

Chapter 3

Carving up Australasia: the quest for natural biogeographic regions

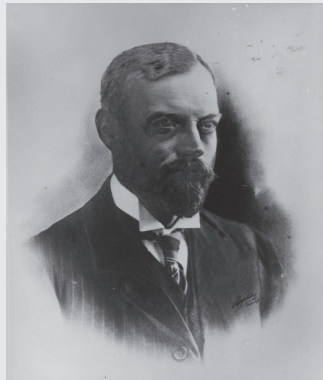
Most systematists will squirm at inferences derived from a non-monophyletic or artificial taxon. The importance of monophyly is critical to understanding the natural world and drawing inferences about past processes and events. Since the early 19th century, plant and animal geographers have also been 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 Ornithogæan (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, p. 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

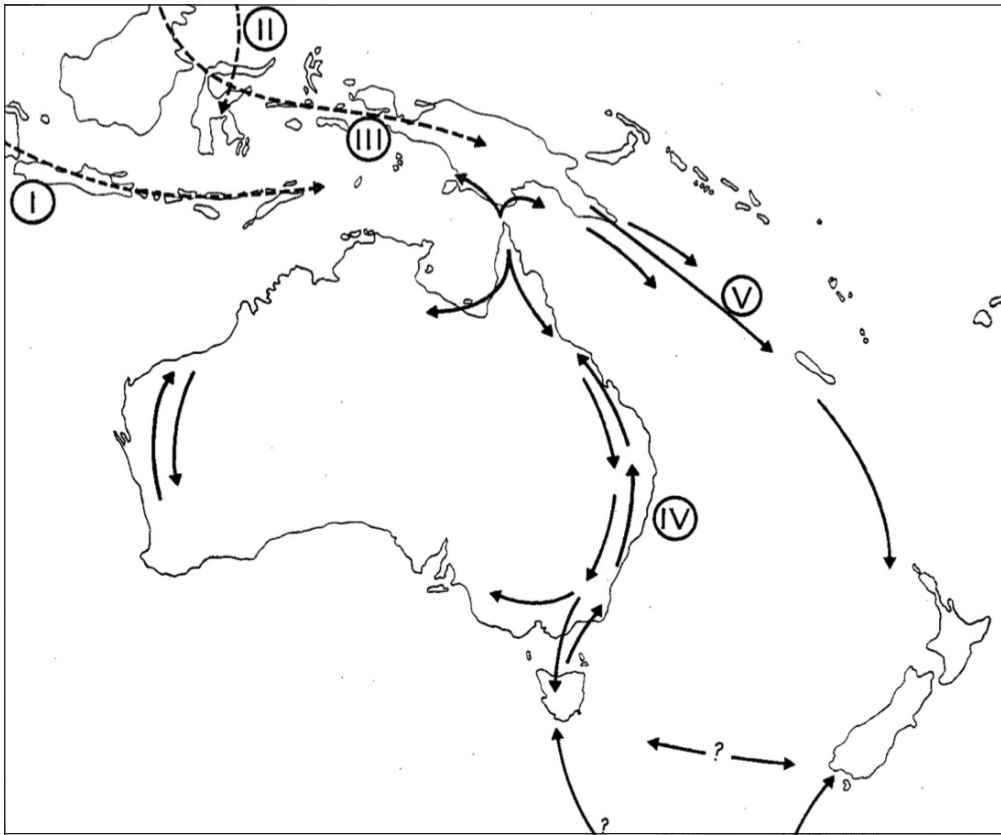


Fig. 3.1. 'Migration tracks affecting the Australian Region. (I) Sumatra track; (II) Luzon track; (III) New Guinea track; (IV) Eastern Australia track; (V), New Zealand track ... Movement within the Australian Region has undoubtedly been in more than one direction and there has been interchange with 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

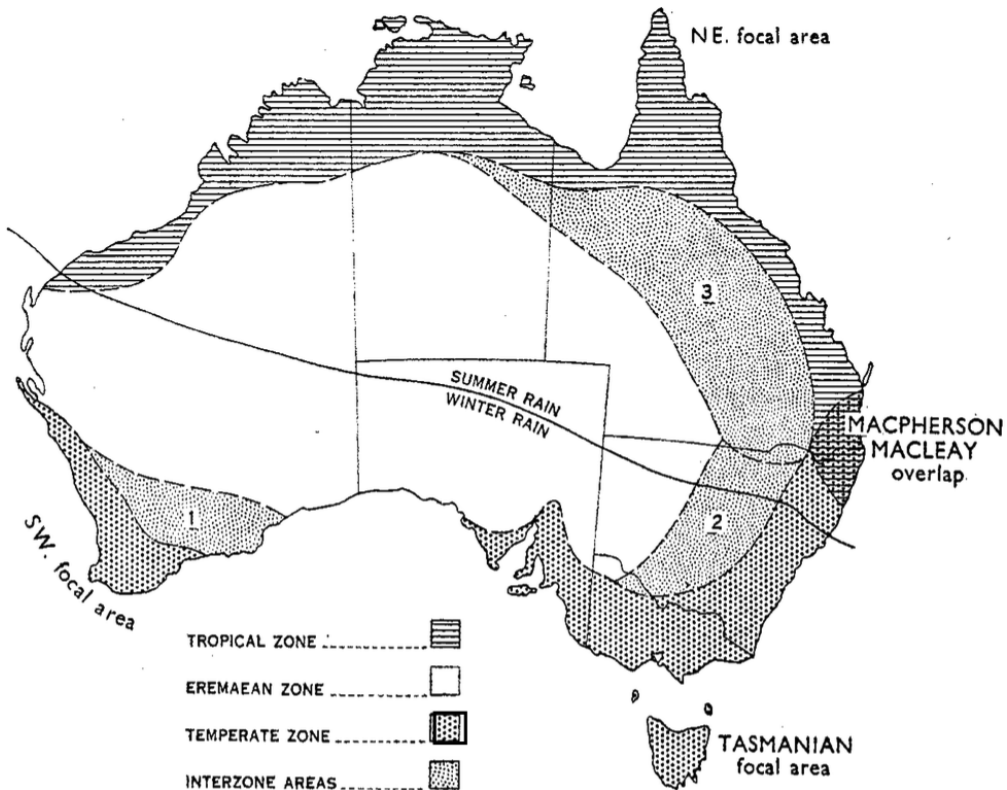


Fig. 3.2. 'The principal floristic zones of the Australian Region' (Burbidge 1960, p. 79, Fig. 1).

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 southwest 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 phylogenetic 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, p. 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-

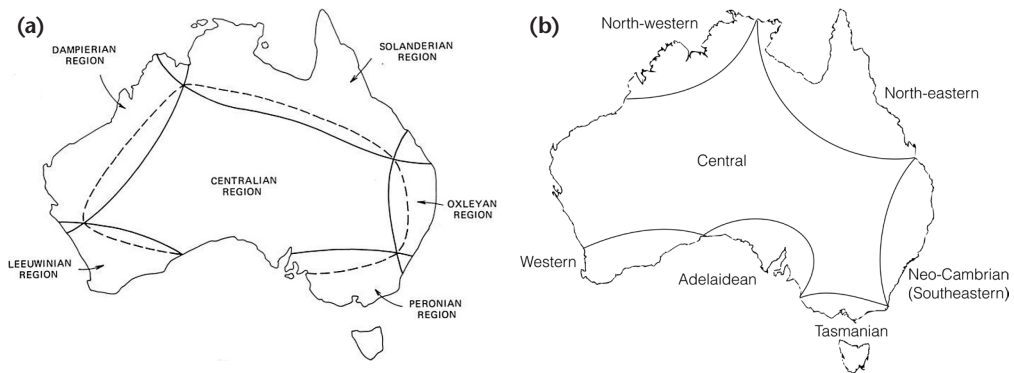


Fig. 3.3. A comparison of (a) ‘The six faunal regions of Australia for the native land mollusc fauna’ (Smith 1984, p. 179, Fig. 1) with (b) the seven zoogeographical areas proposed by Tenison-Woods (1882, pp. 48–49), here drawn for the first time. Tenison-Woods did not assign an area to the central part 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
Veronellidae	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