxonomy. Augustin Pyramus de Candolle and Antoine de Jussieu were able to establish natural plant families, many of which are still considered to be monophyletic today, without a coherent mechanism of evolution. In other words, you don't need any knowledge of evolutionary mechanisms in order to establish natural (i.e. evolutionary) entities. In the same way, distributional mechanisms are not necessary to establish a natural biogeographical regionalisation. For example, Sclater proposed Lemuria, 'a large continent occupied parts of the Atlantic and Indian Oceans stretching out towards (what is now) America on the west, and to India and its islands on the east; that this continent was broken up into islands, of which some have become amalgamated with the present continent of Africa, and some possibly with what is now Asia' (Sclater 1864, p. 219). Sclater's Lemuria is also speculative. But it was Sclater's areas that were free of any hypotheses regardless of what you believed: polygenesis, dispersalism or sunken continents. Alfred Russel Wallace also picked up on the idea of biogeographical areas, and revised Sclater's own areas. If taxonomy has both a classification and evolutionary theory, why can't biogeography do the same? My own view is that many scientists since the 19th century are not interested in the biogeography of areas; rather they are interested in the geohistory of their lineages over space and time. Why would someone interested in the evolutionary history of a single species or genus be interested in area classification or even areas? In the same way, mammalian monophyly has little to no impact on a cell biologist, a dipterist working on the history of a genus of flies will have little interest in whether New Zealand biota as whole is Gondwanan or not. But yet evolutionary biology has had great impact on area classification, particularly in the history of New Zealand biogeography (see Craw 1978).

New Zealand as an archipelago

Seemingly adrift in the south-west Pacific, one would expect 19th century naturalists to think of New Zealand as an oceanic island: one that was slowly colonised by distant migrations since the dawn of time,

> 'Let us in imagination peer into that remote past when New Zealand had finally emerged from the ocean, and when its surface, destitute of all life, was ready to receive its plant and animal immigrations' (Cockayne 1910, p. 4).

The imaginations of 19th century biogeographers, however, were not shared by later 20th century biogeographers (Table 6.1): New Zealand was a continental island that had significant land connections between eastern Australia, Antarctica and South America since the Mesozoic. Furthermore, the notion of a drifting flotsam and jetsam biota seemed unacceptable,

> 'Mr. Wallace's supposition that land and fresh-water molluscs, lizards &c., were distributed over the whole Pacific Ocean by waves of the sea I think to be more than bold' (von Ihering 1892, p. 432).

The idea of the permanence of the oceans and continents was also a sticking point for Herman von Ihering – a confirmed land-bridger. The concept of land-bridges – that is, continental connections such as island chains or sunken continents – is equally *ad hoc* as a

Table 6.1. Biogeographical hypotheses of the origin of the New Zealand flora and fauna by 19th century land-bridgers.

Author	Continental connection hypotheses	Biogeographic area
Hooker (1853)	Former Pacific continent	
Huxley (1870)	Subsided Mesozoic continent in the Pacific	Austro-Columbian
Hutton (1873, 1904)	Gradual subsiding Antarctic Mesozoic continent	
Milne-Edwards (1874)	Land connection between Polynesia and the Mascarene Is.	
Moseley (1877)	Former land extension into Antarctic Ocean (*sensu* Hooker 1853)	
Wallace (1880)	Oceanic island	
Blanchard (1882)	Subsided southern continent	
Hutton (1884)	Subsided Mesozoic continent in the Pacific	
Gill (1893)	Land connection to Tasmania and South America at the end of the Mesozoic	
von Ihering (1892)	Archiplata: Subsided Mesozoic continent in the Pacific	
Forbes (1893)	Subsided Antarctic continent in Pliocene	Continental island
Hedley (1893b, 1895, 1899)	Land connection to South America via Antarctica. Melanesian Archipelago	
Sloane (1915)	Huxley-Hutton Mesozoic Trans-Pacific continent	

hypothesis of chance dispersal by ocean currents or by wind. A land-bridge connected two places and seemingly guaranteed some form of interchange. If, for example, sea level dropped between mainland Australia and Tasmania, Bass Strait would, through sea level changes, become a land-bridge (the Bassian isthmus of Hedley 1904). Compare that with organisms dispersing by wind or water between New Zealand and either northern Tasmania or the southern part of the mainland. Objections to land-bridges, however, came not from biologists; early 20th century geologists were opposed as much to land-bridges as they were to continental drift. No evidence existed for either mechanism other than hypotheses of land connections based on organismal distributions. The whole land-bridge argument was based on the effectiveness of land connections and biotic interchanges. Without concrete evidence for land-bridges, the theory fell into disuse. By the mid-20th century land-bridges were not considered viable. The Earth, still fixed in the mind of 19th and early 20th century geologists and biologists, continued to present the same problems: how did organisms get to where they are? Chance dispersal still remained the dominant paradigm. Regardless, late 19th century naturalists pondering the New Zealand biota still baulked at the idea that it originated completely by trans-oceanic dispersal,

> ‘If the number of plants common to Australia and New Zealand is great, and quite unaccounted for by transport, the absence of certain very extensive groups of the former country is still more incompatible with the theory of extensive migration by oceanic or aerial currents’ (von Hochstetter 1867, p. 129).
>
> ‘It is hardly possible to account for the distribution of frogs, slugs, wingless and feebly flying insects, earth-worms, myriapods, and fresh water animals generally, except by the supposition of land passage’ (Hutton 1896, p. 46, footnote*).

Even though many naturalists agreed that there were some continental connections between New Zealand and the rest of the southern continents, there was little agreement on what the island continent was biogeographically (Table 6.2). Wallace (1876) famously placed New Zealand within the Australasian region, which according to Hedley is misleading,

> ‘The use of political boundaries has much confused the lines of zoogeographical demarcation. “The Australian Region”, meaning the continent of Australia, together with the Islands of New Guinea and the West Pacific, is an especially misleading term, and has tended to obscure natural boundaries … I am unable to recognise New Zealand and other West Pacific Archipelagoes as appanages [sic] of Australia’ (Hedley 1899, p. 395).

Hedley puts the blame on the zoogeographical classification of William Swainson (1835), in which New Zealand is one of three ‘sub-ordinate districts’ within the Australian Province. Sclater (1858) was also hesitant to separate New Zealand from his own classification of *Regio Australiana*. Hedley’s own classification of Australasia derives from Ralph Tate and Walter Baldwin Spencer, suggesting that the biotic regions within Australia (Euronotian, Eyrean, etc.) share greater affinities with parts of New Guinea than they do with each other.

Frederick Wollaston Hutton (1836–1905)

Hutton was a British-born captain serving abroad in the Royal Welsh Fusiliers. Upon arriving in New Zealand, Hutton was taught geology and zoology and rose to the ranks of the country's academic elite. As a professor and supporter of Darwin's theory of evolution, Hutton had offended the clergy who had funded his position. Hutton also supported the view that a land-bridge or sunken continent existed in the south-west Pacific, which explained the disjunct distributions of similar taxa between Australia and New Zealand. Hutton's 'researches on the origin of the fauna and flora of New Zealand' meant that he 'became a recognised authority on questions of bio-geography' (Farr 1905, p. 597).

Frederick Wollaston Hutton (in Jenkinson 1940). University of Wellington, http://nzetc.victoria.ac.nz/tm/scholarly/JenNewZ-fig-JenNewZP004a.html.

In this sense, the Papuan fauna extended down into Australia via the now submerged Torres Straits, mingling with the older Antarctic fauna. A similar land-bridge leading from the Solomon Islands extends down to New Zealand with a detour to Lord Howe Island. Unlike Australia, this fauna extends into a different, albeit older, Antarctic fauna. There was no connection between New Zealand and Australia: their faunas were merely a result of similar faunas extending north from Antarctica and south from New Guinea at different times. As for the relationship between New Zealand and Australia,

> 'Upon detailed examination, it appears that although the fauna of New Zealand sometimes approximates to that of Queensland, yet it could not have been derived therefrom; that, in short, the relation is not that of mother and daughter, but that of sisters' (Hedley 1893b, p. 188).

The sister relationship of Hedley forms a wedge between the south-west Pacific and Australia and resembles a distinct biogeographical fork (Fig. 6.1).[51] A combination of plausible land-bridges and dispersal over time presents a complex, but neat, solution to the origins of Australian and south-west Pacific biogeography. By the turn of the 20th

Table 6.2. Authors featured in text who treat New Zealand as an archipelago, land or island continent, biogeographic region and the dominant distribution mechanism.

An asterisk indicates a New Zealand or New Zealand-based biogeographer.

Author	Island type	Biogeographical region	Distribution mechanism
Hedley (1899)	West Pacific Archipelago	Not in the Australian region	Land-bridge
Hutton (1904)*	Archipelago	–	Land-bridge
Cockayne (1910)*	Island	New Zealand botanical region	Dispersal
Cockayne (1921, 1928)*	Island archipelago (former semi-continent)	New Zealand botanical region	Dispersal
Oliver (1925)*	Continental island	–	Dispersal
Mayr (1943)	Island	Separate region (?)	Long-distance dispersal
Falla (1953)*	Island archipelago	–	Dispersal
Forster (1961)*	Island	–	Long-distance dispersal
Fleming (1962)*	Island archipelago	–	Long-distance dispersal
Caughley (1964)*	Island	–	–
Gaskin (1970)*	Island archipelago	–	Long-distance dispersal
Skipworth (1974)*	Island	–	Long-distance dispersal
Fleming (1975)*	Island archipelago	–	Long-distance dispersal
McDowall and Whitaker (1975)*	Island	–	Long-distance dispersal
Udvardy (1975, 1987)	Archipelago	Neozealandia sub-realm (in Antarctic realm)	–
Mildenhall (1980)*	'Long narrow landmass'	–	–
McGlone (1985)*	Island	New Zealand	
Fleming (1987)*	Island archipelago	Neozealandia sub-realm (in Australasian realm)	–
Pole (1994)* and neodispersalists	Oceanic island	–	Long-distance dispersal

century, Hedley (1899) had dismantled Huxley's, Hutton's and von Ihering's Mesozoic Pacific continent as both implausible (i.e. no geological evidence) and unnecessary.[52] No complex geological hypotheses (land-bridges) were necessary to explain post-Cretaceous New Zealand biogeography:

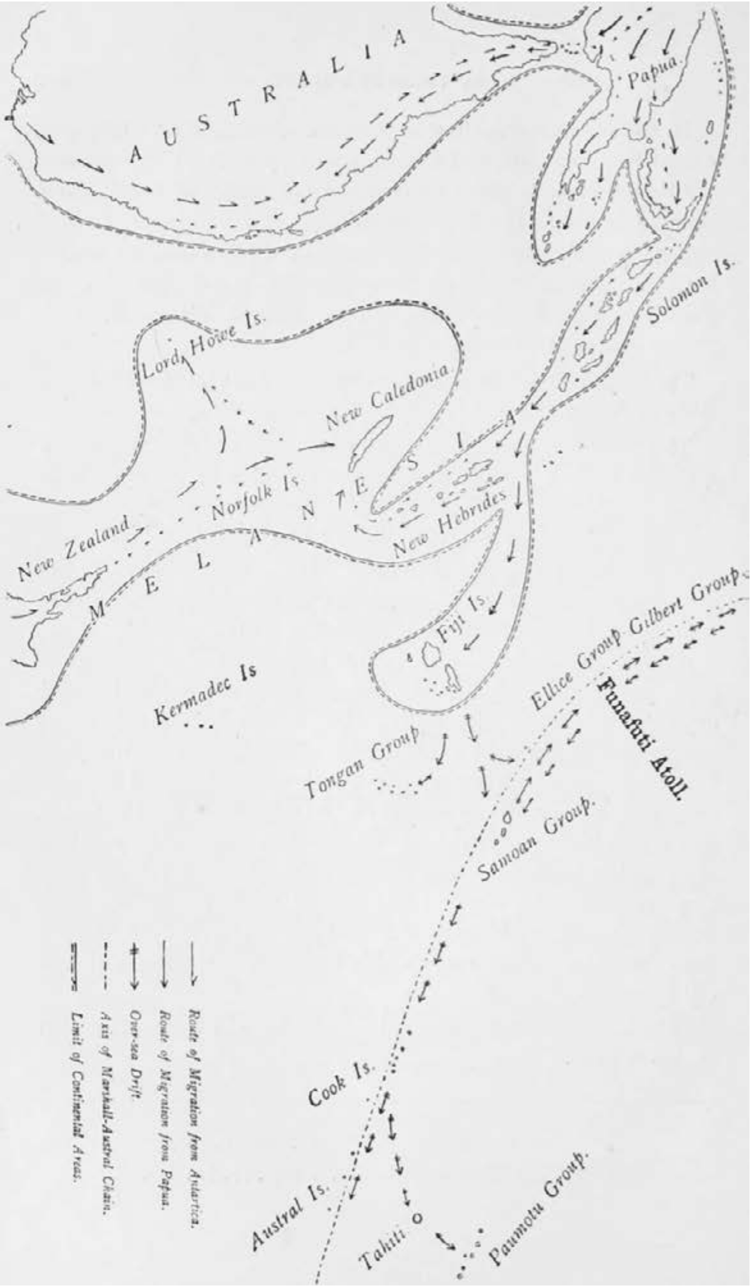


Fig. 6.1. A biogeographic 'scheme' or 'fork' outlining the history of Australasian mollusc faunas. 'The foregoing account of the migration and classification of different faunas, usually confounded together as Australian, is diagrammatically reprinted in the accompanying map' (Hedley 1899, p. 404). In a review of Hedley (1899), AEO approves of the connection: 'the explanation of the connection of the continental faunas of Australia, New Guinea, etc., to New Zealand seems very acceptable' (AEO 1900, p. 596). Also note the similarity between Hedley's and Burbidge's 'Migration tracks affecting the Australian Region' (Fig. 3.1 herein). Both maps are representative of the invasion hypothesis, which has dominated Australia's biogeographic thought for over a century.

> ‘The map given by Hedley represents precisely what, judging from the present New Zealand flora and the evidence gradually accumulating of the flora of New Guinea and the islands of the western Pacific, I think necessary for a land connection in the Cretaceous’ (Oliver 1925, p. 135).
>
> ‘Zoo-geographers who have expressed views on the origin and nature of the New Zealand fauna have often invoked hypothetical land bridges or continental drift. If, however, the more obvious facts of the situation are taken as a starting point, it must be admitted that the fauna of the New Zealand archipelago conforms, in the main, to what should be expected on large oceanic islands … However, if hypotheses of land bridges and of drift are to be rejected, either must be substituted in their place a very thorough taxonomic analysis of the fauna, and a very careful examination of all dispersal factors’ (Falla 1953, pp. 36–37).

Lacking a geological hypothesis and mechanism, such as extensive land-bridges and sunken continents, 20th century New Zealand biogeographers adopted chance dispersal wholeheartedly (Oliver 1925; Forster 1961; Gaskin 1970; Skipworth 1974; Pole 1994).

New Zealand as an island continent

A theory of continental evolution, such as the development of New Zealand flora and fauna wedged between two large continental plates, also provides the mechanisms for distribution. Land-bridges, such as the Melanesian Archipelago, for example, provide a dual-carriageway to and from New Zealand. Organisms can disperse, variate, evolve or go extinct along an archipelago. But island continents are another matter. There are basically two ways to get to an island continent: via island hopping or long-distance dispersal. Other mechanisms such as vicariance are also valid due to former land connections. Effectively island continents contain older continental (i.e. Australasian) taxa as well as local endemics. As part of a larger continental region (i.e. Australasia), dispersals from sub-regions may result in a mixed biota. For example, Cockayne (1921, 1928) described seven elements in the New Zealand flora: endemic, paleozealandic, Australian, subantarctic, palaeotropic, cosmopolitan, and Lord Howe and Norfolk Islands. Fleming (1962, 1975) described six: Malayo-Pacific, Australian, austral (including palaeoaustral and neoaustral), endemic (archaic), cosmopolitan and holarctic. Neither author agrees which element dominates New Zealand. For instance, Cockayne (1921) believes that while New Zealand flora is strongly endemic and ‘is not one floristic entity, but consists of a combination of the palaeozealandic and subantarctic elements of the flora, now difficult to disentangle’ (Cockayne 1921, pp. 322–323), while Fleming (1962, 1975) agrees that the present day biota is dominated by the Australian element, in which ‘it is sometimes hard to distinguish Australian from Malayo-Pacific elements’ in older groups (Fleming 1975, p. 71). Later authors describe the Australian and Malayo-Pacific elements becoming more prominent in the New Zealand flora (Mildenhall 1980), while others feel the connection between Australia and New Zealand is mostly Antarctic (Takhtajan 1986; Thorne 1986). Describing New Zealand in terms of elements tells us little about what it is biogeographically. Place New Zealand in an area classification and we immediately determine *whether it is a natural area or not*, as opposed to identifying elements. For example, Mayr thought that 'Most of the birds of New Zealand, for example, apparently arrived there from Australia. But some of the endemics are so unique and the unchanged Australian element is so small, that it seems hardly justified to include New Zealand in the Australian Region' (Mayr 1943, p. 45). Mayr considered New Zealand, like Hawaii, to be placed into its own region. Fleming agrees: 'There could well be a case for treating New Zealand as a distinct realm or subrealm, as implied by Mayr (1943)' (Fleming 1987, p. 198). To paraphrase English poet John Donne – No region is an island / Entire of itself / Every region is a piece of the continent / A part of the main – New Zealand is not a lone region separate to all other regions and realms. Like all other biogeographic regions, New Zealand belongs within an area hierarchy and within a higher classification.

Fleming hotly debated the classification of the New Zealand sub-region in the late 1980s in a reply to Miklos Udvardy (1987). Fleming objected to Udvardy placing the existing neozealandic sub-region into the Antarctic region,

> 'There is much evidence that New Zealand's biogeographic relationships with Australia are closer than they are with the rest of Gondwanaland, and especially with the rest of Udvardy's Antarctic Realm' (Fleming 1987, p. 196).

Fleming provides nine examples of the strong connection New Zealand has with Australia, including plants (e.g. conifers, *Nothofagus*, Proteaceae), invertebrates, freshwater fish and the arrival of recent 'colonists' such as 'plant pathogens, birds and insects' (Fleming 1987, p. 197). But Fleming also rejects the proposed revival of von Ihering's Archiplata, or cold-temperate biogeographic relationships between Australasia, Antarctica, South Africa (Cape), Patagonia and southern Chile (including islands) as proposed by Kuschel (1960). Fleming considered a region based on such relationships to be '"living in the past", and not a satisfactory solution to the problem of classifying the biogeographic areas of the contemporary world' (Fleming 1987, p. 198). Kuschel's main point, not highlighted by Udvardy (1987), was that these areas are related based on present day phylogenetic relationships between individual taxa.[53] Fleming, however, fails to deal with this vital point, confusing phylogenetic relationship with biotic similarities between elements. For Fleming, the degree of similarity between elements is based on the 'number of plant and animal taxa they have in common, now and in the geological past, particularly during the Neogene' (Fleming 1987, p. 198). This, Fleming believes, warrants New Zealand (Neozealandia) to be a sub-realm of the Australasian realm. But what happens when we do uncover the phylogenetic relationships (rather than biotic similarities) between New Zealand and Australia?

In a review of the New Zealand biogeographical literature, Gaskin (1970) cites Brundin's famous 1966 monograph in which a phylogenetic systematic analysis revealed no connection between south-eastern Australia and New Zealand in midges, leading Gaskin to declare: 'The importance of Australian influence in the composition of the New Zealand biota has been exaggerated by some previous workers' (Gaskin 1970, p. 420). Gaskin reintroduces the idea of Hedley's pre-Cretaceous Melanesian archipelago in which the majority of New

Zealand taxa arrived via Melanesia (Indo-Malay) and earlier radiations from South America via a land-bridge connecting Antarctica and the Antarctic Peninsula to New Zealand,

> 'It is of an island archipelago far enough removed from the nearest landmass to be considered oceanic, but with a large enough surface area to allow prolific speciation and evolution in isolation at least to the generic level. Although a number of ancient endemic elements of uncertain affinities exist, the majority of the precursors of present taxa came from outside New Zealand by way of pre-Cretaceous direct land connections, of early and mid-Tertiary archipelagic links, or of transoceanic dispersal by air or water throughout the history of the archipelago' (Gaskin 1970, p. 434).

Gaskin's explanation of what is seemingly an island continent presented a good middle ground for most biogeographers. But the issue of area classification still lingered. If we take Fleming's area classification of both Australia and New Zealand as sub-regions within the Australasian region, then how are they related? Perhaps we should return to Hedley's criticism, that within 'Australasia are several regions, peopled by distinct and unrelated faunas. To a zoologist, Australasia is not an entity, and may with advantage be dismissed from this vocabulary' (Hedley 1899, p. 395). Rather than understand where New Zealand fits into the regions and sub-regions of the world, greater emphasis has been for New Zealand biogeographers to isolate it from the rest of the globe.

New Zealand as an oceanic island

There is a myth, of sorts, that states New Zealand's 'flora is popularly seen as a living example of "Gondwanan" vegetation isolated by sea-floor spreading in the Late Cretaceous' (Pole 1994, p. 625). The claim, often referred to as the Moa's Ark,[54] is quite recent and has its origins in the dispersalist literature of the 1990s. The claim that some New Zealand taxa are relicts with a Gondwanan origin, particularly *Nothofagus,* leiopelmid frogs and the ratites, is not new and has been acknowledged by both international and New Zealand authors. To suggest otherwise, would be to deny that New Zealand has no connection to pre-Cretaceous taxa. But this is exactly what Mike Pole is suggesting, that the 'entire forest-flora of New Zealand arrived by long-distance dispersal',

> 'The evidence is now clear that at least a significant proportion of New Zealand's flora arrived by long-distance dispersal; in fact, there is no compelling reason why all of it may not have arrived that way' (Pole 1994, p. 632).

This extraordinary claim by Pole serves as an explanatory tool to justify New Zealand biologically as an oceanic island, even though geologically it is continental. Unlike an island continent, which may contain relict taxa, an oceanic island consists of a newly formed oceanic landmass, or atoll, which shares its biota with a nearby continent that had reached it via long-distance dispersal. Biogeographers focused on oceanic islands have little time with ancient distributions, relict taxa or tectonics. But neither did many 20th century New

Zealand biogeographers. The conclusion to *Continental Drift and the New Zealand Biota* by Skipworth (1974) makes little of the effects of drift on New Zealand biota:

> 'It appears likely that New Zealand might well have received its oldest faunal and floral components when it was part of, or immediately adjacent to, that Gondwanaland supercontinent. These could have included *Glossopteris*, Podocarps, *Sphenodon*, *Leiopelma*, and the Ratites' (Skipworth 1974, p. 11).

Even with the acceptance of plate tectonics, Gondawanan relicts were considered a result of dispersal:

> 'It could be fairly stated that transoceanic dispersal provides a reasonable explanation for the appearance of the bulk of genera occurring first within the last 60 million years' (Skipworth 1974, p. 10).

Revisiting these statements helps to remind us that 20th century New Zealand biogeographers did not consider plate tectonics and vicariance to be the main distributional mechanisms shaping biotic distribution (see Table 6.2). Even so, panbiogeographers such as Craw denied *Nothofagus* was Gondwanan, suggesting instead that it was a 'member of a non-Gondwanan trans-Pacific fagalean alliance' (Craw *et al.* 1999, p. 27). Then where does the view that large parts of the New Zealand flora (and fauna) are Gondwanan come from? Certainly not from the vicariance biogeographers or panbiogeographers of the 1980s or 1990s. There is a possibility that it derives from a misunderstanding of an area classification: one that places New Zealand into a broader Austral region, which is often misinterpreted as being 'Gondwanan'. In the southern beech genus *Nothofagus,* for example, the relationship (southern South America, (Australia, New Zealand)) occurs three times, thereby forming a pattern (i.e. geographical congruence) (Fig. 6.2). The relationship, seen in context to classification, would place Australia, New Zealand and southern South America in an Austral region. The classification is explained by vicariance – namely that the biota in each area shares a relationship. Dispersal is not necessary or useful to create biotic classifications. They are simply subsumed into vicariance. After all, when a species has dispersed from one area to another and speciated, both species are vicariant (i.e. allopatric). Whatever the distributional mechanism, Australia, New Zealand and southern South America share the same flora, meaning they share a common area and a common history (i.e. Gondwanan). In other words, stating that New Zealand and Australia are Gondwanan means they connected biogeographically regardless of whether vicariance or dispersal was the dominant distribution mechanism. A Gondwanan distribution does not equate to vicariance. That comparison is simply untrue and seemingly manufactured by some neodispersalist agenda. The Gondwanan connection since the Mesozoic is still there – even if the genetic barrier is absent for some recent species – as many New Zealand and international biogeographers have observed. One would think neodispersalists would applaud this result. Quite the opposite is true.

> 'The argument is simple – if the bulk, characteristic, or even all of the New Zealand plants arrived by dispersal, after the supercontinent of Gondwana had ceased to exist, what gain is there in describing New Zealand's flora as

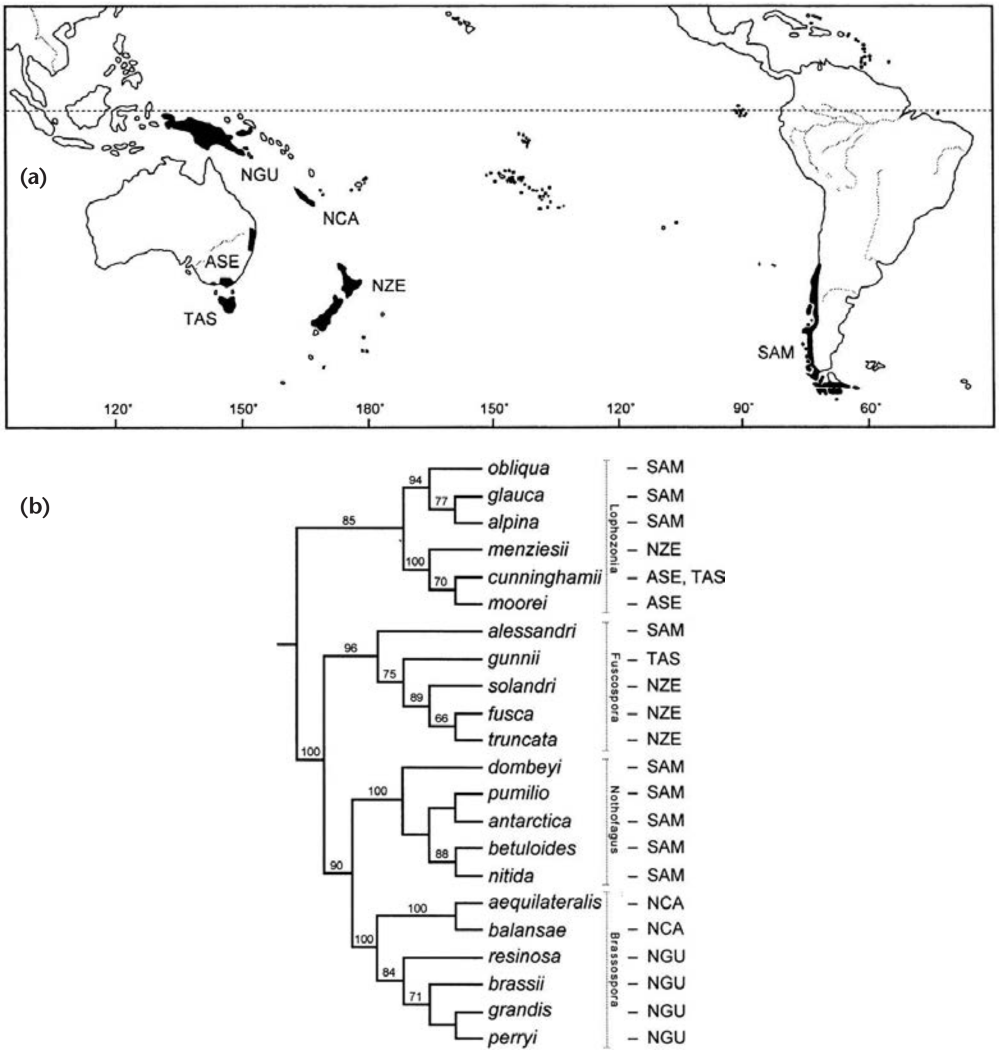


Fig. 6.2. (a) The distribution of living species of *Nothofagus* ASE = south-east Australia; NCA = New Caledonia; NGU = New Guinea; NZE = New Zealand; SAM = South America; TAS = Tasmania (Swenson *et al.* 2000, p. 470, Fig. 1); (b) cladogram of *Nothofagus* including the areas in which each species occurs (Swenson *et al.* 2000, p. 471, Fig. 2).

> Gondwanan? Shall we call a seagull migrant from Australia "Gondwanan"? Would it not make more sense to call it "Australian"?' (Pole 1994, p. 632).

Why are dispersal biogeographers at odds with the concept that the genetic link between New Zealand and Australia has not been severed? Australia has been part of Gondwana for over 500 million years. To say that New Zealand is independent of Gondwana is to say that it has a completely separate biogeographic and geological history. A far better argument would be that recently arrived Australian species have evolved in a post-Mesozoic Australia, but a majority of their genera have their origins in Gondwana, such as *Nothofagus* (Sauquet *et al.* 2012). The problem is neither a lack of evidence nor a lack of explanation, but rather the idea that New Zealand is an oceanic island, with no historical association – geologically speaking, a relatively new, isolated and separate region. But Pole goes one step further,

> 'If New Zealand was completely submerged [during the late Oligocene], then all these organisms had to disperse there over a wide ocean gap. The moa (*Dinornis*) and kiwi (*Apteryx*) ancestors may have flown to New Zealand and then lost the power of flight, like so many other birds living on islands' (Pole 1994, p. 628).

A submerged island continent would guarantee that all old relict species were literally washed away. New Zealand would have 'emerged from the ocean' as bare rock 'ready to receive its plant and animal immigrations' (Cockayne 1910, p. 4). Given this, 'a significant proportion of New Zealand's flora arrived by long-distance dispersal; in fact, there is no compelling reason why all of it may not have arrived that way' (Pole 1994, p. 632). Pole's idea of a formerly submerged continental island colonised by long-distance dispersal since the late Oligocene seems extraordinary. The south-west Pacific is the most complex tectonic region on Earth and one may think New Zealand's biogeographical history would be utterly unique, but not so. Pole extrapolates his hypothesis in the same way Darlington had. If this is true for New Zealand, then,

> '… plants and animals that have reached New Zealand crossed water gaps, no land connections are needed anywhere across the southern end of the world to explain the distribution of far-southern terrestrial life' (Darlington 1965, p. 107).

Compare this to Pole (1994),

> 'The significance of this should not be missed – if the flora of New Zealand, even most of it, can be shown to have arrived over the sea since this isolation, biogeographic hypotheses the world over which invoke any kind of land connection must be reconsidered' (Pole 1994, p. 625).

Imagine, for one moment, the impact of Pole's statement. Most, if not all, biogeographical regions have at some time had a land connection, meaning that a total reappraisal of the global biogeography would be needed in light of long-distance dispersal biogeography. To see the effect of such an audacious statement, we need to return to the New York School of biogeography of the mid-20th century.

Nelson and Ladiges (2001) noted a distinct similarity between the ideas of the New York School on biogeography and modern day long-distance dispersal biogeography.[55] The New York School included several influential heavy-weights of 20th century Modern Synthesis: William Diller Matthew (1871–1930), Karl P. Schmidt (1890–1957), George Gaylord Simpson (1902–1984), Philip J. Darlington (1904–1983), George S. Myers (1905–1985) and Ernst Mayr (1904–2005). The New York School was influential in suppressing the ideas of continental drift in 20th century biogeography and for downplaying the role of land-bridges.

Table 6.3. The biogeographical mechanism assumed to occur on archipelagos, island continents and oceanic islands.

	Vicariance	Land-bridge/hopping	Long-distance dispersal
Archipelago	✓	✓	✓
Island continent	✓	✓	✓
Oceanic island			✓

Rather, the New York School represented a wholly dispersalist view of distribution – one that did not sit well with a new generation of rebels who were influenced by the works of Léon Croizat and Lars Brundin. The rebellion against the New York School was in the form of cladistic and vicariance biogeography: the very same ideas that present-day dispersalist biogeographers claim to dominate New Zealand biogeographic thought during the 1970s to 1990s (de Queiroz 2014, p. 101). Clearly vicariance had hardly dominated New Zealand or Australian biogeography. The notion that it had works well to further promote the revival of the New York School of long-distance dispersal (Table 6.3).

The New Zealand drowning hypothesis: towards an integrative biogeography

> 'Put simply, "the drowning hypothesis" states that the geological evidence for the continuous existence of land in the New Zealand region during the latest Oligocene to earliest Miocene time is so weak that rational contemplation of the opposite is admissible and that it is therefore logically conceivable (from a geological point of view) that there may have been a moment during this timeframe that Zealandia was totally submerged' (Campbell 2013, p. 3).

By the 1990s biogeographers had produced many methodological refinements. Every year, historical biogeographers were introduced to new methods, techniques and computer software (see Morrone 2009). Regardless, these new methods found no common ground, and even fewer were certain if a consensus on biogeographical patterns existed at all,

> 'The recent upsurge of interest in vicariance biogeography and application of cladistic methods to biogeography … have provided a rich variety of conceptual frameworks and methodological techniques but little agreement' (McGlone 1985, p. 746).

A scientific field that had reached Ball's analytical stage was unable to find a methodological consensus or an agreed biogeographical history. The infighting between cladistic biogeographers and the vicariance-dispersal debate seemed to distract researchers from the task of uncovering real biogeographical patterns. But for biogeography to truly enter the analytical phase, it required a total reengineering of its foundations – theory and method – something that takes decades. The other problem is the issue of time. Biologists are not familiar with temporal problems that geologists and palaeontologists encounter. For example, in palaeontology floras and faunas determine geological periods. Present a fossiliferous rock to any palaeontologist worth their salt and they will be able to determine the age and location, simply by identifying the fossils. But some faunas seem to have characteristics of older types. These are called holdovers. For example, the early Devonian trilobite faunas of eastern Australia have a late Silurian holdover. The early Devonian trilobites of central Victoria contain Silurian taxa that are already extinct in New South Wales (Dowding and Ebach 2016). Such holdovers are common the world over. However, the biogeographers working on extant taxa seem to be unaware of, say, Eocene or Miocene holdovers in their present-day distributions. The problem with taxic holdovers is that they present us with temporal overlap. This means that the same geographical region can be host to two unrelated temporally overlapping biota that may have responded to different barriers. These biota may not share the same history. They just happen to share the same space. An extreme example is that of the present-day Sydney rock warbler and the Triassic labyrinthodont *Paracyclotosaurus*. The distributions of both taxa are in the Sydney basin, they overlap geographically but are temporally separated by 200 million years. Reduce that figure to 20 or 10 million years and biogeographers will be unable to tell these two distributions apart.

The problem of temporal overlap is not discussed in the biogeographical literature. Rather individual cases are targeted, meaning that each individual species within a phylogeny is given a unique history. The problem with unique histories of individual taxa is that they often fail to uncover general biotic patterns. For the biogeographer working on extant biota, a similar age would help in uncovering patterns. Take New Zealand, for example. A similar biotic age would make for a better, more integrated biogeographical hypothesis. If all taxa are no older than, say, the late Oligocene, then you would only need a single biogeographical hypothesis, not several that conflict, as is the case with relict taxa.

Biogeographers the world over have been calling for an integrative biogeography since Ratzel (1891). Unfortunately, integration has failed at many levels. Biogeographers still argue about various, and often conflicting, aims, goals and methods. But the drowning of New Zealand presents a unique case that may be applied elsewhere. What if all taxa within a biota are of a similar age and a hypothesised maximum age for the oldest known taxon? This would mean fewer distributional mechanisms, perhaps even just one. Moreover, with only a single distributional mechanism, for instance, you could reduce the number of methods to those that model for one or maybe two of these distributional mechanisms. In effect, the drowning hypothesis had integrated New Zealand biogeography as never before – one distributional mechanism and one biogeographical hypothesis. Together they had taken the shape of a biogeographical synthesis, called neodispersalism.

Neodispersalism: The New York School revival

The rise of neodispersalism in the early 1990s in New Zealand is not, as some claim, a counter-revolution to panbiogeography,

> 'Its [panbiogeography] decline became noticeable after the turn of the century as the dispersal counterrevolution began to have its effect' (Briggs 2007, p. 273).

The 'counter-revolution', rather, is a dispersalist New York School revival, in which tectonics and historical biogeographical patterns (i.e. 'Gondwanan distributions') play no role in the biogeography of an oceanic island. Moreover, the revival harks back to a time when there was better integration within the biogeographical community. In the 1949 Society for the Study of Evolution (SSE) Fourth Annual Meeting in New York, the topic of the meeting was 'The role of the South Atlantic Basin in biogeography and evolution, with special reference to the Mesozoic', chaired by New York School biogeographer Ernst Mayr:

> '… the symposium was organized, not to defend or disprove any particular hypothesis, but for the presentation and discussion of current evidence in one restricted but critical field of a much broader subject … Dr. Mayr is satisfied … that there is no need to postulate former land connexions between South America and Africa to explain the distribution of mammals and/or birds, the available facts being "diametrically opposed to the possibility of such a connection"' (Holmes 1953, pp. 669–670).

A similar symposium was held over two decades later in Monaco at the XVIIe Congrès International de Zoologie in 1972. The symposium, titled Biogéographie et Liaisons Intercontinentales au Cours du Mésozoique, was held at a time when plate tectonics was firmly established, however, the biogeographical hypotheses and mechanism had not changed at all,

> 'Providing the concepts of continental rifting and actual drift are not confused, new data from sea-floor spreading and application of tectonic plate theory to the area do not very appreciably alter the previously published picture of the New Zealand Mesozoic largely developed by Fleming' (Gaskin 1975, p. 94).

Plate tectonics is not a necessary assumption in biogeographic theory, certainly not in the period pre-dating vicariance biogeography and panbiogeography. But this comes as no surprise. In effect it was the vicariance biogeographers and panbiogeographers who put the 'geography' into biogeography. The period between 1980 and 1990 saw many attempts at introducing geographical concepts to biogeographers, but largely the venture was not wholeheartedly adopted.

Given this, it is surprising that New Zealand neodispersalists claim that,

> 'Dispersal is increasingly recognised as a dominant biogeographic mechanism … Although many biogeographers still interpret biotic distributions as passive phenomena shaped largely by geology … recent evidence shows that dispersal is common' (Waters and Craw 2006, p. 354).

Really? A large part of the biogeographical literature, from the 1940s to the 2010s, favours dispersal as the dominant biogeographical mechanism (Ebach and Williams 2016). Why make such a false claim? Neodispersalism is not new in terms of its methodology, as I will show below. The insistence that long-distance dispersal is the only, or dominant, means of distribution differs marginally from the traditional New York School. Neodispersalism discounts any relict taxa, effectively making all dispersal events arrivals to *terra nullius*. Another tactic is to cite the older vicariance literature 'Croizat *et al.* 1974; Rosen 1978; Craw *et al.* 1999', which looks archaic to the recent neodispersalist output 'Pole 1994; Waters *et al.* 2000; Wright *et al.* 2000; Price and Clague 2002; de Queiroz 2005'.

Vicariance (later cladistic) biogeography has served neodispersalism well. First, the name suggests vicariance was the only biogeographical mechanism accepted by vicariance biogeographers (which is untrue if you actually read the literature). Second, vicariance biogeography is associated with tectonics, meaning that biogeographic studies that used tectonism to explain distributions, such as those in the 1972 symposium, are associated by guilt with vicariance theory even though dispersal is the dominant explanation. A new straw man had been erected by the neodispersalists – the dominant vicariance biogeographer – who had monopolised historical biogeography, a *doctrinaire vicariance*, if you like: one that has muddied the waters of biogeographic thought since the 1970s (see de Queiroz 2005, 2014; Waters and Craw 2006).

With a target in sight, neodispersalism just needs a methodology that looks new – one that has evolved away from '… the construction of hypotheses about the location of ancestral species. Such a procedure would necessarily follow a phyletic analysis and would then permit statements to be made about centers of origin and pathways of dispersal' (Cracraft 1975, p. 36). Enter molecular clocks and their fossil calibrations.

Molecular clocks, fossil calibrations and biogeographical models

The original New Zealand drowning hypothesis is based on fossil evidence in the form of fossil pollen and some plant macro-fossils (Campbell and Landis 2001). However, this evidence is used to support highly speculative assumptions: something that the New York School was very good at doing.

What many palaeontologists and biologists fail to communicate is what the appearance of a fossil can tell us. A fossil is merely a shadow of its former self – an impression or an organism that has been replaced by other material, be it sediment or minerals. Not only fossils are indicators of former environments that were ideal for preservation, their parts are crucial for understanding the inter-relationships of extinct taxa. For instance, the presence of feathers (i.e. their impressions) in theropods relates it to birds rather than to any other taxonomic group. That relationship means that birds and theropods share a common evolutionary history – a common ancestor – but we do not know the identity of that common ancestor. The oldest known fossil is not necessarily the oldest ever. That evidence is missing from the fossil record. It could be the fossil we are holding or something else entirely. But it is this assumption on which the majority of inferences are made, such as the identity of ancestors, centres of origin and the direction of ghost lineages. In other words, there is no evidence in the fossil record or elsewhere to definitely identify ancestors, centres of origin and the direction of ghost lineages. For example, theropods are found earlier in the fossil record than birds are worldwide. The immediate reaction is to suggest a ghost lineage: a direct line of unseen evolutionary descent between theropods and birds, which might very well be the case. But what if we found an even older bird? If we stick to Occam's Razor, we would be better erring on the side of caution and believing we do not have all the information available to us. This means that any assumptions of ancestry taken from the fossil record are speculative. With this in mind, we come to molecular clocks and their calibrations:

> 'Although a range of molecular dating methods is now available, they all share a vital dependence on age calibrations. DNA sequences only record the number of substitutions that have taken place, inferred from the degree of genetic divergence among taxa. These sequences do not provide separate information about the amount of time over which genetic variation accumulated or about the rate of substitution. Therefore, an absolute timescale is required in order to calibrate molecular date estimates, and geology usually represents the ultimate source of all absolute age data' (Sauquet *et al.* 2012, p. 289).

Molecular clocks are completely reliant on determining the maximum or absolute age of a known fossil or lineage, which harks back to the days of the New York School: molecular clocks of the 21st century are not equivalent to dating hypothetical lineages in early 20th century palaeontology. But yet, molecular clocks are hailed as a new and sophisticated method for determining the ages of lineages, but many fail to see the connection to 20th century palaeontology and its inherent problem,

> 'Curiously, even as molecular dating approaches have improved dramatically, some still maintain that dating should not enter into biogeographic analyses … Fortunately for the growth of the discipline, this outlook is fading fast as molecular phylogeneticists, using so-called relaxed clock methods, are discovering that many plant and animal groups are simply too young for their disjunctions to have been caused by continental drift' (Donoghue 2011, p. 6342).

Molecular clocks are no different than the pre-clock speculations of the 20th century,

> '… from a few cases in which arrivals have actually been recorded, transoceanic dispersal is difficult to prove and one can only resort to paleontological evidence such as that cited by Fleming (1962) which indicates time of first known appearance in the fossil record. It could be fairly stated that transoceanic dispersal provides a reasonable explanation for the appearance of the bulk of genera occurring first within the last 60 million years' (Skipworth 1974, p. 10).

Regardless, molecular clocks provide the pivotal element in neodispersalist thought, 'many plant and animal groups are simply too young for their disjunctions to have been caused by continental drift'. With this, the neodispersalist synthesis is complete: molecular clocks (young ghost lineages) provide the evidence for long-distance dispersal. However, the drowning of New Zealand comes into this at an earlier date, before molecular clock methods, by a New Zealand palaeontologist, Mike Pole, who assumed the first appearance of fossil pollen and macro-fossils to be the oldest possible date for each group. The assumed ages, with assumptions about the dispersal abilities of extinct and extant plants together with their possible dispersal routes, form the basis of neodispersalist meta-narratives,

> 'Palynological interpretation is clear on three points: (1) trans-Tasman dispersal has been a reality; (2) important genera and families of the extant flora arrived

> in New Zealand post Tasman Sea rifting; and (3) the present character of New Zealand's vegetation can only be traced into the Pleistocene … During the Paleogene, New Zealand itself was progressively submerged beneath a marine transgression until the Late Oligocene, when there is little indication in the marine sediments of any land. Debate continues among researchers as to whether or not New Zealand went "completely under". C. A. Landis (*pers. comm*., 1993) believes that much, if not all of the Tertiary "peneplain", which can be seen throughout much of central New Zealand, is in fact a wave-cut platform, rather than its classical interpretation as representing a long period of subaerial erosion' (Pole 1994, p. 627).

Ironically, with all that said, Pole ends his paper on a peculiarly sober note,

> 'I see oceans not as barriers to plant dispersal but hurdles which, given time, are overcome. How some plants dispersed long distances is irrelevant; that belongs to the realm of speculation' (Pole 1994, p. 632).

Pole's 'realm of speculation' was the driving force behind the drowning hypothesis. After all, if you *believe* New Zealand to have completely submerged (as opposed to *assuming* it has) then long-distance dispersal is the only mechanism available, heralding a new way at looking at continental islands, even though evidence for drowning is lacking,

> 'A paradigm shift is needed to approach the biology of New Zealand from the perspective of a relatively young, dynamic evolutionary environment rather than the assumption of an archaic ark' (Trewick *et al.* 2007, p. 4).

The paradigm shift became part of the neodispersalist synthesis (McGlone 2005; Waters and Craw 2006; Bunce *et al.* 2009; *ad nauseam*). But did the geological evidence support the drowning hypothesis? Pole (1994) noted that 'Debate continues among researchers as to whether or not New Zealand went "completely under"', but at some point the argument tipped in favour of Oligocene submergence. But where? I remind the reader of Pole's statement that 'Arguments by geologists against total submergence are usually intuitive, based on biogeographic assumption' (Pole 1994, p. 628). So too, it seems, are the arguments by biogeographers for total submergence – they are intuitive. There is no concrete geological evidence for complete submergence, just speculation by Campbell and Landis (2001) and biogeographical hypotheses presented by Pole (1994) and Cooper and Cooper (1995). Perhaps Waters and Craw (2006) should practise what they preach,

> 'A form of cosy "reciprocal illumination" has resulted in biogeographical interpretations settling into a comfortable self-fulfilling prophecy – flimsy knowledge of geological history fits with assumptions about natural history (Waters and Craw, 2006)' (Trewick *et al.* 2007, p. 2).

The drowning hypothesis so ardently promoted by neodispersalists, particularly those in New Zealand, ended up in Pole's 'realm of speculation'. Almost 20 years after it was proposed in 1994, the hypothesis finally sunk at the VII Southern Connections Congress in 2013,

> '… well over 100 years it has been known that what is now New Zealand was substantially underwater during the Oligocene geological period, about 24 million–34 million years ago … It was thought that only a few areas remained above the sea at this time and these became life rafts on which many of the distinctive biota we have today survived as island refugees … So this was the established theory, but then a few geologists began to raise doubt and, in the 2007 book, *In Search of Ancient New Zealand*, Dr Hamish Campbell claimed that the geological evidence for sustained land during the Oligocene was very weak. And he went further: "In the absence of any substantive geological constraints for the placing of a shoreline anywhere within Zealandia 23 million years ago, the inevitable conclusion is that it was empty, open ocean", he claimed.
>
> What a possibility.
>
> "Outrageous!" cried the biologists (and a good number of geologists). But was this just a storm in a prehistoric teacup?
>
> Definitely not! This was important and the implications were huge. It would mean that New Zealand's biota was much younger than we thought and what is more, as most of the plants and animals would have had to come from the nearest big land mass, much of what we hold so dear would be nothing more than recycled Australians. How could we ever live that down?' (Penniket 2013, pp. 51–52).

To be fair to Mike Pole and Hamish Campbell, many pro-drowners changed sides in light of the geological evidence. The hard evidence against the drowning hypothesis has appeared as individual papers (e.g. Climo and Mahlfeld 2011), and in 2014 in the form of a special issue of the *New Zealand Journal of Geology and Geophysic*s,

> 'The articles in this Special Issue demonstrate how a provocative suggestion (Campbell and Landis 2001) can lead to intensive research identifying new geological localities of interest, discovering new species and making new tests of interpretations – the way science progresses. Our goal for this issue was to present both sides of the debate but almost all of the submitted articles present evidence for some Oligocene land in different parts of New Zealand' (Mildenhall *et al.* 2014, p. 107).

What impact does a no-longer submerged New Zealand have on the neodispersalist 'synthesis'? Not much. It is clocks that are providing the so-called evidence for early dates that are explained by long-distance dispersal. The drowning, while helpful in the early days of neodispersalism, is no longer required. Just with the New York School, the fossils will just do fine.[56]

As with the New York School, neodispersalism is stuck firmly within Ball's narrative phase. The analytical phase, with its minimum molecular divergence dates, fails to test our hypotheses. Modelling alone does not constitute the analytical phase, even though it uses sophisticated computer software. So do geospatial information systems, which do no more than map empirical data onto maps. Such approaches belong in Ball's descriptive phase. Neither of these approaches moves biogeography into the analytical phase as is seen in the recent call for an integrative biogeography – or a field, such as neodispersalism, that has a single synthesis.

Integrative biogeography: an undisciplined discipline?

Given the multidisciplinary nature of biogeography and its many aims and goals, biogeographers have made calls to find a meta-narrative – one that would unify biogeography under a single synthesis. The result is integrative biogeography – an approach that was first offered by Donoghue and Moore (2003) to include temporal data in cladistic biogeographic analysis. Since then, integrative biogeography has now come to mean the incorporation of all possible data in proposing new biogeographic hypotheses. Although an integrative biogeography has potential to bring to light new evidence and to make discoveries about the world, it also has the ability to confuse the results of different methods with different aims as correlations in the data (e.g. confusing biomes as phylogenetically informative or as biotic regions). Moreover, integrating as much data as possible comes across as arbitrary and undisciplined. What are the aims of an integrative biogeography and what method reflects these aims? A scientific field that has this integrative nature is palaeontology, and it too has a problem with unifying its aims and method.

Integration in palaeontology

Incorporating fossils, palaeoecology, geochemistry, cladistics, morphometrics, systematics and evolutionary taxonomy into a single field has its problems. For instance, evolutionary taxonomy and cladistics have opposing world-views: what is considered non-monophyletic in cladistics may well be considered to be 'monophyletic' in evolutionary taxonomy. Meta-narratives in palaeontology may also conflict. In any given biostratigraphic reconstruction, for example, the oldest known taxon is linked to the next youngest taxon in a hypothetical temporal sequence. The direction in which these taxa evolve is 'up', with the most primitive being at the bottom and the more derived appearing at the top. Placed in order, these taxa can be linked by hypothesised lines of ancestry that form a ghost lineage (Fig. 6.3). In this example, we see that the oldest horse fossil is *Hyracotherium* and the youngest *Equus*, the modern horse, with the other genera linked in a ghost – ancestor-descendant – lineage (Fig. 6.3a). *Merychippus*, for example, is considered to be older, and therefore an ancestor of the younger *Hipparion*. When we look at their morphological relationship independently of time, we find that *Merychippus* is more closely related to the modern horse, *Equus*, than it is to *Hipparion*. The independent evidence states that *Merychippus* cannot be the ancestor to *Hipparion* (Fig. 6.3b). Independent morphological evidence in the form of a cladogram has shown the hypothesised narrative to be wrong. But cladistics was not an accepted methodology in palaeontology until only recently. Rather, palaeontologists relied on time and assumptions of relationship based on 'expert' opinion (Hedley's 'testimonies') to be sufficient to show that a preferred hypothesis was correct. When no independent evidence is available, such as cladistic relationships, we defer to our meta-narrative from which our

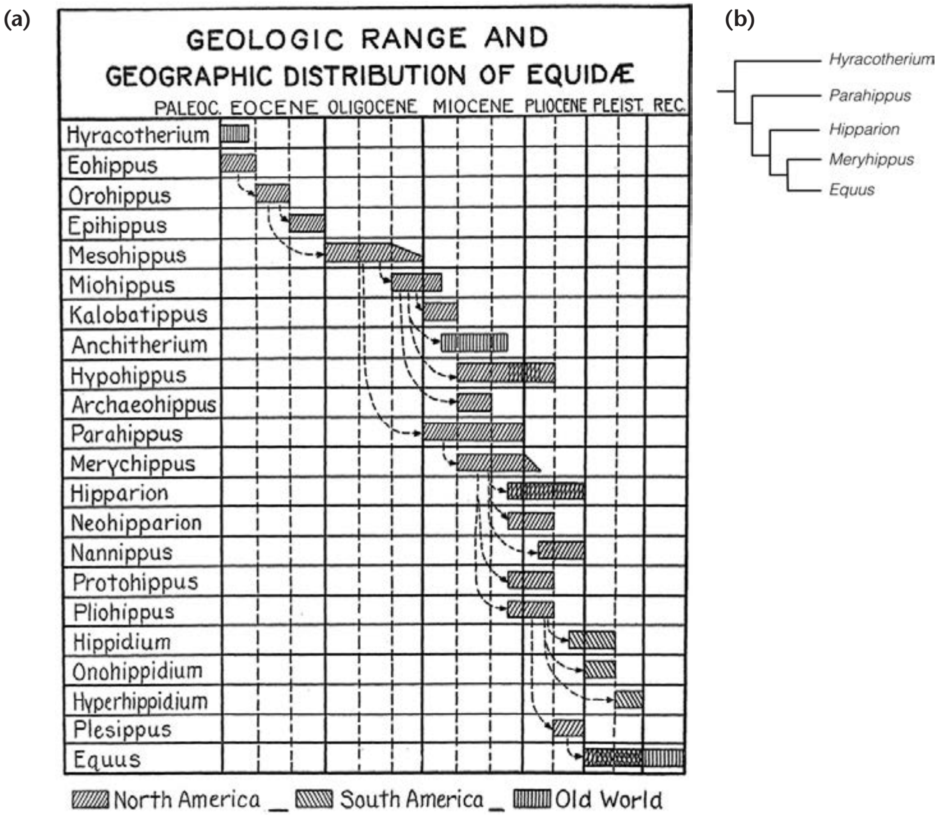


Fig. 6.3. Horse evolution. (a) A ghost lineage based on similarity of form in addition to the age of the taxon (reproduced from Matthew 1926, p. 167, Fig. 25). For instance, *Merychippus* is considered to be the ancestor of *Hipparion* and *Pliohippus.* The modern horse, *Equus*, is the descendant of *Pliohippus* and *Merychippus*; (b) a cladogram based on the relationships of the morphological characteristics indicates that older *Merychippus* cannot be the ancestor of the younger *Hipparion* (MacFadden 1994, p. 100, Fig. 5.15).

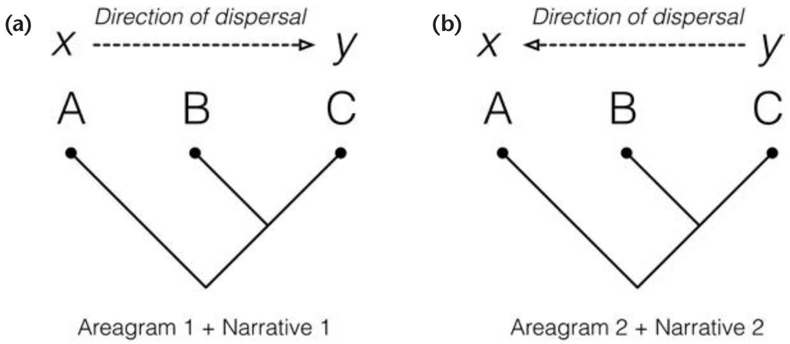


Fig. 6.4. The narrative drives the result. In both areagrams, A is ancestral to B and C, in (a) areagram 1, the narrative suggests that the descendants disperse away from the centre of origin, namely area *x*; (b) in areagram 2, the narrative states that it is the ancestors that move away from the ancestral area (*sensu* Matthew 1915), meaning that the centre of origin is area *y*. The narrative can completely alter the meaning of the empirical evidence.

hypothesis derives. But even without this evidence derived from cladistic analysis, should an integrative field such as palaeontology take other evidence into account? The problem here is that our hypothesised narrative of 'primitive' horses evolving into derived forms lacks independent evidence. Integration of other methods and data also means we integrate many different narratives. For instance, in the above example we have two hypotheses: (i) time's arrow: older taxa are more likely to be ancestral, and (ii) all taxa are part of a single lineage. Together these two hypothesised narratives result in a chance correlation. We may also add a third hypothesised narrative: species evolve in a centre or origin and, over time, disperse to new areas where they evolve into new species. Together, these narratives form a meta-narrative that states the oldest species resides in the ancestral area from which some species disperse to new area and evolve into descendant species. Integration without independent evidence means our meta-narratives grow untested. The point here is that meta-narratives are part and parcel of science; however, confusing correlation for independent evidence is problematic and is more likely to occur when we integrate more and more data and methods.

Correlation in integrative biogeography

Our meta-narrative above can be further correlated with cladograms, providing of course they do not conflict. The matter of conflict is simple: alter the meta-narrative slightly to accommodate the cladogram. In the horse example, we may state that while *Merychippus* is older, but not ancestral to *Hipparion*, it may well be part of a different lineage and derived from yet undiscovered fossil ancestors. In cases where the cladogram provides evidence for multiple lineages, we may apply our meta-narrative to choose the lineage we prefer. Essentially, this is what happens in the progression rule (Hennig 1966). The cladogram, rather than a biostratigraphic column, provides the structure from which we derive time's arrow. For instance, the most basal taxon in cladogram (A,(B,C)) is A, which is interpreted to be the oldest and part of the ancestral area *x*. Taxon C is younger and resides in area *y* to which members of Taxon A dispersed, giving rise to the intermediate Taxon B (Fig. 6.4). The meta-narrative in the resulting areagram 1 cannot be tested, because it is applied after cladistic analysis, and not proposed before. Rather the cladogram and areagram are part of a correlation in which taxon relationships are interpreted as real phyletic lineages. What happens when we change our meta-narrative? Let's say we use William Diller Matthew's theory of evolution, namely, 'At any one time, therefore, the most advanced stages should be nearest the centre of dispersal, the most conservative states farthest from it' (Matthew 1915, p. 180). Matthew means that the most derived taxa remain at the centre of origin and the ancestral taxa move *away* from it. Apply this narrative to the same cladogram and we get a very different story. Taxa B and C, the descendants of Taxon A, stayed, meaning that Taxon C resides in the ancestral area. In other words, areagram 2 says the opposite to areagram 1, namely that area *y* (and not *x*) is the ancestral area. The information in the original cladogram supports both narratives. See the problem? There is no hypothesis testing, just correlation driven by a favoured or popular narrative. I call this narrative-driven biogeography, because it is the narrative and meta-narrative generating the result. The narratives are supported not by evidence, but by 'expert opinion' derived from a meta-narrative, very much like the hypotheses of early 20th century palaeontologists.

Integrative biogeography is developing its own meta-narrative, from which it draws its own conclusions. For example, in a paper that attempts to 'illustrate the benefits of an integrated approach', Wiens and Donoghue set up their meta-narrative, namely that 'biogeographical patterns result from ecological processes that influence dispersal (or "dispersion") at different spatial and temporal scales' (Wiens and Donoghue 2004, p. 640).

Already this integrative approach has excluded several biogeographic approaches and their aims. Rather than 'integrate' biogeography, Wiens and Donoghue are assimilating certain popular narratives into an exclusive biogeographical meta-narrative. In this sense, integrative biogeography denies the multidisciplinary nature of biogeography by selecting popular aims and goals and approaches and disqualifying others. Wiens and Donoghue's 'expert opinion' is no different to those of Matthew or Darlington. Testing within these parameters means that alternative narratives cannot be considered as viable explanations, regardless if you test your hypothesis or not.

Another form of integration is the reliance of molecular clocks,

> 'Historical biogeography will be most effective as a means both for generating and testing hypotheses if methods that allow for accurate calculation of organismal divergence dates can be incorporated within its methodological framework' (Riddle *et al.* 2008).

The incorporation of time into analysis has been plagued with problems since the emergence of ghost lineages in biostratigraphic columns. Time is difficult to incorporate into any analysis as an objective 'fact'. For example, time is often confused with ancestry. In the palaeontological meta-narrative, the older a fossil is, the more likely it will be the ancestor. Even if this were true, *how do you know you have the oldest fossil*? You don't. A molecular clock is nothing more than a set of proposed ages, based on fossil taxa and a model of substitution rates that are mapped onto a cladogram. Together, the cladogram, the fossil calibration and model are combined to form a correlation. The problem is how the correlation is interpreted. Are these absolute dates for when two unidentified ancestral taxa diverged or are they simply a suggested maximum age for that clade? Many choose the former: namely a maximum absolute age for an actual divergence event between two ancestral lineages. Again, it is our meta-narrative driving the evidence. Just like hypothetical lineages in palaeontology, the ages of the fossils are interpreted as the oldest (i.e. the real ancestral ages). Also the cladogram, or branching diagram, is interpreted as a phylogenic lineage, where common ancestors are located at the nodes. The similarity between the palaeontological approach of drawing ghost lineages and the molecular approach of dating branching diagrams are striking. Rather than advance biogeography, we have placed it firmly within the past practices of early 20th century palaeontology.

Integration in biogeography is not a bad thing once it is done with Ball's criteria in mind – namely clarity, comparability and rigour (Ball 1990). For example, using geospatial software to propose areas for hypothesis testing using cladistic biogeography is a form of integrative biogeography. But there is no over-arching meta-narrative that enforces one world-view over another. Instead of setting up our hypotheses for testing using meta-narratives, we should stick to single testable hypotheses that are tested against independent evidence. Our meta-narratives, vital in science, can be adjusted and corrected as we discover more about our evidence. What is needed is exactly what Ball (1990) proposed – a set of criteria that test the link between our evidence and our narratives. According to Ball, this is the way into the analytical phase – one that moves biogeography forward to an *evidence-based* science. The analytical phase, as discussed in Chapter 1, may only be reached if, and only if, we search for patterns (multiple overlapping area relationships). The tools, methods and theory to do biogeography within the analytical phase are all available, so too are biogeographical hypotheses. There is no longer any need to start new cycles of reinvention.

Chapter 7

All possible futures

Proposing narratives for the data we have is not in itself 'bad biogeography'. At some point we do need to make a call. For instance, are the organisms of New Zealand mostly migrants from elsewhere or are they endemic? Whatever the explanation, the result is a meta-narrative that together forms a biogeographical story of a continent.

Meta-narratives help us understand what may have happened, even in the light of little to no evidence. Quantum physics works in the same way – a meta-narrative serves as a way to explain how quantum particles interact, but it is not a discovery. Our discoveries come from independent evidence that supports or denies our hypotheses. This is why so much emphasis is placed on testing hypotheses, rather than proposing meta-narratives. Discoveries move a science forward and beyond the meta-narrative towards something true we can say about the world. Take plate tectonic theory, for example. It uses evidence from many different sources – geology, geophysics and chemistry – to confirm the claim that both continental and oceanic plates are indeed moving. Before plate tectonics, when we only had circumstantial evidence based on fossil distributions and the matching of continental margins and geology across ocean basins, there were multiple and equally plausible hypotheses that could both confirm and deny continental drift. The distribution of *Glossopteris* may have been through break up and subsequent drift, or it could have been due to a series of dispersal events. Until the discovery of palaeomagnetic data – mid-oceanic ridges, and so on – continental drift served as a meta-narrative for the distribution of fossil and some living taxa. Now that we have confirmation of plate tectonics, biogeography can move on and propose tectonic meta-narratives, such as the drowning of New Zealand, for example. The discovery of independent evidence is the key, without which we are not able to test our hypotheses. Can we break out of the cycle of proposing the same meta-narratives again and again? Here I return the reader to Ian Ball's analytical phase, in which biogeographic methods falsify proposed narratives: namely, our hypotheses. Is 21st century Australasian biogeography in a position to reform itself and break the cycle of reinvention?

Entering the analytical phase: testing the link between evidence and hypothesis

The influence of Popper in the 1980s and 1990s on biogeography had for a time led to the notion of testability in the historical sciences, but one that was not based on observation and experimentation. The historical sciences are at best blind to process and immune to experimentation. With these limitations, falsifying a hypothesis becomes almost impossible. Considering that science, at least in Popper and Ball's view, was one narrative replacing another, we are left with narratives attempting to 'falsify' other narratives, based on argumentation or authority. Without going into a deep philosophical discussion, what is needed is a way to test hypotheses without correlating our hypotheses to other more popular narratives: that is, enter another cycle of reinvention. Quite simply, we have the explanation (our narratives) and the thing to be explained (taxa and their distributions). Finding the link between the thing that needs to be explained and the explanation is possibly the most challenging task in historical science. Even if we do find that link, will it explain everything or just a small part? Earlier I made the connection between cladistics and cladistic biogeography: homologies provide us with biological relationships in the same way that endemic area relationships (area homologues) provide us with area relationships. A pattern of area relationship, or geographical congruence, is a discovery. But it tells us little more than whether a named area is part of natural classification, and that closely related areas share a common history. In other words, our link between evidence and explanation tells us little more than what we may have already expected. Yet the link is strong. We can test this link using Ball's criteria,

> 'Clarity – The units of study should be clearly denoted and be of logical status of individuals, whether they be taxa or areas' (Ball 1990, p. 5).

The areas and taxa are clearly denoted and have the status of individuals. Geopolitical areas or continents are vague concepts, in the same way that fowl and shellfish are vague notions of taxa.

> 'Comparability – The hypothesis should be presented in such a way that direct comparison with hypotheses derived for other organisms in the same area can be made' (Ball 1990, p. 5).

In other words, a unified history of areas is needed. Area monophyly would be an ideal test. We may ask, do the sub-regions within region X form a monophyletic region?

> 'Rigor – Hypotheses should be presented in such a way that potential observations that would serve to refute the hypotheses may be assessed' (Ball 1990, p. 5).

Here Ball calls for additional data, such as 'phylogenetic, distributional, or geological data'. Again, the cladistic parameter serves as independent evidence in regards to the relationship between the taxa of each of the areas in our study. If there were no overlap, there would be no pattern.

Clearly pattern is what is providing us with the evidence that passes each of Ball's three criteria. In 'clarity', pattern will tell us which areas overlap (i.e. endemicity area overlap); in 'comparability', we are finding the overlap of patterns across different taxa; and in 'rigour' we find that the pattern in the cladograms serves as the independent evidence to test the relationships of our biotic areas. Why then has pattern received such bad press?

The problem is how pattern is perceived. As humans we are hard-wired to recognise patterns. This is why we classify. But we also see non-patterns, or objects and processes that do not conform to a common pattern, and we identify these as anomalies. Here lies the problem: scientists are more interested in explaining anomalies than they are in searching for patterns. For example, if we discover patterns that show our conclusions to be wrong, it jars with us. Many established taxonomists (e.g. Brummitt 2002) have rejected cladistics just because it has shown their own taxonomies to be wrong. It takes a brave scientist to admit they are wrong, particularly after a life-time of doing taxonomy. Rather than tackle the possibility that we may, after all, have been doing poor taxonomy, we would rather focus on the peculiarities, such as non-monophyly and non-homology. Discussing why something isn't there means that all possibilities are open to us and the best explanations (or greater authorities) win (e.g. Hörandl and Stuessy 2010). The other problem is that patterns are erroneously thought of as being equivalent to narratives: that is, they are merely explanations in need of testing. Deriving narratives from patterns isn't the problem. Treating them as equivalents is where problems arise.

In Fig. 7.1a and b we see that our cladogram contains a series of conflicting, but equally plausible, phylogenetic narratives. Let's see if we reverse the situation and recover our regional classification from our narratives. What we find is that while some narratives recover the original classification, others don't (Fig. 7.1c). Narratives as explanations cannot recover the original classification because it is the classification that is the thing to be explained. Natural classifications themselves are not narratives or meta-narratives, rather they are statements of relationship from which multiple (and at times conflicting) narratives may be drawn. An artificial classification, however, contains no information about natural relationships, and in turn may not lead to plausible narratives. This take us to Ball's first criterion, clarity: namely the 'units of study should be clearly denoted and be of logical status of individuals, whether they be taxa or areas' (Ball 1990, p. 5). Artificial units or non-monophyly are not clearly denoted because they do not represent real taxa or areas. Ball's criteria work in recovering natural areas and taxa, but can they extend to more explicit narratives about process and historical events? Ball was cautious, claiming that 'narratives are rarely so testable …' (Ball 1990, p. 7). But we may, using other forms of independent evidence, be able to extend Ball's criteria to at least test the plausibility of some biogeographic hypotheses, even if we are unable to give a clear 'yes' or 'no' answer.

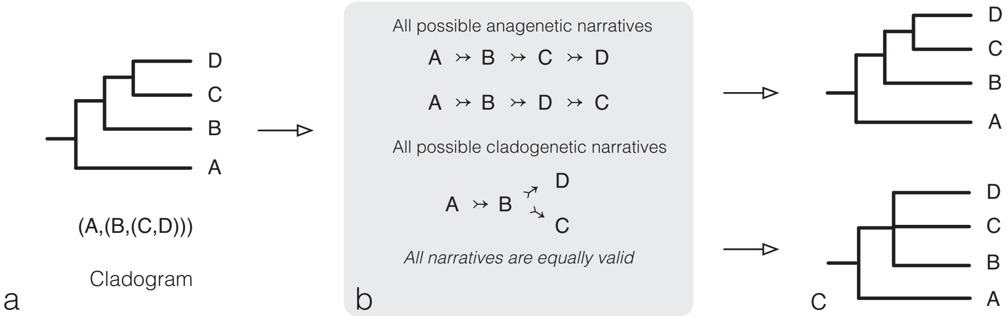


Fig. 7.1. The power of classification over narratives. In (a) our cladogram depicts the relationship between A–D. A single cladogram contains (b) multiple narratives, of which some (c) find the original cladogram, while others do not.

Certain criteria fit certain types of questioning. Are we, for instance, testing for natural areas? If so, we are looking for patterns, rather than a plausible narrative. Once we ask questions about specific types of processes, such as dispersal or vicariance, we start asking for more evidence that lies beyond cladistic and distributional data. Let us take several hypotheses from earlier chapters and put them to the test, such as the invasion theory, the drowning of New Zealand hypothesis and neodispersalism.

Extending Ball's criteria: invasions, drowning and neodispersalism

The invasion hypothesis stems from the meta-narrative that the continents are fixed and that the Australian flora and fauna contain elements of other areas (including an older Autochthonous or Antarctic element). The notion is that organisms dispersed to Australia. Any endemicity is seemingly dismissed as older elements. By the 1980s, Australasian biogeographers started to abandon the invasion hypothesis due to a lack of evidence (e.g. Webb and Tracey 1981; Archer and Fox 1984; Martin 1984; Schodde 1989). With Australia having both an endemic biota (with tropical elements from the north), the invasion theory was merely flipped around. Rather than having older tropical and Antarctic elements, Australia is now considered to be the centre of diversification for areas such as New Zealand, New Guinea and Wallacea (e.g. Winkworth *et al.* 2002; Sanmartín and Ronquist 2004; Sanmartín *et al.* 2007). The cladistic relationships between modern and ancient organisms helped to identify the endemicity of the Australian biota, thereby revising the elements. The direction of the invasion hypothesis and Australian endemicity was confirmed using Ball's rigour criterion. The discovery and eventual acceptance of plate tectonics also helped in changing the direction of the invasion hypothesis, again falling under the rigour criterion. But the invasion hypothesis of New Zealand had only changed direction. Rather than receiving elements from South America via an Antarctic land-bridge and the Melanesian archipelago, New Zealand had an Australian element, with Pacific and Melanesian elements. By the 2000s, the invasion hypothesis had not been invalidated in New Zealand, as many still believed that much of the biota had arrived from elsewhere. The evidence used was lack of evidence indicating a pre-Oligocene holdover, or terrestrial depositional environments. This evidence would again fit under Ball's criteria, but it failed in two ways. First, there was evidence to suggest that New Zealand had terrestrial land during the Oligocene; and second, it failed on comparability, because there was no shared pattern or history between taxa. Had the majority of taxa come from Australia via chance dispersal along the west wind drift (i.e. Antarctic Circumpolar Current), then the currents would move in a west to east direction across the Tasman Sea. However, oceanographic evidence points to currents moving from New Zealand to south-eastern Australia (*contra* Fell 1962) and currents moving from central NSW and Queensland to New Zealand (Rintoul *et al.* 2001). The west wind drift, originally conceived as 'an epiplanktonic dispersal agent' (Fell 1962, p. 759), may not be the great driver of long-distance dispersal of organisms from southern Australia and Tasmania to New Zealand; therefore the taxa from Australia that did get to New Zealand would come from further north. But there are stronger cladistic relationships between New Zealand and Tasmania than to other areas in Australia, particularly in *Nothofagus*. If dispersal occurred from New Zealand to Tasmania, then the meta-narrative that New Zealand was colonised by Australian elements is incorrect. Again Ball's rigour criterion (i.e. evidence from oceanography) and comparability (i.e. cladistic relationships in *Nothofagus*) have shown the west wind drift not to be a driver of dispersal to New Zealand. These three simple criteria can help us decide which hypotheses are least plausible. But the explanatory narratives of neodispersalism, however, are much harder to test, because they require strict adherence to a fairly reactionary meta-narrative: taxa disperse long distances regardless of any contradictory evidence. The neodispersal meta-narrative includes the hypothesis that the moas, for example, came to New Zealand via an ancestor that could fly great distances. The evidence here was presented in a phylogeny by Phillips *et al.* (2010) based on a cladogram showing the close relationship between the flightless moa and the flighted tinamous of South America. Based on this relationship, and molecular divergence dates, it is assumed that South America may be the source of Australasian ratites. When we look at the area relationships, we get a different story. The areagram of Phillips *et al.* (2010) contains two area relationships, namely, (Eurasia/Africa,(South America, New Zealand)) and (Eurasia/Africa,(Australia, New Zealand)). Added together we find that the relationship between Australia, New Zealand and South America is unresolved: (Eurasia/Africa,(South America, Australia, New Zealand)). Until more information can be found to resolve this issue, nothing more can be said of ratite biogeography. Once again the comparability criterion has helped us determine the link between the data and the narrative presented in Phillips *et al.* (2010), namely that the link is uncertain because we do not have conformity between the evidence (i.e. the area relationships) and the narrative (i.e. molecular dates and dispersal direction).

Ball's criteria are robust and work on a variety of testable biogeographic hypotheses. Over time they can be refined: each criterion could be divided into smaller sub-categories. Until Ball's criteria are refined and broadcast to a wide audience, we are stuck with so-called 'tests', such as 'maximum likelihood significance tests'. Rather than confuse hypothesis testing for statistically quantifying correlation, biogeography will need criteria for linking independent evidence to explanatory narratives.

The future of hypothesis testing is a hot subject in biogeography. For instance, Crisp *et al.* (2011) have pointed out the need for testable hypotheses, and Ball (1990) has clearly stated the significance of using criteria to test for plausible biogeographic narratives. But little has been done to find an expedient way to apply the criteria to sort out which of our testable hypotheses are plausible and which can be falsified and discarded (Ebach and Michael 2016). One solution would be to map the biogeographic work process and identify areas where these criteria could be applied. That way, computer algorithms could be used to automate the criteria and quantify them in the same way that current biogeographic models choose between one model and another. I am sure there are a myriad of ways to implement Ball's criteria, but until we do, we are left with mere correlations.

Towards the analytical phase and biogeographic discovery

Imagine a world where all testable biogeographic narratives can be tested for plausibility. What would that world look like? You don't have to look too far. Presently natural classification can be tested, which on its own can help existing biogeographic modelling programs chose between plausible models. But the search for natural classification has larger ramifications, which has captured the minds of naturalists as far back as the 19th century, and one where 'we require a far more extended knowledge of zoology and botany than we as yet possess, before it can be told with certainty what *are* the primary ontological divisions of the globe' (Sclater 1858, pp. 131–132, original emphasis).

Biogeography, evolutionary biology, ecology and conservation biology would all be impossible if we didn't have a classification of life. But now, with greater demands for more data, we can extend our classification to include the 'tree of life': namely natural classifications. In biogeography, however, we make do with point data, arbitrary areas and rough maps. Could a natural area classification, an 'areagram of life', be the basis for an 'integrative' biogeography rather than a meta-narrative driven biogeography? It is well known that it works in taxonomy and phylogenetics, so why not in biogeography? Discovering natural areas is the main problem – there are few methods that can find general congruence and there is not much data. Regardless, this has not deterred modern biogeographers from identifying possible areas of endemism and biotic regions. Although this is considered part of the descriptive phase, it is a right step towards an analytical biogeography.

Bioregionalisation and the descriptive phase

When Sclater proposed his bird regions of the world, he was not concerned by the lack of data,

> 'There is no reason, however, why attempts should not be made to solve the question [what are the primary ontological regions?], even from our present imperfect data, and I think the most likely way to make good progress in this direction, is for each inquirer to take up the subject with which he is best acquainted, and to work out what he conceives to be the most natural divisions of the earth's surface from that alone' (Sclater 1858, p. 132).

The same is true of attempts at proposing natural regions today,

> 'The inclusion of data (when they become available) on reptiles, invertebrates, and/or plants may also affect the boundaries of our realms and regions and the relationships among them' (Holt *et al.* 2013, p. 77).

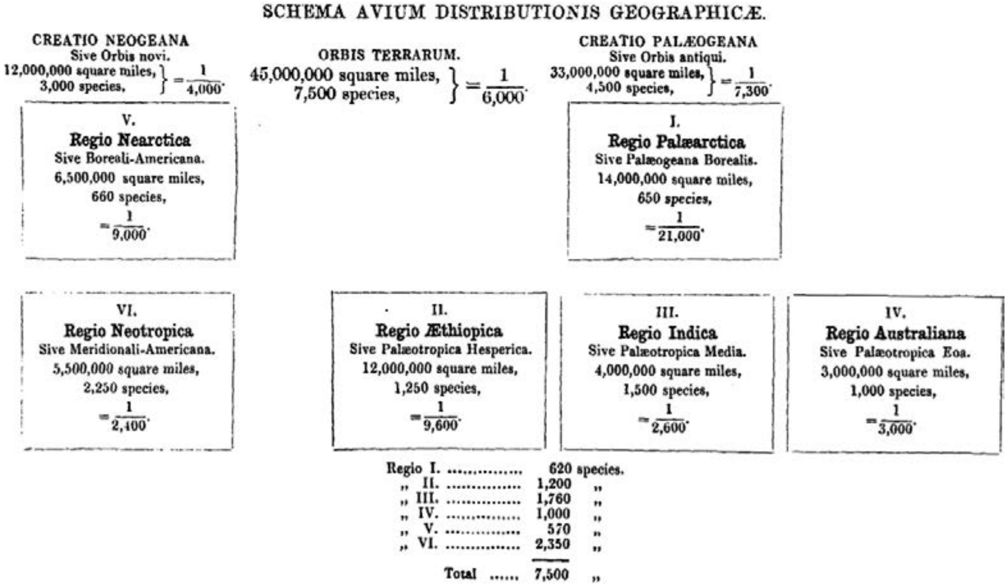
Proposing areas will always be a challenge, particularly when it is done statistically as in Sclater (1858) and Holt *et al.* (2013). Although the methodology of Holt *et al.* (2013) is sophisticated, it is still a model with which to propose areas. In a reply to Holt *et al.* (2013), Kreft and Jetz (2013) correctly point out that 'biogeographers must be aware that expert- and algorithm-drawn boundaries are ultimately only arbitrary, although helpful, constructs that are inherently limited in fully capturing the biogeographical complexity' (Kreft and Jetz 2013, p. 343). While this is true, it should not halt the search for potential natural areas. In fact, there are many sophisticated algorithms that have the ability to propose endemic areas and regions based on many different types of data, including phylogenetic turnover (Kreft and Jetz 2010), area similarity based on taxic distribution (Rosen 1988), spatial turnover (Gaston *et al.* 2007) and similarities between nested sets (Templeton 1998). Proposing potential natural areas can be as sophisticated or as basic as you like. Sclater's 1858 regions, adopted by Wallace (1876), were recovered, in part, by Holt *et al.* (2013). The degree of sophistication only helps biogeographers to delimit their areas at much finer scale.

> 'Such being done, we shall see how far the results correspond, and on combining the whole, may possibly arrive at a correct solution of the problem – *to find the primary ontological divisions of the earth's surface*' (Sclater 1858, p. 132, original emphasis).

But how we can discover which classifications are real or not? Sclater hinted at a possible solution,

> '… little or no attention is given to the fact that two or more of these geographical divisions may have much closer relations to each other than to any third, and, due regard being paid to the general aspect of their Zoology and Botany, only form one natural province or kingdom (as it may perhaps be termed), equivalent in value to that third' (Sclater 1858, p. 131).

Sclater knew certain regions had a closer affinity to other regions based on the composition of their flora and fauna (Fig. 7.2). Some might argue this is an early form of area similarity, as in Parsimony Analysis of Endemicity (Rosen 1988), but read Sclater's passage clearly, you get the sense of something else – 'no attention is given to the fact that two or more of these geographical divisions may have much closer relations to each other than to any third'. To my mind, this is a general statement of area relationship (based on



SCHEMA AVIUM DISTRIBUTIONIS GEOGRAPHICÆ.

CREATIO NEOGEANA
Sive Orbis novi.
12,000,000 square miles, 3,000 species, $\Big\} = \frac{1}{4,000}$.

ORBIS TERRARUM.
45,000,000 square miles, 7,500 species, $\Big\} = \frac{1}{6,000}$.

CREATIO PALÆOGEANA
Sive Orbis antiqui.
33,000,000 square miles, 4,500 species, $\Big\} = \frac{1}{7,300}$.

V.
Regio Nearctica
Sive Boreali-Americana.
6,500,000 square miles,
660 species,
$= \frac{1}{9,000}$.

I.
Regio Palæarctica
Sive Palæogeana Borealis.
14,000,000 square miles,
650 species,
$= \frac{1}{21,000}$.

VI.
Regio Neotropica
Sive Meridionali-Americana.
5,500,000 square miles,
2,250 species,
$= \frac{1}{2,400}$.

II.
Regio Æthiopica
Sive Palæotropica Hesperica.
12,000,000 square miles,
1,250 species,
$= \frac{1}{9,600}$.

III.
Regio Indica
Sive Palæotropica Media.
4,000,000 square miles,
1,500 species,
$= \frac{1}{2,600}$.

IV.
Regio Australiana
Sive Palæotropica Eoa.
3,000,000 square miles,
1,000 species,
$= \frac{1}{3,000}$.

Regio I.	620	species.
„ II.	1,200	„
„ III.	1,760	„
„ IV.	1,000	„
„ V.	570	„
„ VI.	2,350	„
Total	7,500	„

Fig. 7.2. *Schema Avium Distributionis Geographicae* (Sclater 1858, p. 145). A hierarchical classification of the bird regions of the world. The Palaearctic, Ethiopian, Indian and Australasian regions are part of *Creatio Palaeogeana*, whereas the Nearctic and Neotropical regions are part of the *Creatio Neogeana*. The figures represent the approximate area and number of species living in each region. The Australasian region (IV) contains 100 species, with one species per 3000 square miles. The table at the bottom gives the total number of species per region and for the world.

taxic similarity), and in 1858 few people would have given it any attention. Perhaps Sclater was on to something? Sclater didn't propose explicit area relationships, but his Creatio Palaeogeana seems to suggest that the Regions Ethiopica, Indica and Australiana are more closely related to each other. What did it mean? Sclater (1864) did think that 'as a general rule, such tracts of land as are most nearly contiguous have their Faunæ and Floræ most nearly resembling one another; while, vice versâ, those that are farthest asunder are inhabited by most different forms of animal and vegetable life'. Most biogeographers still believe this to be a general rule, because taxa that are more related to each other will in general be found closer together. This is why we can find endemic biota in places such as Australia. But Sclater knows there are exceptions to this rule: when 'two regions far apart exhibit similar forms, it is the task of the student of geographical distribution to give some reason why this has come about, and so to make the "exception prove the rule"' (Sclater 1864, p. 213). The exception to the rule may have jarred with Sclater's notion of area relationship. The single bit of information that was missing was that the continents are mobile. If Sclater had been a strong supporter of continental drift, then perhaps a method of determining area relationship may have arisen earlier.

It isn't the lack of quantity, but a lack of different types, of data that has held back biogeography. Without the verification that continents are mobile, we would, for example, still be trying to work out how *Glossopteris* dispersed across the Indian Ocean. The same is true for modern biogeography. The lack of geographically overlapping area relationships has made it impossible to test for area monophyly. Instead, we use more sophisticated methods and algorithms to propose the same old areas again and again. Are we forever stuck in a cycle of proposing new potential natural areas? It certainly seems that way when we look at Australian bioregionalisation and find examples such as the areas of Tenison-Woods (1882) being unwittingly redescribed by Smith (1984). But things are changing. It is true that biogeographers have developed rigorous methods to test for geographical congruence since the 1970s, but, with recent developments in molecular systematics, more and more geographically overlapping phylogenies are being published, meaning that we can finally test for area monophyly at a finer scale – the analytical phase has finally arrived.

A future of Australasian biogeography ending the cycle of reinvention

Australasian biogeography has not dealt with the bigger issues of natural regions, and their area relationships. For instance, what are the inter-relationships of Australasian biotic areas? Will Australasia fall out as a natural monophyletic area on the areagram of life? Just knowing this alone separates out the plausible meta-narratives. Let me propose three passable meta-narratives, from the most to the least plausible, and propose the types of area relationships we would expect to find.

Australasia as an artificial region

Of the few large-scale studies made of Australasia, this is perhaps the most plausible narrative. Assuming that an area the size of Australasia is natural has its problems: first, what do I mean by Australasia? Do I include the Antarctic islands, which Udvardy (1987) thought

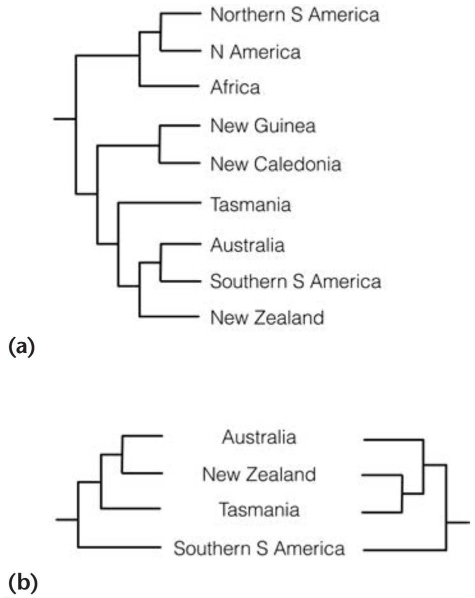


Fig. 7.3. Australasia as a composite region: examples redrawn from the volume *Austral Biogeography* (Ladiges *et al.* 1991). (a) General area cladogram (i.e. geographical congruence) obtained under assumption 2 (Crisci *et al.* 1991, p. 124, Fig. 24); (b) 'The two alternate positions of New Zealand supported by *Nothofagus*' (Seberg 1991, p. 131, Fig. 3C).

belonged in a separate region along with New Zealand? How far north does it extend – to Wallace's line or Weber's line? The question whether Australasia is natural depends on what we test. In an analysis I did with Lynne Parenti in 2009, we found that although the two Australian sub-regions were more closely related to each other than to any other area, Melanesia, which included Papua, had greater affinity to the African and Samoan sub-regions. In fact, going back as far as Hedley (1900), we find that both New Zealand and Australia were considered to be parts of two separate regions – an argument that continued into the latter half of the 20th century (Fleming 1987; Udvardy 1987). The early results from cladistic biogeographers in the late 1980s and 1990s confirmed the relationships not only between Australian and New Zealand sub-regions, but also the relationships between New Zealand and South America. In the papers resulting from the 1990 Austral Biogeography Symposium (Ladiges *et al.* 1991), it is clear that Australasia was a composite region. In comparing the areagrams from the same volume, we get a unique insight into both the inter-relationships of Australia and New Zealand (Fig. 7.3). These results even lead to the question, 'are Australia and New Zealand natural areas?' The evidence is clear: treating Australia as a single area is not going to reveal a pattern. Yet, since 1991, biogeographers have insisted on treating Australia as a single region, most notably in the analysis of Sanmartín and Ronquist (2004). The analysis of '54 non marine and 19 plant groups' consists of multiple conflicting relationships (Sanmartín and Ronquist 2004, Table 2). An artificial Australasia (or Australia) will not form a single pattern; rather it would result in multiple contradictory area relationships as shown in Sanmartín and Ronquist (2004, Fig. 7).

Australasia as one or more temporally overlapping natural regions

The concept of temporally overlapping areas is not new. Hedley (1893a) was perhaps the first to propose the idea that the Autochthonian, Euronotian and Papuan were 'superimposed one above another' (Hedley 1893a, p. 446). However, not much was made of overlapping areas until Burbidge (1960), who nonetheless focused on the timing of plant migration routes rather than on the age of the areas themselves. In fact, biogeographers have complained at the 'lack of temporal information' in cladistic biogeography: a catch-phrase used in integrative biogeography (see Donoghue and Moore 2003). The lack of temporal information in cladistic biogeography is both intentional and useful. Temporality interferes with the primary data, namely the homologues and the homologies, because a relationship is difficult to date, particularly at the internal node. Imagine dating the internal node in the relationship: (Devonian trilobite, (Triassic labyrinthodont, living rock warbler)). The internal node could be dated anywhere between 395–201 Mya. Unless there is a precise maximum age, dating nodes remains problematic. But if you date the organisms and the areas they live in, however, you keep the morphological and temporal information separate and independent, just like in a cladogram. In other words, if you treat time as a condition of the taxon or area, rather than arbitrarily placing it on a node, you can add multiple realms together to find patterns. If each gene tree in a molecular systematic analysis is given a different time stamp, then it would seem impractical to compare them in order to find an aggregate pattern: namely the consensus tree. The reason we do find a consensus tree is because we do not date the nodes, but rather the taxa.

In dating areas, rather than the nodes, we are able to find aggregate patterns and fulfil each of Ball's criteria. Moreover, we can treat the same geographical space as two or more temporal areas. For example, the trilobite, labyrinthodont and rock warbler may inhabit the exact same geographic space, meaning that three separate areas with separate histories are overlapping geographically – namely, temporal geographic overlap. The trick is to pick these separate histories apart, which is easy in our example (and in palaeobiogeography), but difficult in living biota. The first problem is how to date accurately two potential overlapping temporal biotic areas. Next is how to identify potential biotic holdovers – this is why I place temporal geographic overlap as a possible alternative to Australasia as an artificial region.

Finding temporal geographic overlap is difficult to do and few biogeographers, if any, have attempted to do so. We may never know if a biotic area has a temporal sister area until a reliable method arises that can date taxa and the areas in which they live. One way would be to date the age of a distribution, based on fossil data (e.g. palynological data). Doing so is common practice in palaeobiogeography, and in the palaeontological literature holdovers are a common phenomenon. Within the Sydney Basin, at least, we have a great, be it extreme, example of temporal geographic overlap between the Triassic labyrinthodont and the living rock warbler, because both taxa are only found within the sandstone outcrops of the Sydney Basin (Fig. 7.4).

Australasia as a natural region

The reanalysis of Wallace's regions by Holt *et al.* (2013) revealed a modified Australasia: one that includes Australia and New Zealand with the exclusion of Papua and Sulawesi (Fig. 7.5).

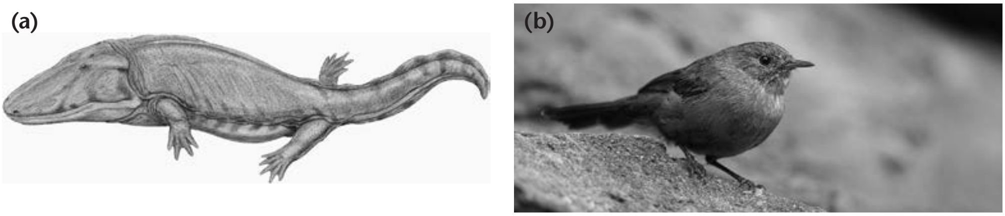


Fig. 7.4. Two taxa that inhabit the same geographical space at different times: (a) the Triassic fossil labyrinthodont *Paracyclotosaurus davidii* (Creator: Dmitry Bogdanov). This image is licensed under the Creative Commons Attribution 3.0 Unported licence (https://creativecommons.org/licenses/by/3.0/). Available at https://en.wikipedia.org/wiki/File:Paracyclotosaurus1DB.jpg; (b) the living Sydney rock warbler, *Origma solitaria.* This image is licensed under the Creative Commons Attribution 3.0 Australia licence (https://creativecommons.org/licenses/by/3.0/au/). Available at http://images.ala.org.au/image/viewer?imageId = 73951321-0a6c-4f2d-a759-73fba74a3449.

As in Sanmartín and Ronquist (2004), known conflicting area relationships within existing cladograms were ignored (i.e. phylogenetic diversity accounts for area relationship). If conflicting area relationships are ignored, then Australasia appears to be a 'natural' region as in Holt *et al.* (2013). What if we redrew the boundaries of Australasia? Just as dinosaurs would become monophyletic if we included birds, could we not include all the areas that would make Australasia a natural region? The analysis by Parenti and Ebach (2009) would mean we include parts of Africa. The analysis by Sauquet *et al.* (2012) and Phillips *et al.* (2010) would mean we would include the southern part of South America, Papua and New Caledonia. Combine these together and we get an area that resembles Gondwana. Is a monophyletic Australasia equivalent to Gondwana?

The term 'Gondwana' seemingly stirs up much debate, particularly among New Zealand biogeographers (e.g. McGlone 2005; Waters and Craw 2006). The reason, at least from their perspective, is that the default distribution mechanism in biogeography is vicariance and that clashes with the neodispersal meta-narrative, namely, biogeography is nothing more than long-distance dispersal.[57] Even if we exclude vicariance as a plausible mechanism, the fact that a monophyletic Australasia encompasses a 'Gondwanan' distribution is difficult to deny. If the cladistic biogeographic meta-narrative states that on the one hand every taxon is endemic to a single area and, on the other, that closely related taxa evolved near each other, then you would expect a monophyletic Australasia to encompass neighbouring areas over time. If we invoke Sclater's 'exception to the rule' as the default explanation, then we would find that closely related taxa would inhabit areas further away. Looking at the geological evidence, we know that Australia, New Zealand, Africa and South America were geographically closer to each other the further back we go in time. If neodispersalists are correct, then over time we would find that closely related taxa would gradually be found further away as the drifting of continents would mean long-distance dispersers would occupy more distant areas. But would there be a pattern? Neodispersalist say 'yes'. Dispersal corridors between two or more areas would mean that different types of taxa would follow the same dispersal route, leading to geographical congruence. For the sake of the argument, let's accept this as a 'plausible' narrative. What these corridors would reflect would be an extension of one area to another, say of a continent to an oceanic island. If we see this being about areas,

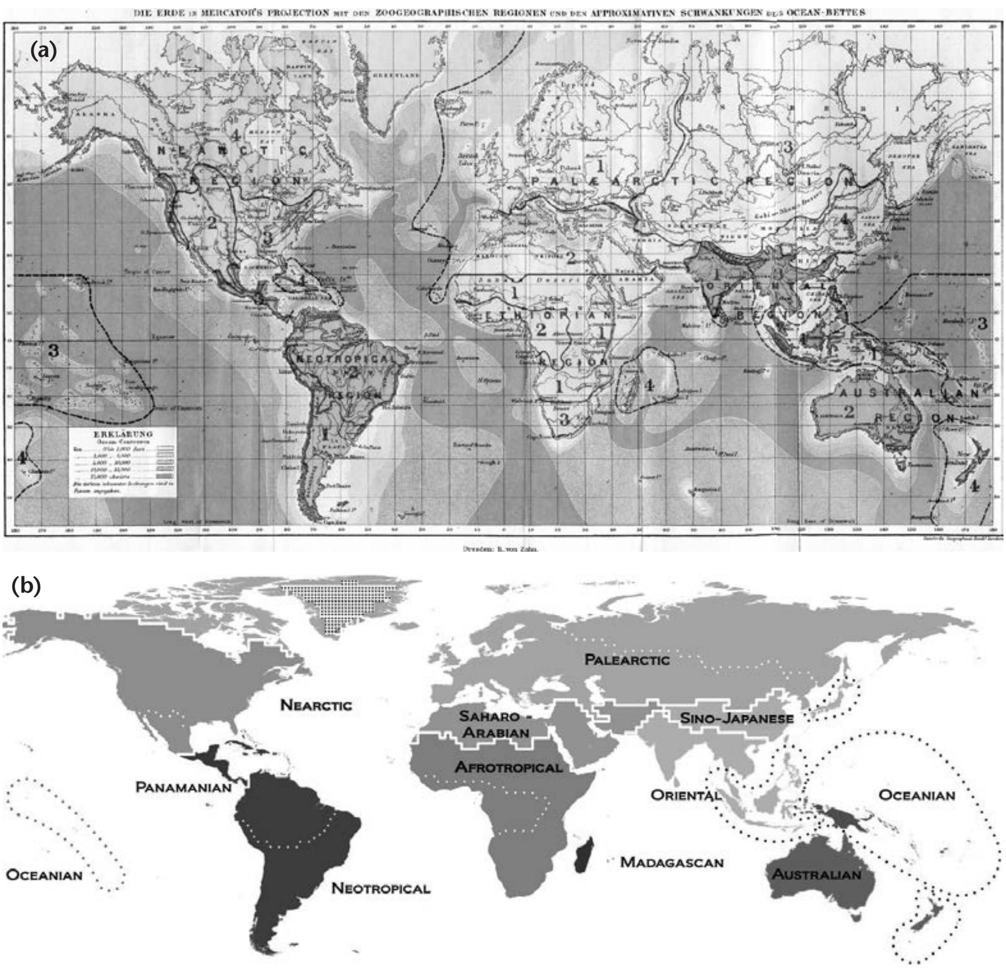


Fig. 7.5. A comparison between (a) *The Geographical Distribution of Animals* (Wallace 1876). Note this is the 1876 German edition. Image: http://upload.wikimedia.org/wikipedia/commons/2/2c/Wallace03.jpg; (b) map of the terrestrial zoogeographic realms and regions of the world (Holt *et al.* 2013, p. 75, Fig. 1).

rather than about dispersal ability, we see that the corridor is nothing more than a taxon's area of distribution. Taxa cannot move outside of their areas of distribution, because the taxon defines its own distribution. If we know, for example, that an iguana has the ability to traverse the Pacific Ocean, then the Pacific Ocean would be part of its area of distribution. If this is true, Sclater's general rule – namely that taxa in neighbouring areas are more closely related to each other – holds true. Neodispersalists are simply ignoring areas of distribution and focusing on dispersal. Treat major disjunct distributions as areas, then the problem is easier to resolve. If a monophyletic Australasia encompasses areas formerly part of Gondwana, then 'Gondwanan' becomes a term for identifying Australasia distributions, in the same way birds are described as being dinosaurs.

Framing biogeographic problems using the taxonomy analogy

Throughout this book I have used taxonomy as an analogy for resolving common problems in biogeography, both at the implementation and theoretical levels. Treat biogeography as an area taxonomy, and we dispense with certain assumptions regarding our hypotheses. Discovering natural biotic areas becomes the main focus of our study, while narratives about the distribution mechanisms of our taxa and individual taxon histories become secondary. This is not to say that narratives are bad. Some can be tested and others are untestable. Biogeographic narratives and hypotheses require areas. The use of arbitrary areas only confuses the hypothesis and makes specific hypotheses untestable. Use natural biotic areas and our biogeographic narratives become more plausible and may be open to testing. The reciprocal illumination between the areas and taxa, or taxonomic analogy, can only work if we have a 'common language' (Rosen 1978); that is, a natural classification and a robust approach to find and test our natural classifications. That approach in my view is the cladistic parameter: the search for patterns. Once we have patterns we can derive our narratives (and hypotheses) from them, in the same way we derive multiple phylogenetic narratives from a single cladogram, we derive biogeographic hypotheses from our general areagram. The taxonomic analogy gives us the systematic and stable concept of area monophyly and a natural area classification: namely the areagram of life. Rosen's approach of using the cladistic approach in biogeography has also made it easier to formulate an analytical phase: one that can use criteria to test for plausible narratives. Together this taxonomic analogy serves as a biogeographic work-flow process or schema for biogeographers to create plausible and testable models, ideally being a potential way forward for future biogeographic research.

A biogeographic schema for example would also use the taxonomic analogy to draw equivalences between the problems and solutions in taxonomy and biogeography. For example, fish are a non-monophyletic taxon: one that is need of taxonomic revision. The same is likely true for Australasia. If our biogeographic tests show that Australasia is indeed non-monophyletic, then we can easily revise it in light of new evidence: namely the pattern of area relationships (i.e. area monophyly). The taxonomic analogy serves as a framework for Australasian biogeography. We have the methods and much of the data to establish a biogeographical program to find the natural regions of Australasia, and start to discover the areagram of life.

Glossary

Analytical phase. A phase in biogeography where tests exist to test for plausible narratives within proposed hypotheses. The analytical phase can be implemented as the same time as the descriptive and narrative phases.

Aphyly. A named taxon or area that may or may not be monophyletic; that is, the '-phyly' is unknown. See **non–monophyly**.

Areagram. A statement of **area relationship** depicted as a branching diagram, Venn diagram or as a set of parentheses.

Archipelago. Appendage to a continental landmass that shares a biota or part of a biota.

Area monophyly. A **clade** or set of clades in a general areagram that indicates a natural biotic area.

Area relationship. The relationship of three or more **endemic areas** based on the **taxic relationship** of the **taxa** that inhabit them.

Artificial classification. An arbitrary hierarchy of taxa or areas that does not represent a natural order in the natural world.

Australasia. The biogeographic area encompassed by the Australian continent and offshore islands, New Guinea, the Melanesian Archipelago, New Zealand and several of the subantarctic islands (The Snares, Auckland, Campbell and Chatham Islands) (*sensu* Australian region Morrone 2015). While biogeographers worldwide use Australasia to denote all or some of the areas above, it is not known whether Australasia is a natural or artificial area.

Bioregionalisation. An area classification.

Biota. The organisms that live in a natural **biotic area**.

Biotic area. A natural region that is endemic to many unrelated organisms.

Branching diagram. A hierarchical diagram consisting of three or more homologues, taxa or areas. Branching diagrams are often used to depict phenograms, phylogenetic trees or cladograms.

Clade. A group of taxa or areas that are more closely related to each other than they are to anything else.

Cladistic biogeography. An approach in biogeography that equates taxa with areas using the **cladistic approach**.

Cladistic parameter. A framework for natural classification in which homology and monophyly are equivalent parts of a **natural classification**.

Cladistics (cladistic approach). The approach that uses the cladistic parameter to find (or test for) a **natural classification**.

Cladogram. A pattern of taxic relationship, usually depicted as a branching diagram or in a parenthetical format.

Descriptive phase. The phase in biogeography in which taxic distributions and areas are proposed based on measurements and observations.

Dispersal. The migration or movement of an organism away from its centre of origin, to another area in which a new species is derived.

Drowning hypothesis. The theory that New Zealand was submerged during the Oligocene and reemerged as an island that has retained none of its original biota.

Ecological biogeography. The study of vegetation, populations and individuals that live in small areas and have evolved there over short periods of time. Ecological biogeography is reliant on ecological methods and can be considered to be a synonym of ecology.

Element (biogeographic). A taxonomic assemblage typical of an endemic or foreign biota (equivalent to an ancestor in biogeography).

Endemic area. The geographical space occupied by two or more overlapping taxic distributions.

Geographical congruence. A pattern of area relationship; area monophyly. Geographical congruence is evidence for a common history. See **monophyly**.

Geographical paralogy. The duplication of areas in areagrams. In the areagram (A,(A,(B,(B,C)))), areas A and B are geographically paralogous, meaning that only one instance of an area is necessary.

Historical biogeography. The study of taxa (e.g. species, genera, families) that have evolved in regions and/or continents over long periods of time. Historical biogeography is usually reliant on phylogenies and/or on Earth processes.

Holdover. An overlapping geographical distribution of two biota that have different temporal geographic histories.

Homologue. Morphological or molecular part of an organism.

Homology. A statement of relationship between one or more **homologues**.

Hypothesis (biogeographic). A narrative involving an unseen process or event that is responsible for the distribution and subsequent evolution of a taxon or area.

Integrative biogeography. An attempt to integrate as many biogeographic approaches as possible regardless of their purpose, aims or goals. Integrative biogeography is an attempt to support a meta-narrative.

Invasion theory (Australia). The notion that the bulk of the Australian biota has its origins elsewhere (see **elements**), with a minority being a holdover from the Paleogene. The concept supports the notion that the present-day Australian flora and fauna dispersed here from South-East Asia.

Island continent. An island land mass that is part of a continent and a larger biogeographic region. The biota could be partially relict, endemic or dispersed via island hopping or via long-distance dispersal.

Long-distance dispersal. The hypothesised distribution of successive individuals over time across a great geographical distance, usually an ocean.

Mast (multiple areas on a single terminal-branch). A mast occurs when a single terminal-branch in an areagram contains more than one area. Masts are resolved by separately relating each area. A mast is underlined – for example, in the areagram (A(B,C(C,D))), B,C is a mast.

Meta-narrative. A synthesis based on multiple narratives.

Monophyly. A pattern of taxic relationship within a named taxon. Monophyly occurs when two or more taxa are more closely related to each other than they are to any other taxon.

Narrative (biogeographic). An explanation, usually in the form of a process or event, to explain a biogeographic distribution.

Narrative phase. A phase in biogeography in which the distribution mechanisms and events are hypothesised to form a meta-narrative or synthesis.

Natural classification. A taxonomy that is representative of a natural order of taxa or areas.

Node. A junction between two branches in a branching diagram.

Non-monophyly. When a named taxon or area is not monophyletic.

Oceanic island. A newly formed oceanic landmass, or formerly sunken island, which shares its biota with a nearby continent. All taxa dispersed there via long-distance dispersal.

Orthogenesis. The assumption that evolution is driven in part by external (e.g. geography) and intrinsic (e.g. mutation) processes. ‘In the panbiogeographic synthesis, evolution is recognized as having an internal component that produces a tendency for evolutionary change without natural selection being required as a driving force’ (Grehan 1985, p. 174).

Overlap zone. An area where two biota overlap.

Phylogenetics. The study of ancestor–descendant lineages of taxa and their characteristics.

Phylogenetic tree. A hypothetical branching diagram that depicts a lineage.

Taxic relationship. The relationship of three or more taxa based on **homology**.

Taxonomy. The study of biological classification.

Temporal overlap. When the same geographical space is occupied by two biotic areas with different temporally disjunct histories.

Vicariance. When an ancestral area and its biota is broken up into smaller areas that are geographically isolated over time and give rise to new species.

Vicariance biogeography. A term used to describe cladistic biogeographers pre-1990s.

Endnotes

1. Other mechanisms were considered to be far more likely, such as the west wind drift, which 'supplies the only acceptable distributing mechanism … and it would be plainly absurd to postulate land-bridges or continental drift' (Fell 1962, p. 761).
2. To my knowledge, the term 'biogeography' was first used in the New Zealand literature by British-born William Blaxland Benham (1860–1950), Professor of Biology at the University of Otago, Dunedin: 'The study of the geographical distribution of organisms or Biogeography, as it has been called …' (Benham 1903, pp. 319–343).
3. These few branches could be physiology and cell biology. But even so, physiology has been used to describe the different types of dispersal capabilities, such as the winglets on seeds or torpor in lemurs. Cell biology remains perhaps untouched by geographical distribution.
4. For the purpose of this example, I have ignored vestigial wings.
5. Jorge Luis Borges also talks of a 1:1 scale map in his single paragraph story 'On Exactitude in Science', 'The following generations, who were not so fond of the study of geography as their forebears had been, saw the vast map was useless …' (Borges 1974, p. 847).
6. Island biogeography of MacArthur and Wilson is also known as 'insular biogeography' (Whitehead and Jones 1969).
7. In a book review for the journal *Nature*, Colinvaux reaffirms his earlier claim, 'They named a terrestrial unit with characteristic climate a "biome", a name that has stuck, even though it is a mere abstraction' (Colinvaux 2005, p. 479).
8. The original reads: 'Acacia-arten, dem tropisch-afrikanischen Element angehörig, von den südafrikanischen Arten getrennt' (Drude 1890, p. 146).
9. I am uncertain if Burbidge (1960) did attribute all three floristic elements to Hooker (1859). I am, however, certain that Burbidge did not attribute the three floristic elements to Diels (1906) because there is no mention of it. More bizarre is this statement: 'Schwarz (1928) has discussed the phytogeography of the flora of northern Australia with special reference to the plants of Arnhem Land. While much of his data must be regarded as superseded by those available to Specht (1958) it is interesting to see how he distinguishes between the elements represented in the flora' (Burbidge 1960, p. 169). I suspect Burbidge, and other Australian biogeographers such as Crisp *et al.* (1999), may have missed a significant passage in Schwarz (1928), namely: 'Since Diels [1906, p. 36] the Australian floristic elements are perfectly oriented, and his list is still valid today in its entirety. Therefore it is reproduced below with a few minor changes' (Schwarz 1928, p. 84). The original reads: 'Über die Zusammensetzung des australischen Florenelements sind wir seit Diels [1906, p. 36] ausgezeichnet orientiert, und seine Liste gilt such heute noch fast in ihrem vollen Unfang. Darum its es nachstehend, mit wenigen, unwesentlichen Änderungen wiedergegeben (Schwarz 1928, p. 84).
10. The original reads: 'Gut bekannt waren die floristischen Elemente; dagegen wußste man nichts darüber, wie sie sich zum Vegetationsbilde ordneten. Ihre äußeren Affinitäten

hatte schon Hooker gesichtet … Die Analyse der australischen Flora, deren Grundlagen wir Sir J. Hooker un F v. Müller verdanken, ergibt drei Haupt–Elemente, die man als australisches, malesisches, antarktisches unterscheidet' (Diels 1906, pp. v and 31).

11. Elements are not always defined in the same way. The 19th century naturalists defined them in terms of their origins (e.g. Indo-Malay element), whereas modern-day researchers define them as vegetation types (e.g. rainforests, Martin 2006) or as individual taxa (Bowman *et al.* 2010).
12. New Zealand biogeographers, however, do not misattribute elements to Hooker, who in his *Introductory Essay to the Flora of New Zealand* does not use the term 'element' to signify a biota.
13. Fleming had earlier defined element as 'the sum total of organisms that came to New Zealand along a given dispersal avenue, but ecological bonds between the different organisms that used the same dispersal avenue are neither implied nor denied. Classification of organisms by dispersal avenues implies their immediate place of origin, but not their ultimate place of origin' (Fleming 1963, p. 15).
14. Craw *et al.* (1999) define a track as '… a line drawn on a map that connects the different localities or distribution areas of a particular taxon or group of taxa … These lines explicitly give shape or expression to the space and time that necessarily intervenes between disjunct localities … The drawing of a track identifies the spatiotemporal coordinates most closely associated with the origin of that distribution. The shape or geometry imparted by these coordinates can then be compared to those of other patterns, and hypotheses or predictions about their origin proposed (e.g. specific historical events or processes)' (Craw *et al.* 1999, p. 20).
15. Hedley (1893a) summarises the earlier invasion theory, 'Superimposed one above another may be distinguished three divisions of Australian life. The earliest is the *Autochthonian*. Possibly this arrived from the Austro–Malayan islands in or before the Cretaceous era, and spread over the whole of Australia. The next is the *Euronotian*. Probably this reached Tasmania from South America not later than the Miocene epoch; many of the original inhabitants, particularly on the east coast, probably disappeared before the invaders. Thirdly, a contingent of Papuan forms seized on the Queensland coast late in the Tertiary, and likewise exterminated their predecessors' (Hedley 1893a, p. 446).
16. Two new Australasian elements, the 'Malesian or Irian rainforest biota and the old Australian Tertiary or Tumbunan rainforest biota' (Schodde 1989, p. 11), were introduced by Schodde and Calaby (1972).
17. In New Zealand the same was true. Bioregionalisation was driven by molluscan workers such as Fischer (1880–1887), Cook (1895) and Solem (1968) (see Climo 1975).
18. Tenison-Woods notes that 'The north-western and western divisions may be considered arbitrary, as of these regions so little is known' (Tenison-Woods 1882, p. 49 footnote*; see also Ebach 2012). Hedley rejected the areas by Tenison-Woods, as 'neither natural nor well-defined, and has been overlooked by Tate, Spencer and other writers on Australian zoogeography. The meaning I attach to "Adelaidean" is not that of Tenison-Woods' (Hedley 1904, p. 880).

19. Smith (1984) does not cite Tenison-Woods (1882), and may not have known of his rare monograph.
20. Australian botanist David Morrison recalls Carolin: 'I was first taught systematics in 1978 in Australia, by the person who seems to have published the first cladistic analysis of any endemic Australian biota (Carolin 1977). So, to me cladistics was "normal science," and it took me some years to find out what people had done before they invented cladistics (and phenetics)' (Morrison 2014, p. 847).
21. Classifying the eucalypts has been an age old problem: 'Considerable thought and much patient experimental investigation has been given to devising schemes for the classification of the 150 species or so of our eucalypts. Every possible aspect has been under consideration – the woodman's, the chemist's, the histologist's, and the systematic botanist's, and, nevertheless, no satisfactory system has been evolved' (Tate 1898, p. 544).
22. In another unfortunate post-production bungle, the paper by Ladiges *et al.* (1995) appeared in print *before* that of Udovicic *et al.* (1995).
23. Many, including myself, have been guilty of confusing transformed and pattern cladistics, particularly in historical treatments. I am grateful to David M. Williams for pointing out this confusion in an earlier draft of this chapter.
24. Humphries had not completely joined the other side for long. While referring to himself as a 'pattern cladist', Humphries still collaborated with numerical cladistics on high-impact projects such as the Angiosperm Phylogeny Group (APG) at Kew Gardens, Kew, UK (APG 1998; Endersby 2001). The APG used numerical methods including Farris' method 'Jac': something that would have been abhorrent to a pattern cladist.
25. Peter Cranston suggested the idea at the Australian National University (ANU) Zoology Department pre-Christmas party in December 1987. The first meeting was held in January at the ANU Staff Club (Old Canberra House) and, the first paper for discussion was '*Nothofagus* and its parasites*:* a cladistic approach to coevolution' by Humphries *et al.* (1986). John Trueman has written an unpublished account of Coopers and Cladistics (Chris Reid *pers comm*. 2015).
26. In 1992 *Systematic Zoology* changed its title to *Systematic Biology*.
27. I attended the Sydney Branch meetings between 1996 and 1999. Influenced by the success of Coopers and Cladistics, I started the Perth Systematics Forum, which ran in 2000 (held at the University of Western Australia). In 2001, I co-founded the Melbourne Systematics Forum with Robin Wilson (Melbourne Museum) and then PhD students Dan Murphy and Rod Jones (School of Botany, University of Melbourne). The Forum is held at the Melbourne Museum and has been running every year since: http://researchdata.museum.vic.gov.au/forum/
28. The Tumbunan and the Irian divisions were first proposed by Schodde and Calaby (1972, pp. 294–295, fig. 14.1).
29. The *Austral Biogeography* volume is a reproduction of the 1991 issue (volume 4, number 1) of *Australian Systematic Botany.*
30. There are a few exceptions, such as Kenneth McNamara (formerly Western Australian Museum).

31. The story of Croizat and his relationship with the AMNH cladists was dramatised by David Hull in his *Science as a Process* (Hull 1988). I refer readers to Grehan (1989) for a more sober account of the exchange between Croizat and Nelson.
32. Craw had personal communication with Croizat in 1976 'about the problems concerning Croizat *et al.* 1974' (Craw in letter to Peter Weston dated 18th May 1982).
33. The authors include Charles A. Fleming, J.D. Coulter, Q.W. Ruscoe, E.J. Godley, P.C. Bull, A.H. Whitaker, R.M. McDowall and B. Reid.
34. Compare this with Allen Keast's review: 'So fascinating and well written is the account that it is probably the best in the W. Junk regional series' (Keast 1977, p. 112).
35. In Australia cladists such as Roger Carolin, Jim Armstrong and Judy West had an interest in vicariance biogeography.
36. Craw originally intended to work on the taxonomy of geometrid moths.
37. In reading correspondence from Craw, it is evident that he did not consider vicariance biogeography '… the methodological child of panbiogeog[raphy]' (Craw in letter to Peter Weston 13th September 1982).
38. An article about Frank Climo and panbiogeography appeared in the New Zealand lifestyle magazine *North & South*, 'New Zealanders are in the forefront of international thinking in this field. They publish their findings in an Italian journal, *Revista* [*sic*] *di Biologia*, and write each other extraordinary-looking letters full of diagrams, patterns and imagery. The letters themselves are a challenge to how we imagine scientists think' (McLeod 1989, p. 103).
39. The symposium was organised by Frank Climo.
40. The documentary was shown in New Zealand on the TV program *Science Express* on Tuesday 16 August 1983, on TV One (Grehan *pers. comm.* 2015).
41. The analysis was later dismissed by Sibley and Ahlqvist (1990) as UMPGA analysis alone resulted in the Rhea–Ostrich relationship.
42. Danish botanist Ole Seberg (1986) puts it like this: '… it is beyond question that panbiogeography has inspired the development of vicariance or cladistic biogeography … It suffices to note that the simple, but ingenious, leap-changing Croizat's concept of track into what might be termed the generalised area cladogram – was foreshadowed by Nelson (1973) and finally taken by Nelson and Rosen …' (Seberg 1986, p. 369).
43. Croizat does discuss homology in terms of affinity and analogy.
44. The only specific place Craw claims Croizat discusses a homology concept for biogeography is in the '… entry on p. 572 of Index, "Homologies in dispersal", and compare fig. 6 with fig. 10 … In much of his later work (especially Croizat 1968: 226–257), Croizat also discussed the problem of homology in relation to biogeography' (Craw 1983, p. 432).
45. In proposing a panbiogeographic analysis, Craw would defer to Croizat, even though much of the methodology was his own. For example 'The distribution patterns of these taxa and their relatives [ratite birds, *Nothofagus* and the *Leiopelma* frog] are reexamined using Croizat's panbiogeographic method' (Craw 1985, p. 1). The reanalysis involves the use of areagrams and geograms not present in 'Croizat's panbiogeographic method'.

46. Craw did not stop publishing. Although he returned to publishing *Panbiogeography: Tracking the History of Life* (Craw *et al.* 1999) and a few biogeographical articles (Craw 1992a), he spent time researching society and culture (Craw 1990, 1992b, 1999; Craw and Hubbard 1993) as well as art history (Craw 1993).
47. Heads does discuss current biogeographical methods with empirical examples in the introduction of his two books *Molecular Panbiogeography of the Tropics* (Heads 2012) and *Biogeography of Australasia: a Molecular Synthesis* (Heads 2014). However, panbiogeographic concepts such as geographical homology and area classification are not touched upon.
48. Craw's job was endangered due to a 'letter of reclassification' at the former DSIR (Department of Scientific and Industrial Research) entomology, now Landcare, in 1992 (*The Dominion Sunday Times*, 26 July 1992, 'Top scientist faces redundancy'). Regardless, Craw's reclassification does not explain the drop in scientific publications between 1991 and 1992 (Macfarlane *et al.* 1991).
49. In contrast, compare the demise of panbiogeography in New Zealand with the following text from an up-beat paper by Page (1989) titled *New Zealand and the New Biogeography*: '… New Zealand has become the cradle for the development of some exciting, if somewhat unorthodox ideas on biogeography' (Page 1989, p. 471). One wonders whether the fall of panbiogeography a year later was unexpected.
50. The aversion New Zealand publishers have to panbiogeography is extreme. For example, the Royal Society of New Zealand, which is the main publisher of New Zealand scientific journals, including the *New Zealand Journal of Zoology*, has not published articles on panbiogeography since 1989.
51. Hedley's Melanesian arc or 'fork' can still be seen in modern day literature, such as Solem (1968, p. 242, fig. 8) and Holloway (1984, p. 133, Fig. 1).
52. Although there were some avid supporters in the following 20th century: 'There are entomological reasons for supporting the existence of the Huxley–Hutton Mesozoic Trans-Pacific continent in warm latitudes' (Sloane 1915, p. 140).
53. I am unsure whether Kuschel (1960) means phylogenetic relationships in terms of phylogeny rather than areas sharing taxa.
54. The term 'Moa's Ark' was a natural history television series produced by Natural History New Zealand and shown on TVNZ in 1990 and hosted by David Bellamy. A book also accompanied the TV series (Bellamy *et al.* 1990). The term, however, was most likely first used in the book *Te moa–the Life and death of New Zealand's Unique Bird* (Brewster 1987), and eventually made it into the scientific literature (e.g. Knapp *et al.* 2005; Trewick *et al.* 2007; Tennyson *et al.* 2010).
55. Croizat coined the 'New York School of Zoogeography' (Croizat 1958, p. xi; see Nelson and Ladiges 2001, p. 397).
56. Some New Zealand biogeographers, such as Graeme Caughley, did resist the urge to name centres of origin, 'centres of evolution tend to be near the larger universities. Stated in this way, these axioms are obviously absurd and would mislead no-one. But the

student of zoogeography must continuously guard against being seduced by them in their more plausible guises' (Caughley 1964, p. 56).

57. Ebach and Williams (2016) have shown that this claim is false. In fact, dispersal has been the default narrative in biogeography since the mid-18th century. The notion that vicariance dominated biogeography is part of the neodispersal meta-narrative.

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