# 5. MAJOR COMPONENTS AND DISTRIBUTIONS OF THE TERRESTRIAL FAUNA

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## INTRODUCTION

The Australian terrestrial environment is diverse. The climate varies from moist tropical and monsoonal in the north to arid in the centre and west, Mediterranean in the southwest and cool temperate along the southeastern seaboard, grading to alpine at the higher elevations. Accordingly, vegetation ranges from tropical and temperate rainforest through various forest and woodland types to savannah, grassland and desert scrub (Specht, 1981; Chapter 4, this Volume).

Despite this diversity, many of the climatic and vegetative regions are peripheral and the vast majority of the continent is semi-arid or arid. Widespread aridity is probably the predominant single feature that most characterizes Australia. It probably began in the northwest or the centre in the Tertiary and progressively spread to envelop much of the central part of the continent (Beard, 1976; Lange, 1982).

Associated with aridity is the prevalence of fire, a phenomenon that probably began to be of major ecological importance in the Miocene, as progressive aridity developed. Fire constituted part of the environment in which Australia's biota evolved and it still has a profound effect (Recher & Christensen, 1981).

The Great Dividing Range provides some topographic diversity on the eastern coast, but the lofty mountains of other continents are absent and the general character of the landscape is one of slight relief (Nix, 1981).

Another characteristic of the Australian environment is the general deficiency of nutrients (especially phosphates) in the soils, a condition to which the Australian sclerophyllous biota is highly adapted (Beadle, 1966; 1981). The fauna of Australia must be viewed in the perspective of these features.

## GEOLOGICAL HISTORY

Throughout its geological history, Australia has been partially covered by seas, has moved through different latitudinal belts, suffered changes in climate and has been variously isolated from, been in proximity to or formed part of other land masses. This history has resulted in an extant fauna of widely different geographic origins, modes of adaptation and lengths of residence in Australia.

### Pangaea

In ancient times, all the continents were aggregated as the single landmass of Pangaea (Fig. 5.1). By the middle of the Jurassic (about 160 mybp), however, the large Tethys Sea partly divided Pangaea into a northern supercontinent called Laurasia and a southern one, Gondwana. Laurasia later fragmented into North America, Europe and part of Asia and Gondwana into the remaining more southerly land masses (Estes, 1983).

### Gondwana

Gondwana remained intact until the Early Cretaceous. At that time Australia was broadly in contact with Antarctica, more narrowly so with India and, indirectly through those two continents, with South America and Africa. There also were small landmasses included in Gondwana: New Zealand, New Caledonia, Madagascar and some of the Pacific islands (Fig. 5.2).

There was undoubtedly regional faunal divergence within Gondwana, just as there is today in different regions of any continent. Those parts most distant from the regions now represented by Australia would more likely have shown greater faunal divergence from Australia than geographically closer areas, subject of course to modification by effects of topography and of climatic or vegetational zonation within the super-continent.

Whatever these pre-breakup faunal geographical differences, the sequence in which various land masses fragmented would have influenced markedly the degree of faunal relatedness among the present derivative continents. India was the first to break away, northwards at the beginning of the Cretaceous (about 140 mybp). Africa followed soon thereafter (about 120 mybp). New Zealand moved away about 80 mybp leaving an axis of Australia-Antarctica-South America (Powell et al., 1981; Keast, 1981c; Archer, 1984a). Australia did not break away from Antarctica until about the Late Paleocene (less than 60 mybp). From this sequence, one would expect that Australia would have the least faunal similarity (among taxa of Gondwanan origin) with India and Africa, but with greater affinity in increasing order with New Zealand, South
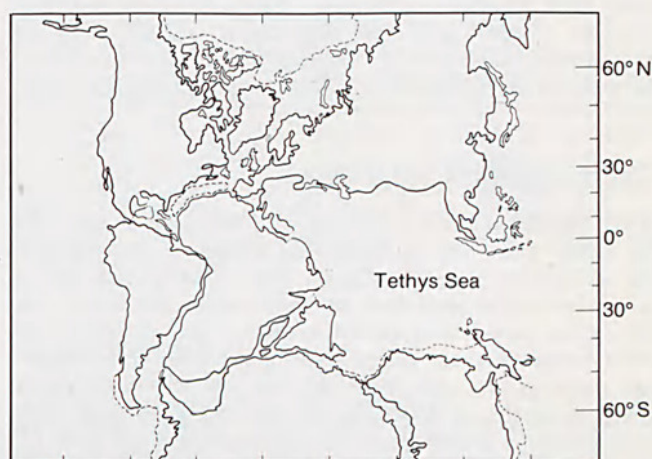


Figure 5.1 The continent of Pangaea as it appeared in the Early Jurassic (Mercator Projection). Dashed outline represents outlines of ancient continents. Solid lines indicate present continental outlines. Dot indicates South Pole. Only broad outlines indicated; outlines of epicontinental seas or of possible archipelago of Antarctic mainland ignored.                                            [L. Bridges]
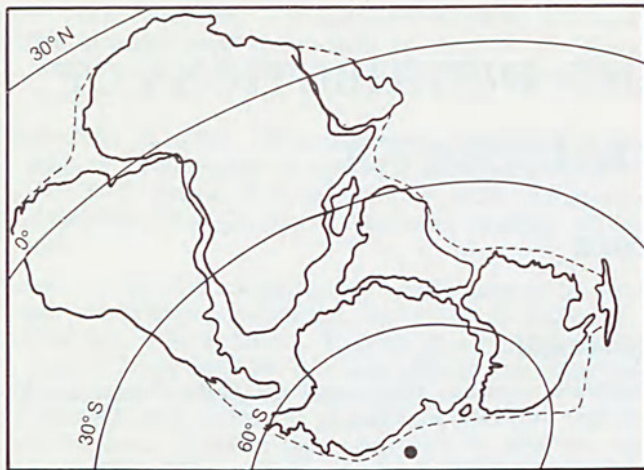
Figure 5.2  Gondwana as it appeared in the Early Cretaceous (Oblique projection). Dashed outline represents outlines of ancient continents. Solid lines indicate present continental outlines. Dot indicates South Pole. Only broad outlines indicated; outlines of epicontinental seas or of possible archipelago of Antarctic mainland ignored.                                                    [L. Bridges]

America and Antarctica. The special circumstances of Antarctica, now largely ice-covered and inimical to most terrestrial life, combined with a rather meagre available fossil record, make a test of the degree of its relationship with Australia tenuous. These circumstances, however, do not apply to the other continents derived from Gondwana and, in general, the predictions are fulfilled. Australia and South America have the greatest faunal affinity, despite having been on opposite sides of Gondwana. There is less faunal similarity between Australia and either India or Africa. There are, however, particular groups in which Australia shows greater affinity with Africa and India than with other southern continents. These may have been distributed only in the northern part of Gondwana. If so, present affinities may reflect ancient regional distributional patterns within Gondwana. Keast (1981c) suggests that when Australia began to drift northward it contained the vestiges of an older (Paleozoic and Mesozoic), northern, subtropical, Gondwanan biota with African and Indian relationships and a newer (Eocene), southern and more cold-adapted one with affinities with Antarctica and South America. These various continental relations are discussed in relation to particular taxa below.

## The Northward Migration

After separation from Antarctica, Australia spent more than 20 million years moving northward through a span of about 30° of latitude (Fig. 5.3) (Crook, 1981). During that time, it was relatively isolated from all other major landmasses and would not have been expected to receive new terrestrial taxa from outside sources except by long-distance oceanic dispersal. Consequently, one would predict that during the northward movement of Australia, the land fauna would be characterized by a divergence of the Gondwanan fauna from that of other southern continents, with little or no input from elsewhere. Faunal change would have occurred mainly by *in situ* evolution rather than from exchange with other places.

The extent of change in the isolated, ancient fauna may have been rather great. The movement of Australia northward was accompanied by passage through different climatic zones and there were major alterations in the patterns of wind systems and the circulation of ocean currents.

The Paleocene climate of Australia, while the latter was connected to Antarctica or shortly after separation, is problematical and opinions vary from cool to warm temperate with a high rainfall (Kemp, 1981) to subtropical or tropical (Lange, 1982). During the Eocene, Australia maintained widespread humid tropical conditions, even in the south, but cooled toward the end of the epoch. The Oligocene in Australia was characterized by marked cooling, especially at high latitudes, as well as by a reduction in rainfall. Parts of Australia probably were relatively arid. In the Early Miocene there was a warming; conditions were relatively moist. In Middle to Late Miocene (about 12 to 15 mybp), however, there was a rapid expansion of the Antarctic ice sheet. Conditions became colder and rainfall decreased; central and northwestern Australia became dry. In the Pliocene, there were wide fluctuations in climate. There seems to have been a brief, warm, moist period in the Early Pliocene, followed by progressive aridity and perhaps coolness over most of the continent, with wetter and warmer conditions perhaps persisting in southern coastal regions. The Pleistocene saw worldwide fluctuation in sea-level and climate associated with alternating periods of glaciation (glacials) and glacial retreat (interglacials) at higher latitudes and altitudes. In general, the aridity of the Late Miocene and much of the Pliocene continued through the Pleistocene, although there was considerable fluctuation in climate, from wetter and warmer interglacial conditions to cooler and drier glacial ones (Bowler *et al.*, 1976; Frakes *et al.*, this Volume; Galloway & Kemp, 1981).

Associated with the rather rapid fluctuations in climate in the Tertiary and Quaternary were corresponding changes in vegetation (Smith, 1982; Lange, 1982; Singh, 1982). During the earlier, warm and moist periods, tropical and subtropical rainforests were widespread in Australia, but temperate forests and rainforests predominated in the cooler moist periods. With the generally progressive aridity in the Tertiary, there was a shift to grassland and xeric vegetation, with pro-



Figure 5.3  Position of the southern continents in the Eocene (South Polar stereographic projection). Arrows indicate paths of movement of continents. Dashed outline represents outlines of ancient continents. Solid lines indicate present continental outlines. Dot indicates South Pole. Only broad outlines indicated; outlines of epicontinental seas or of possible archipelago of Antarctic mainland ignored.                                                    [L. Bridges]

nounced regional differences (Lange, 1982). Aridity was most pronounced in the centre and west and moister conditions prevailed toward the eastern, southeastern, southwestern and part of the northern periphery. All of these climatic and vegetational changes undoubtedly affected the adaptive radiation and evolution of the Australian fauna.

## Contact With Asia

With the approach of Australia towards southeastern Asia in the Miocene, the long period of isolation came to an end. As the distance between the two plates closed, the likelihood and frequency of overwater dispersal of fauna would have increased; one would predict an increasing impact of the Asian fauna upon the Australian one.

The marked climatic and sea-level fluctuations of the Tertiary and Quaternary undoubtedly influenced the immigration of Asian fauna into Australia, the likelihood of their establishment upon arrival and the subsequent course of their distributional spread and adaptive radiation.

Based on the above geological scenario, one would predict that the Australian terrestrial fauna is a mixture of two major elements, an ancient one derived from Gondwana (and with an affinity with South America) and a vastly more modern assemblage with southeastern Asian affinity. This theory has the support of data from various taxa.

## THE FAUNAL ELEMENTS

The present terrestrial faunal elements in Australia can be divided into five categories. The oldest two contain those taxa that are relicts from former, larger continents and are referred to as the Pangaean Element (Archaic Element) and the Gondwanan Element (Old Southern Element).

Those more recent taxa with an Asian origin can be subdivided according to the time of their arrival in Australia. The oldest members of this group began to appear in the Tertiary fossil record and, therefore, have had considerable time to undergo adaptive radiation within Australia. These are designated as the Asian Tertiary Element. Later arrivals, in the Pleistocene and Recent, although of ultimate Asian derivation, primarily have a more specific local origin such as New Guinea or Timor. They will be called the Modern Element.

The fifth category, the Introduced Element, includes those species introduced by man. Obviously, these are newcomers to the Australian scene and have not adaptively radiated within Australia. Their distribution and success depends partly upon the extent of their preadaptation to existing local conditions rather than upon evolution in an Australian historical and climatic context and partly upon human modification of Australian environments. Their regions of origin are various.

## Pangaean Element (Archaic Element)

There are Australian animal groups that are represented in the fossil record of various continents, including northern ones, prior to the mid-Jurassic break up of Pangaea, or whose present distribution and primitive status suggest that they were distributed widely in Pangaea and that their present occurrence in Australia dates from the time Australia was a part of Pangaea. A continuous residency in Australia since Pangaean times is implied. These animals constitute the most ancient of the terrestrial faunal elements of Australia. Often, their worldwide distribution is disjunct and isolated

relicts occur in widely separated localities on different continents, extinctions having long since occurred in the intervening areas.

If extinction of a Pangaean group was widespread, leaving representatives on only a few southern continents, and if that group was soft-bodied and not easily fossilized, there might be difficulty determining if that group was part of the Pangaean rather than the Gondwanan Element. The Onycophora, for example, has no fossil record and is now primarily on southern continents or peripheral to them. Their primitive structure and undoubted antiquity place them in the Pangaean Element. Other Australian groups of Pangaean origin are the Symphyla, Diplura, Blattodea (cockroaches), the relict ant *Nothomyrmecia*, the Tasmanian endemic spider family Hickmaniidae, mecopterans of the family Meropeidae, the fly genus *Nemopalpus*, the beetle genera *Cupes* and *Rhysodes* (Mackerras, 1970) and the earthworm tribe Acanthodrilini (Main, 1981b). Note that many of these examples are at the higher taxonomic levels.

The distribution of Pangaean taxa within Australia has no consistent pattern. Time, subsequent adaptive radiation into new habitats and extinction over large parts of the continent have obliterated original distribution patterns, except perhaps for some relicts maintained in ancient refugia.

## Gondwanan Element (Old Southern Element)

Several animal groups (1) have fossil records extending back to Gondwanan times, (2) have their closest relatives in other continents of Gondwanan origin with no, or very distant, relatives in Asia or other northern continents, (3) are primitive and found only in Australia or (4) have some combination of the above. Examples are marsupial mammals, ratite birds, chelid turtles, diplodactyline geckos, megascolecine earthworms, terrestrial molluscs of the families Athoracophoridae, Cystopeltidae, Megaspiridae, Rhytididae, Bulimulidae and Acavidae, spiders of the taxa Hexathelinae, Migidae and Actinopodidae, many insects, the scorpion genus *Cercophonius* and several genera each of Opiliones and Pseudoscorpionida (Mackerras, 1970; Main, 1981c).

In contrast to the Pangaean fauna, many of the Gondwanan taxa are at the familial or generic level, rather than at higher ones.

The Gondwanan Element entered and developed in Australia at a time when the environment was relatively cool and humid. There has been considerable subsequent adaptive radiation and a number of taxa has become adapted to drier regions (for example, many marsupials, the mygalomorph *Missulena*, the snail *Bothriembryon*, some dynastine beetles, the pseudoscorpion genus *Austrochorus*) (Main, 1981c) or have invaded the tropical north. Many of the more sedentary and evolutionarily conservative taxa, however, tend to occupy the cooler, more humid regions in the southern part of the continent.

## Asian Tertiary Element

Presence of a particular Asian taxon in Australia does not necessarily indicate a single entry and subsequent adaptive radiation from one established species. Nor is it likely that at any time in history was there a mass flow of all species of Asian taxa into a newly accessible Australia. The vagaries of overwater dispersal probably acted as a species filter.

As the Australian and Asian tectonic plates closed during the Tertiary, finally abutting, opportunity for invasion of Australia by an entirely new fauna became possible. This was, of course, not a momentary event. Continental drift is a very slow process, in the order of only about 60 mm per year

(Archer, 1984a). One would expect that with closer approach there would be increasing frequency of overwater transport, the incidence varying greatly among taxa depending on their vagility and resistance to the conditions of aerial or flotsam transport. Overwater dispersal is fortuitous, relatively rare and, for a given taxon, may occur at widely spaced intervals. An early immigration and establishment by a particular taxon thus may have resulted in rather extensive adaptive radiation before a second invasion by another member of that same taxon. For a higher taxon (say family), there may have been multiple invasions, widely spaced in time and with the degree of speciation and adaptive radiation decreasing from the older to the newer immigrations. The older and more widely separated the different immigrations, the more easily can they be distinguished. With close contact between Asia and Australia and increased frequency of faunal exchange, such distinctions would become blurred. Examples of the Asian Tertiary Element include most families of lizards and snakes, the conilurine rodents, many birds, buthid and scorpionid scorpions, theraphosid spiders and many insects.

## Modern Element

Whereas the break between the Gondwanan and Tertiary Asian Elements involves a gap of more than 20 million years, the distinction between the Modern and Tertiary Asian Elements, which are merely opposite ends of a continuum, is less marked. The separation, nevertheless, is useful and distributional patterns of the two elements may be quite different.

Taxa of the Modern Element have scarcely diverged, if at all, from their New Guinean or Indonesian relatives. Where there is divergence, it is usually only at the specific or subspecific level.

Selected examples include the ranid frog, *Rana daemeli*, the turtle *Carettochelys insculpta*, native rats (*Rattus*) and the Rainbow Bee Eater (*Merops ornatus*) as well as various spiders and insects.

Some modern immigrants with great powers of overwater dispersal, such as small arthropods carried as aerial plankton by wind, may come from sources other than Asia.

## Comparison Of Elements From The North

One of the distinctions that might be made is that the oldest Asian immigrants have widespread Asian affinities. These sometimes are called the Old Northern Element and may be difficult to distinguish in some cases from Pangaean taxa. Later immigrants have a more restricted relation with the oriental part of Asia and are called the Oriental Element. By contrast, the Modern Element usually has a relationship specifically with (1) the secondary radiation that centred in New Guinea and whose Australian representatives occur in northeastern Queensland or only on Cape York or with (2) the Indo-Malaysian fauna, with the Australian representatives occurring in northwestern Australia and/or the tropical Northern Territory (Fig. 5.6).

There is good evidence in various taxa for successive waves of immigration with each wave having undergone different degrees of adaptive radiation.

Some of the presumably older taxa entered from the north, spread over the continent and then underwent adaptive radiation, often from secondary southern or central centres. A later wave of immigration by related taxa may not have spread so far or radiated to such a great extent, maintaining their ecological affinities with tropical conditions. Competition between members of the successive waves also may have had a limiting effect on distribution. The result is that some

of the older taxa of Asian origin are more southerly in distribution in Australia and have their greatest species richness there. Related taxa immigrating later are restricted to, or have their greatest diversity in, the north.

**Reptiles.** Australian representatives of the lizard families Agamidae and Scincidae and the snake family Elapidae have radiated secondarily from southern and Eyrean centres, whereas most varanids have remained primarily northerly in distribution (Cogger & Heatwole, 1981). Cogger (1961) postulates four agamid invasions of Australia, all via New Guinea, the first in the mid-Tertiary (*Moloch*), the second in the Pliocene (most of the Australian agamid genera) and the final two relatively recently. Those of Tertiary origin are adapted primarily to arid and semi-arid conditions, whereas the later invaders are found only in the wet, forested parts of eastern Australia. Witten (1983) recognizes only two groups, an older radiation and a group of newer arrivals. The varanids probably first entered sometime after the lower Miocene and radiated as the subgenus *Odatria* (of the genus *Varanus*) and its derivative *gouldii* species-group and were followed later, perhaps in the Pleistocene, by the *indicus* group (King & King, 1975).

**Drosophilids.** The fruit-fly subgenus *Scaptodrosophila* entered Australia from the north, but underwent speciation in the south and now is distributed there. Later subgenera of the genus *Drosophila* to arrive remained northerly in their distribution (Parsons & Bock, 1981).

**Lepidoptera.** There was a number of northerly incursions of papilionoid butterflies. Of the Nymphalidae, the subfamily Satyrinae probably entered first, as it has several southern centres of high species density, especially in Tasmania and the southeastern alpine and subalpine regions (Kitching, 1981). In contrast, the Nymphalinae is represented poorly in the south, but has high species densities in the north and may have resulted from a later wave of immigration. The families Riodinidae and Libytheidae are represented only by one species each in the far northern regions and must represent still later intrusions. The most recent immigrants are various species which have northern extralimital distributions as well as occupying parts of northern Australia. Examples are *Cethosia penthesilia* (Indonesia to northern Australia) and *Tellervo zoilus* (New Guinea to Cape York).

**Muridae.** Native murid rodents seem to have reached Australia in three waves (Hand, 1984). The first rodents are referable to the tribe Conilurini which arrived in the Pliocene and subsequently radiated substantially in Australia (sometimes denoted "Old Endemics"). The second wave included the tribes Hydromyini and Uromyini which apparently radiated in New Guinea and then entered Australia within the last two million years. The genus *Rattus* subsequently entered within the last million years and diverged into the modern endemic species of this genus.

The older, southern taxa of Asian origin tend to have distributional ranges with a greater similarity to those of Gondwanan origin than to those of later Asian immigrants. They can be distinguished primarily by whether their phylogenetic affinities are with Gondwanan or Asian taxa.

To place successive waves into precise time scales is not always possible, but only relative to each other. The older ones almost certainly occurred in the Tertiary or earlier; the later ones may have been Tertiary or have occurred later and, thus, spill over into the Modern Element (see below). A major point of controversy at the present time is whether particular immigrations, and divergences within taxa, date back only to the Pleistocene changes in climate and sea-level or whether they reflect Tertiary events.
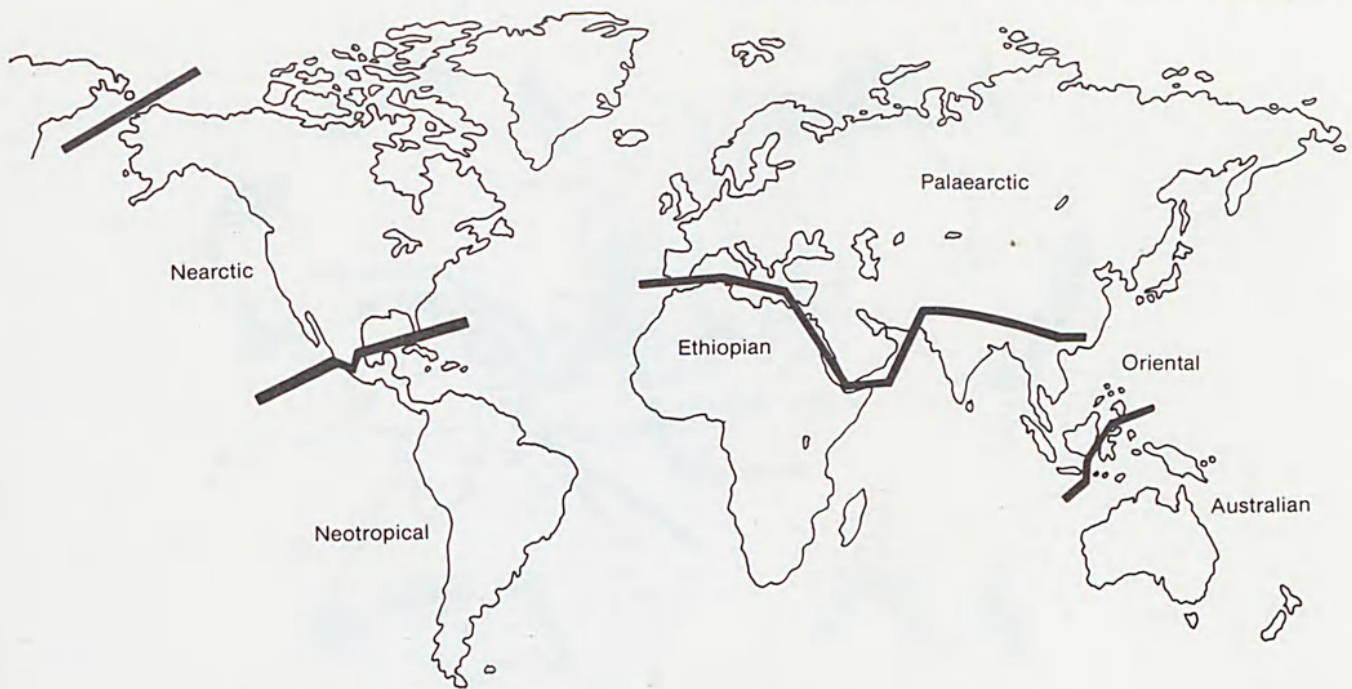
Figure 5.4 Zoogeographic regions of the world.

[L. Bridges]

Many of the affinities between the Asian fauna and Australian taxa of the Asian Tertiary Element are at the familial or generic level.

## Introduced Element

The history of arrival and spread of the recent anthropochorous element is dealt with in Chapter 11 of this Volume.

## DISTRIBUTIONAL PATTERNS

Each species has limits to its geographic distribution. The limiting factors may differ on the various edges of its range. One of the tasks of zoogeography is to identify what those limiting factors are and how they operate upon the species in question. The boundaries imposed by limiting factors may change in time and the distributions of species expand or contract accordingly. In extreme cases, extinction may occur. To assess the role of such changes upon the distributions of individual species is of considerable ecological interest and, if a species is of economic, medical or conservational significance, there may be practical importance as well. Valuable though such autecological information may be, it is important to try to generalize about animal distributions and to see if there are consistent patterns that can be interpreted in historical or ecological terms. Are there recognizable faunal regions in which the inhabitants are linked by similar past history or present environment? Or, alternatively, are species distributed each according to its own response to environment and history, but in a random way with respect to other species?

Of the six world Zoogeographical Regions (Fig. 5.4) the largest is the Palaearctic Region which includes Europe and most of Asia. The Nearctic Region consists of North America. These two together are often referred to as the Holarctic. South America and Central America collectively make up the Neotropical Region. Africa is the Ethiopian Region. The Oriental Region consists of India, southeastern Asia, the Philippines and most of the Indonesian archipelago. The Australian Region includes the rest of that Archipelago, Australia, New Guinea and New Zealand, with declining affinities outward into the Pacific islands.

There are broader transition zones between regions than lines drawn on a map would suggest. Northern Africa and the Arabian Peninsula represent a transition between the African and Palaearctic Regions. Central America shows a grading of fauna between the Nearctic and Neotropical Regions and there is some overlap between the Oriental and Palaearctic Regions (Darlington, 1963).

At one time, the boundary between the Oriental and Australian Regions was considered a sharp one, represented by the Wallace Line (Fig. 5.5). Different authorities, however, have drawn the Wallace Line rather differently and several other lines, equally believed to separate the two regions, have been drawn by other zoogeographers (Muller Line, Weber Line and Lydekker Line) (Muller, 1974). The position of these lines depends on the dispersal abilities and ecological attributes of the taxa on which they are based and no single line serves equally well for all taxa. It is best not to think of a discrete boundary between these two regions (Keast, 1981c; Cox et al., 1973), but rather to consider the area between the easternmost (the Lydekker Line) and the westernmost (the Wallace Line) of the proposed lines as a broad transition zone (Fig. 5.5) sometimes called Wallacea. The Australian faunal influence declines westward in this zone and the Oriental one attenuates eastward; the limits vary among taxa.

New Guinea occupies a special place in this scheme. When the Australian and Asian Plates collided, the leading edge of the former was the southern part of the island of New Guinea. The central mountains originated as a result of a collision of the two Plates in the Miocene and the entire mass pushed against some of the outlying islands of the Asian Plate (the Torricelli and Finisterre Islands) and incorporated them into the northern part of New Guinea. Thus, New Guinea had a three-fold origin: part of the old Australian Plate, old outlying Asian islands and newly formed mountains. The former two components already would have had their resident faunas, providing a mix of the two regional elements; the young mountains provided vacant, qualitatively
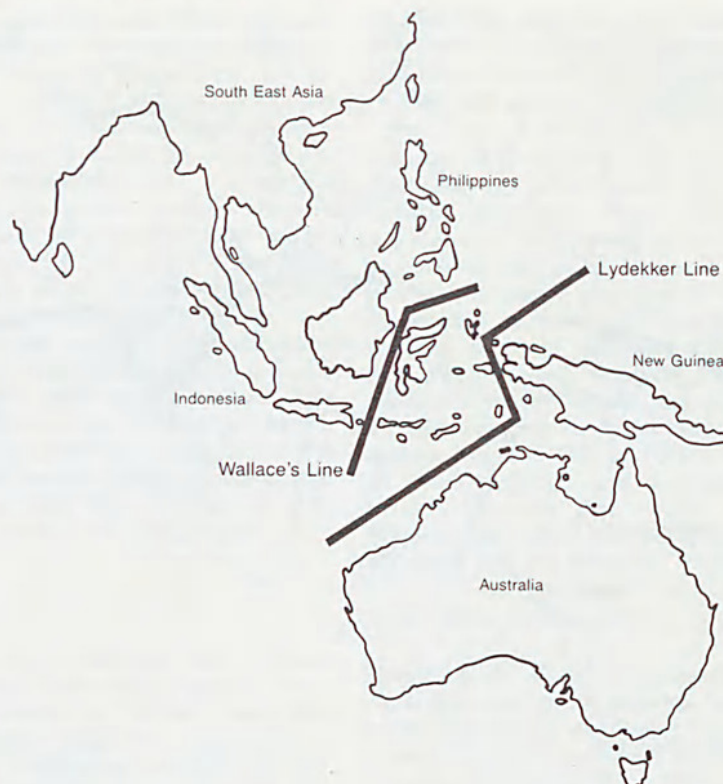
Figure 5.5 The transition from the Oriental Zoogeographic Region to the Australian Region. Wallacea is the area between the Wallace and Lydekker lines. Within it there is a decline in Oriental elements from west to east and a decline in Australian ones from east to west.

different habitats from those either of the Australian or Asian components. This diversity stimulated a rapid and extensive radiation which formed an autochthonous element within New Guinea.

This Volume is not concerned directly with the fauna of New Guinea, but recognition of its tripartite origin and of the subsequent montane adaptive radiation within it, are necessary for an understanding of New Guinean influence on the Australian fauna (Tyler, 1979a).

## Interior Versus Peripheral Distributions and Zoogeographic Subregions

Inspection of a large number of maps of the geographic ranges of Australian terrestrial species immediately suggests that there are two major kinds of distributional patterns, interior (arid-adapted) and peripheral (wet-adapted) (Figs 5.6 and 5.7). A few eurytopic species with sufficient ecological and physiological flexibility to cope with both kinds of environment are found throughout the continent, but the distribution of most clearly falls into one or the other of these general categories.

Within the above two general areas there is a variety of subordinate distributional patterns. Not all species with an interior distribution occur throughout the entire central portion of the continent; many occupy only part. Fragmentation is pronounced even more on the periphery. There are areas where the limits of a number of species coincide at least roughly and recognition of that has led to the delimitation of zoogeographic subregions within the Australian Region.

New Guinea and Australia have markedly different faunas and sometimes are designated as the Papuan and Australian Subregions, respectively, with further subdivisions (provinces)

denoted within Australia. Other biogeographers consider the subdivisions within Australia as subregions rather than provinces and this is the terminology followed here.

Researchers working on different taxa have contributed different schemes and terminologies (Moore, 1961; Kikkawa & Pearse, 1969; Keast, 1959; Horton, 1973; Littlejohn, 1981), each with strengths and weaknesses but all vaguely similar. The number of subregions proposed varies from three to 12. Some of these perhaps reflect the ecological peculiarities of the taxa on which they were based and some of the finer subdivisions, especially, do not seem widely applicable.

No one scheme would fit all taxa and, obviously, even within a given taxon certain species may be effectively blocked by barriers that have little impact on others. There are species that have very narrow tolerances or specific requirements that limit them to extremely local, specialized situations and they will have ranges that do not cover an entire subregion. There are features of climate or topography, however, that serve as a barrier to many taxa and mark the limits of the ranges of many species.

The following are the general subregions most commonly accepted and most generally applicable (Fig. 5.8).

In the moist, tropical north, the western Timorian Subregion is separated from the eastern Torresian Subregion by a seasonally semi-arid tract at the base of the Gulf of Carpentaria. Down the eastern seaboard is a moist, subtropical to temperate area, the Kosciuskan Subregion. It is bounded on the periphery by the ocean and inland by the Great Dividing Range and increasing aridity. The boundary between the Kosciuskan and Torresian subregions has been set at various places. One such demarcation coincided with the Clarence River in northern New South Wales, a boundary rejected by Horton (1973) in favour of the semi-arid gap in the Towns-
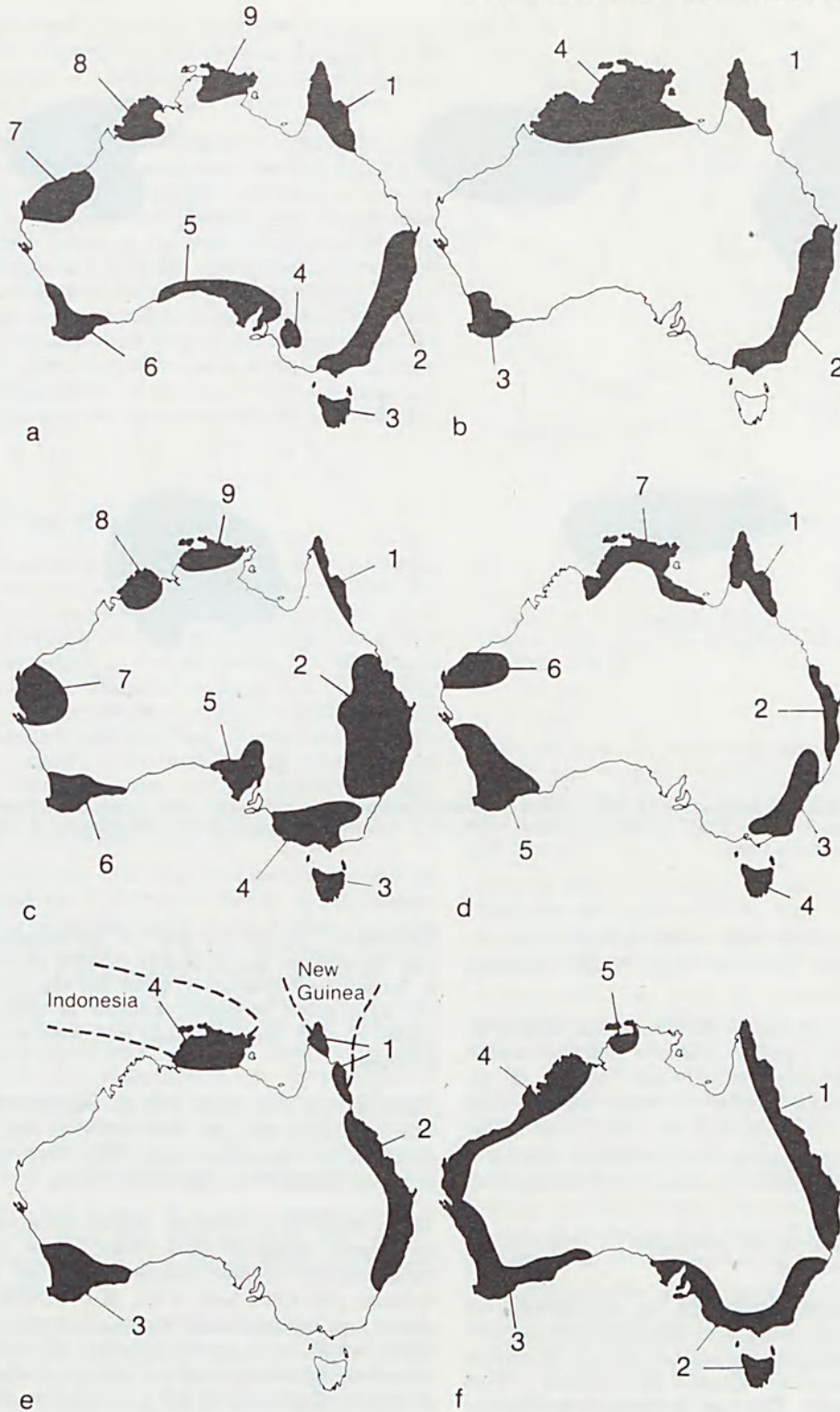
Figure 5.6 Examples of peripheral distribution of species or genera of terrestrial animals in Australia. (Data from Mackerras, 1970; Key, 1976; Koch, 1977; Cogger, 1979; Main, 1981a; Bishop, 1981; Kitching, 1981; Keast, 1981b; Common & Waterhouse, 1981; Strahan, 1983; Blakers *et al.*, 1984).

a. MAMMALS: 1. *Nycticeius sanborni*; 2. *Trichosurus caninus*; 3. *Sarcophilus harrisii*; 4. *Pseudomys apodemoides*; 5. *Lasiorhinus latifrons*; 6. *Macropus irma*; 7. *Ningaui timealeyi*; 8. *Wyulda squamicaudata*; 9. *Antechinus bellus*.

b. BIRDS: 1. *Ramsayornis modestus*; 2. *Climacteris erythrops*; 3. *Eopsaltria georgiana*; 4. *Platycercus venustus* (= *eximilus* northern race).

c. REPTILES: 1. *Liasis amethistinus* (= *Morelia amethistina*); 2. *Pseudechis guttatus*; 3. *Leiolopisma pretiosum*; 4. *Delma impar*; 5. *Amphibolurus fionni*; 6. *Drysdalia coronata*; 7. *Lerista nichollsi*; 8. *Lerista borealis*; 9. *Sphenomorphus douglasi*.

d. AMPHIBIANS: 1. *Rana daemeli*; 2. *Crinia tinnula*; 3. *Litoria citropa*; 4. *Crinia tasmaniensis*; 5. *Pseudophryne guentheri*; 6. *Pseudophryne douglasi*; 7. *Litoria tornieri*.

e. INSECTS: 1. *Tellervo zoilus* (hamadryad butterfly); 2. *Dasybasis cirrus* (a tabanid fly); 3. *Swanea* (a genus of morabine grasshoppers); 4. *Cethosia penthesilia* (Orange Lacewing Butterfly).

f. MISCELLANEOUS INVERTEBRATES: 1. *Isometrus melanodactylus* (scorpion); 2. *Stanwellia* (spider); 3. *Bothriembryon* (snail); 4. *Rhagada* (snail); 5. *Urodacus exellans* (scorpion).

Figure 5.7 Examples of interior distributions of species or genera of terrestrial animals in Australia. (Data from Cogger, 1979; Keast, 1981b; Bishop, 1981; Strahan, 1983; Blakers *et al.*, 1984). 1. *Macropus rufus*; 2. *Stipiturus ruficeps*; 3. *Ctenotus quattuordecimlineatus* (a skink); 4. *Notaden nichollsi* (a frog); 5. *Sinumelon* (a snail).

ville-Mackay area, which not only marks a barrier but accords with distributional patterns. This is the northern boundary accepted here.

Littlejohn (1981) points out that in the Kosciuskan Subregion there is a transition from a preponderance of summer rainfall in the north to a predominance of winter rainfall in the south, with an intermediate zone of seasonally uniform rainfall (Fig. 5.8). This factor, along with its rather large altitudinal and latitudinal extent, gives the Kosciuskan Subregion considerable internal heterogeneity and distributional subgroupings.

The cool, temperate Tasmanian Subregion is restricted to Tasmania and, thus, is insular.

The Southwestern Subregion is located on the southwestern corner of the continent in an area of Mediterranean climate. It is bounded peripherally by the sea and inland by aridity. The Nullarbor Plain forms an extensive gap isolating it from the Kosciuskan Subregion. The final Subregion, the Eyrean, is the largest and incorporates the dry interior of the continent. It is bordered by the sea in the west and along the Great Australian Bight and where narrow tongues of aridity reach the coast elsewhere. Otherwise, it is bordered by the moister areas of the other subregions.

The major modifications of this scheme have been: the inclusion of the Timorian in the Torresian Subregion; the combination of the Kosciuskan and Tasmanian (and sometimes the Southwestern) into a single subregion called the Bassian; the setting of different boundaries between the Torresian and Kosciuskan Subregions; the addition of another subregion along the western coast; the insertion of some other subregions into the transitional gaps between those of the present scheme; or, as mentioned above, the addition of a variety of other regions applicable only to particular taxa.

Refinement beyond the scale of the scheme presented here may be possible and a greater number of subregions erected to reflect the influence of minor barriers on some species or the local effect of slight variation in climate. Such refinements are left for individual treatment in the forthcoming volumes.

These subregions reflect present distributions and barriers. The barriers of the past were different and had a profound effect on the Australian fauna. The effects of temporal shifts in the environment are described below.

There have been botanical regions proposed, just as there have been zoological ones. Since plants are an important structural and trophic component of the habitat of many animals, and since both kinds of organisms respond to climatic and topographical factors, it might be expected that there would be a certain amount of congruence between botanical and zoogeographical regions. Although it is beyond the scope of the present book to dwell on the strictly botanical aspects, it is instructive to compare patterns based on the two major kinds of organisms. Barlow (1984) proposed a delineation of botanical regions for Australia, which he (1985) later modified, largely in response to criticism by Beard (1985). The revised scheme referred to natural regions, rather than botanical ones alone, as criteria in addition to plant distributional patterns were considered. In all, 33 natural regions were recognized. They cannot be discussed in detail here, but the six major floristic zones in which they were grouped, correspond remarkably closely to the zoogeographic subregions described above. These 33 natural regions are described in Chapter 4.

Barlow's (1985) Northern Zone is roughly equivalent to the Timorian Subregion, the North Eastern Zone to the Torresian Subregion, the South Eastern Zone to a combination

of the Kosciuskan and Tasmanian subregion (Bassian) and the South Western Zone to the Southwestern Subregion. Two of the natural zones in combination (Western Shield and Eyre-Murray Basin) correspond to the Eyrean subregion.

Horton (1973) points out that subregions established solely on the basis of clustering of boundaries of animal distribution resulted in nearly the same geographic divisions as occurred when the bases for mapping were climatic and physiographic barriers. The same seems to be true in relation to plant distributions. Congruence of these approaches inspires confidence in the usefulness of the concept. The resultant general patterns recognize the relationships between animal and plant distributions and between those and environmental influences. At the same time, departures from general patterns highlight distributional idiosyncrasies of particular taxa and may lead to greater insights into the environmental factors affecting them.

## Relation To Vegetation Type

Many species of animals are characteristic of a particular vegetation type and may even be restricted to it. Often, the reasons for such a one-to-one correspondence are not clear, but possible explanations include (1) dependence on a food plant restricted to species in that formation, (2) behavioural responses to the unique structural configuration provided by the vegetation (perhaps related to shelter or nest sites), (3) response to associated microclimates, (4) restriction to the same geographic region as the vegetation through common susceptibility to limiting factors, or (5) dependence upon another animal species (perhaps for prey) which is in turn linked to the vegetation in one of the above ways.

Historical considerations also may be important. Tindale (1981) suggests that the Lepidopteran family Agathiphagidae could have evolved at the beginning of the Jurassic or earlier and that its origin may have been linked with such primitive plant groups as the Araucariaceae, which still serves as a food source. He further suggests that the evolution of other Homoneura (given the increasing evidence of their antiquity) may have been associated with ferns and conifers, as some still are, but that the Heteroneura, or more advanced lepidopterans, have a primary association with the expansion and radiation of the angiosperms in the Cretaceous. Howden (1981) suggests that the evolution of the higher families of beetles also is related to the radiation of angiosperms.

The evolution and distributions of various insects and their host plants probably have had historical links that are reflected in the present; others show more flexibility in preferences for host plants.

Animal distributions probably are influenced by many environmental features and no blanket statement can be made. Yet, to emphasize the possible primacy of vegetation as a correlate (if not necessarily a cause) of distributional patterns of animals is not unreasonable. Certainly, analyses of the faunas of particular kinds of vegetation and faunal comparisons among different vegetation types are important exercises. Parsons & Bock (1981), for example, found that Australian *Drosophila* subgenera fall into two groupings. An older invasion radiated in the south and inhabits temperate (or at best subtropical) forests; these species do not come to fruit baits. Species of a newer invasion, restricted to the humid forests of the north, do come to fruit baits. The tropical forests have resources of fleshy fruits that the southern ones lack. Thus, food resources may account, at least in part, for this clear separation by forest type.

There have been few Australian studies of complete faunas of particular vegetation types. Many lists of species of particular taxa for various localities or stands of vegetation have been



Figure 5.8 Zoogeographic subregions of Australia. ▨ = area of winter rain. ▤ = area of seaonally uniform rain. ▥ = area of summer rain.

produced and the increasing popularity of "environmental impact" and "baseline" studies is generating many more such superficial, local approaches to faunal study. These will provide raw data from which future valuable syntheses can be constructed.

There is good information on the relation of some taxa to vegetation and some localities have been surveyed for a few taxa. Seldom has the complete fauna of a particular kind of vegetation been examined on an Australia-wide basis.

A study which can serve as a model of what can be done in this regard is that of Kikkawa *et al.* (1979) on the vertebrate fauna of Australian heathlands. The authors examined each of the terrestrial classes separately and indicated a series of grades of association of species with heathland habitats. They were, in decreasing order of restriction to heathland:

1) Phylogenetic and geographic relicts showing a high degree of specialization in the heathland habitat and confined to southwestern Western Australia, the possible result of radiation at a time of heathland dominance and subsequent extinction of all or most allied forms.

2) Phylogenetic relicts showing a high degree of sedentariness and adaptation to ground-living in dense cover, remaining otherwise unspecialized morphologically and having lost links with modern forms.

3) Species showing a relict pattern of distribution in heathlands as a result of phylogenetic and geographic isolation after radiation into heathlands at a time of heathland dominance.

4) Major taxa showing specialization as nectar-feeders as part of their heathland adaptation and geographic radiation at the time of heathland dominance, but subsequent secondary adaptation to "escape" from dependence on heathlands; some species of these groups still show association with heathland without exclusive dependence on this habitat.

5) Genera showing radiation during arid periods, with some members inhabiting heathlands.

6) Genera showing radiation in a wide range of modern habitats including heathlands as an adaptive zone.
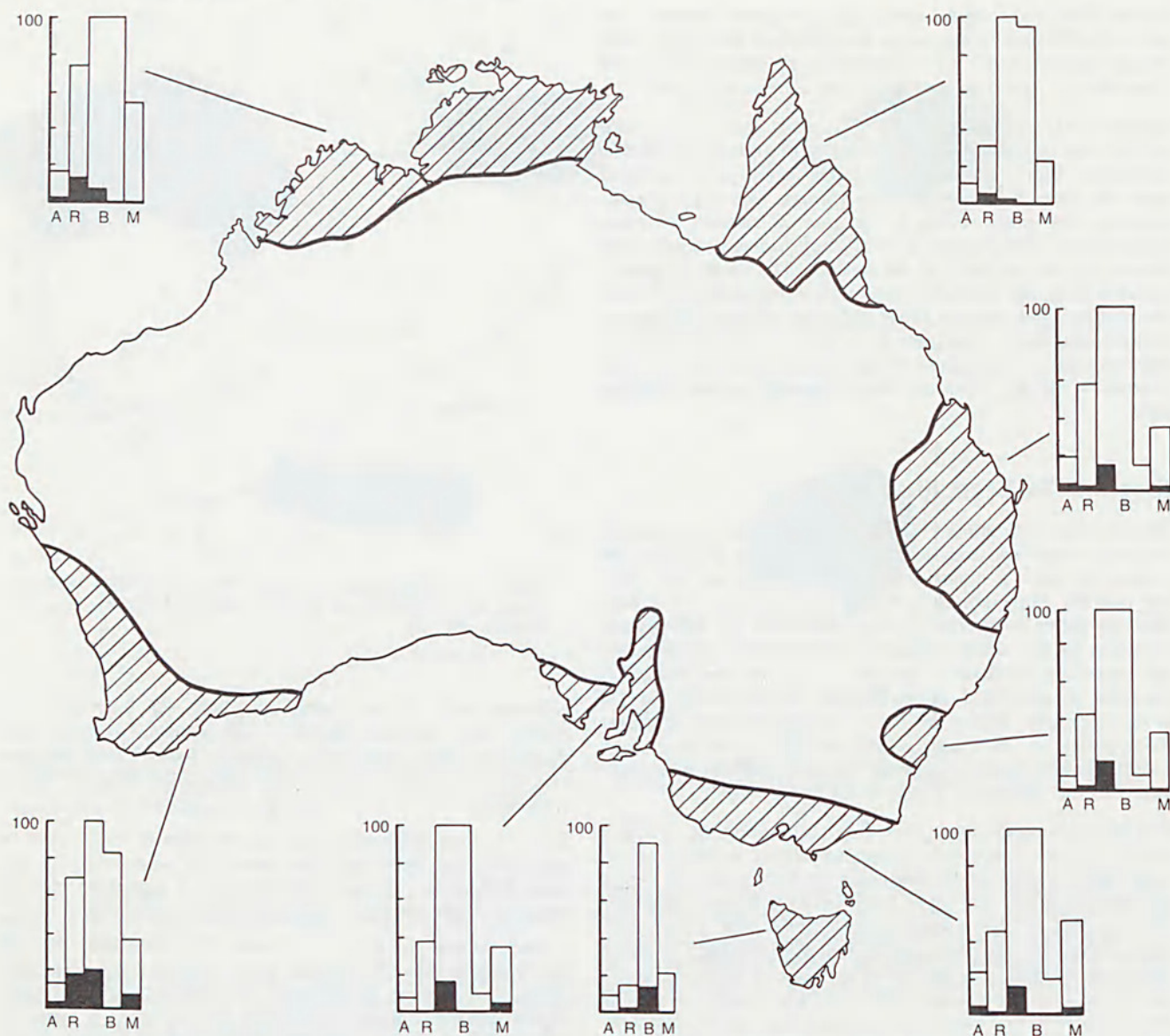
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Figure 5.9  Map of major regions containing heathlands (cross hatched) in Australia. Histograms show the number of indigenous species of vertebrates known from heathlands for each area (white) and with special association with heathland (black). A = amphibians. R = reptiles. B = birds. M = mammals. For birds numbers greater than 100 can be read by summing the columns. (After Kikkawa *et al.*, 1979)

7) Species showing recent adaptation to coastal heathlands in parts of their range.

8) Species showing no obvious association with heathlands.

An important part of this study was the linking of specific animal taxa with the history of heathlands and to show how intertwined were the fates of vegetation and animal life. Heathland habitats are now fragmented in Australia, but were once extensive. Through the Tertiary, heath increasingly became restricted to coastal or subcoastal refugia and in the Quaternary invaded coastal and inland dunes.

The patterns of different degrees of restriction of the fauna reflect this history. Some of the old fauna, already adapted to heathlands, were unable to radiate into other habitats and their distributional history has followed that of the heaths, becoming more narrowly restricted and fragmented. Other taxa were able to adapt to changing conditions and some of their component species moved out to new habitats as those arose. During the ever-shifting dynamism of environmental

change, adaptation in the reverse direction also occurred, some species of otherwise non-heathlands taxa becoming adapted to heathlands. This process of radiation into or specialization within the heathlands is still continuing.

Specialization was found not to be limited to relict species but to be a continual process involving taxa from the oldest to the most recent heathland colonizers. Specialization to heathland living seems to have occurred many times with different chronologies for different taxa.

Two findings of this study deserve further comment. The first is that the majority of vertebrate species recorded from heathlands occur more commonly in other habitats (Fig. 5.9). This casts doubt upon the paramount importance of this vegetation type as a direct determinant of distributions for most species. Other vegetation types with a greater proportion of specialists may exert a greater effect.

The second is that both ends of the sequence in relative specialization and restriction to heathlands involved a variety of taxa. The most specialized and restricted species were

often older, relictual and monotypic (at generic or familial level) forms, but of various taxa. Category 1 contained a frog, a turtle and the Honey-possum (all monotypic at the generic or familial level). Category 2 contained a frog and two birds (Ground Parrot and Noisy Scrub Bird). Relict species, however, also showed secondary adaptation and category 7 included several relict frogs and reptiles as well as recent avian and mammalian colonizers. Kikkawa *et al.* (1979) further point out some of the ecological features of the heathland habitat to which animals have had to adapt. They included low pH in the wetter sites, low soil nutrients, sandy or rocky substrate, restricted and special nature of food resources (such as nectar), low productivity, important role of fire, dense ground cover and high incidence of toxic substances in plant tissues.

This incisive review of the ecological, zoological, evolutionary and historical aspects of the fauna of this vegetation type could well be emulated for other vegetation types. Kikkawa *et al.* (1979) note that the sequence presented for heathlands has parallels in tropical and subtropical each major vegetation type in Australia, great progress would be made in understanding community ecology and evolution on the continent.

There have been a few other attempts at similar studies. Hutchings & Saenger (1987) review the vertebrate and invertebrate faunas of Australian mangrove vegetation.

Mangroves are not the primary habitat for most animals occupying them; many are casual visitors. Possible benefits to be derived from the use of mangroves include fewer predators and competitors in mangroves; abundant food (*e.g.* nectar) at critical times of the year; augmentation of the potential food supply of terrestrial predators by marine invertebrates; the presence of vascular plants with fleshy succulent leaves; and the abundance of detritus on the forest floor (Hutchings & Saenger, 1987).

Terrestrial vertebrates reported from mangroves include mammals, reptiles and especially birds. Over 200 species of the last group occur in mangroves, of which only 14 are restricted to this habitat and 12 others use it as primary habitat only over part of their range. Sixty additional species use mangroves regularly, either throughout the year or in particular seasons. As small as these numbers are in proportion to the total numbers of birds, they represent a much richer avian fauna than in mangroves in other parts of the world.

The greatest number of avian mangrove-specialists in Australia occurs in the floristically richer and structurally more diverse mangroves of the northern tropics, especially in northwestern Australia (Ford, 1982). The mangroves in that area have been more stable geologically than those on Cape York Peninsula where Pleistocene fluctuations in sea level periodically eliminated mangrove areas. The majority of birds endemic to mangroves evolved from rainforest-inhabiting species. As Australia progressively dried during the late Cainozoic, low-lying mangrove areas along the northwestern Australian coast probably served as refugia for the dwindling stocks of formerly widespread rainforest species. As the mangrove areas were patchy, there was a greater probability of isolation, leading to speciation. Along the eastern seaboard, large areas of rainforest and mangroves may have remained contiguous longer, allowing continual interchange between the two environments until recently and minimizing the development of mangrove specialists. Today, mangrove habitat is patchy throughout.

Reptiles and mammals are similar to birds in that only a small proportion of species is restricted to mangroves. Most use it as secondary habitat or as a seasonal refuge. There are more species in tropical than in temperate mangroves.

Less is known of the invertebrates, but most terrestrial arthropods of mangroves are not restricted to that habitat. No species of ants or spiders are known to be so, whereas a few species of dipterans and lepidopterans are.

Heathlands and mangroves are vegetation types that are now fragmented and not in very extensive tracts. More continuous and widespread kinds of vegetation may have a greater number of animal species restricted to them. Generalizations in this regard await further study.

## Refugia

The cyclic fluctuation of Australian climate in the late Cainozoic, superimposed upon a generally increasing and spreading aridity, provided conditions under which refugia played an important role in the distribution and speciation of animals.

During the wetter phases of climatic fluctuation, plant communities characteristic of mesic sites would expand and wet-adapted species would flourish as their habitat increased in area. During the drier phases, however, as mesic vegetation shrank back to the moister parts of the continent and was replaced elsewhere by xeric vegetation, two scenarios are possible. In the first, the ranges of wet-adapted animals would contract into those regions that still maintained a favourable climate and habitat. As the once continuous habitat became fragmented into widely separated pockets, the animal species would be broken up into isolated populations. Alternatively, some species might progressively become adapted to aridity and be able to occupy the new and expanding drier habitats, thereby extending their ranges. In the former case, animals retreat into refugia containing their ancestral environments. In the latter, they adapt to new conditions and radiate into new habitats.

With the return of wetter conditions, the refugia would have expanded and coalesced with a comparable expansion of the ranges of wet-adapted animals and a retraction of the dry-adapted ones into drier central areas or dry refugia — or their adaptive radiation into the expanding wet environments.

The Australian palaeoclimate has undergone a number of such cycles, particularly in the Pleistocene. The isolation of populations leads to their genetic divergence and reproductive incompatibility. During the expansive phase, they may come into contact again, possibly to interact competitively, but perhaps to extend into each other's ranges. When the following contractive phase occurs, both may become split into isolated populations, with each again forming new species in an iterative process. Thus, the alternate expansion and contraction of aridity would favour the proliferation of species. Some isolates may become adapted to new suites of conditions during times of change, only to be isolated in different kinds of refugia at the next cycle (for example, semi-arid habitat). Together, these phenomena should contribute to rapid diversification of fauna.

Countering this trend is the extinction of species at the extremes of climatic cycles. If contraction is extreme, habitat fragments may become too small to support permanent breeding populations and certain species may be lost. In other cases, whole refugia may be extinguished, along with the fauna they contain.

The fact that refugia serve as centres of speciation in fluctuating environments provides a tool for studying the past history of particular taxa. The areas where many species have been generated are likely to be areas where repeated isolation and expansion of distributional ranges have occurred in the past. That is, refugia often are centres of origin and dispersal. Cogger & Heatwole (1981; 1984), Pianka (1981) and Kitching (1981) mapped isoclines of species densities for various

taxa (Fig. 5.10) and identified geographical areas where there were many species (centres of speciation and dispersal) surrounded by areas of relatively few species where there had been adaptive radiation into the more extreme habitats surrounding the centre. Certain areas seem to have served as refugia and centres of speciation for a number of taxa. For some, like the pygopodid lizards, the focus was in southwestern Australia, for others it was located in the north. For some the centre corresponded to one of the zoogeographic subregions such as the Southwestern (pygopodids) or Timorian (varanids). Others, particularly those involving taxa of more recent arrival, were in Cape York. Various older groups (elapids, scincids, agamids) showed a number of foci, perhaps related to different waves of immigration, including radiation of the dry-adapted taxa in the Eyrean Subregion. Some, such as the diplodactyline geckos, had their centres primarily in the arid interior. Similar treatments have been carried out at the generic level as a means of suggesting the centres of origin and dispersal at a lower taxonomic level (Pianka, 1981) (Fig. 5.10).

Given that during Australian Cainozoic history the general trend superimposed over the fluctuating climatic cycles has been one of increasing aridity, wet-adapted species might be expected to become extinct more frequently than dry-adapted ones and that there would be less opportunity for secondary adaptation to wet conditions. Thus, the dry-adapted fauna would be favoured in the long run over the wet-adapted one. This topic is discussed further below in relation to faunal imbalances in various climatic zones.

Another prediction from the progressive drying of the Australian continent is that moist refugia would increasingly become more common than dry ones. That is, moist areas would be reduced in size during arid expansion more than would dry areas during the wetter periods. In this context it is important to consider the kinds of refugia that have been identified in Australia. As predicted, most consist of habitats that maintain moisture during relatively dry periods. In addition to the generally moister peripheral regions, mountain tops have served as refugia. As one goes up mountains conditions get progressively wetter. During generally moist conditions climate and vegetation favouring wet-adapted species are widespread and animal species may have extensive distributions along mountain ranges and perhaps even out onto slopes or plains. With expanding aridity, the moist climatic and vegetative zones move upward and become discontinuous until only isolated mountain tops provide favourable habitat (Archer, 1984e). Habitat and species ranges become fragmented in the classical sense of refugia. A change to wetter conditions would result in expansion of their ranges, perhaps to coalesce or overlap. Conversely, a change to drier conditions might mean their extinction on lower peaks or, in extreme cases, on all mountain tops. There is a number of examples among the amphibians (Tyler *et al.*, 1981), reptiles (Schuster, 1980) and invertebrates (Keast, 1981b) of isolated relicts in the mountain top refugia in the Great Dividing Range. Similarly, the peaks of the Stirling and Porongorup Ranges in Western Australia approach subalpine conditions and contain relict mygalomorph spiders (Main, 1981a).

River banks, gorges and gullies also serve as refugia. During dry periods conditions remain moister there than generally obtain elsewhere and some species may survive only in such limited habitats.

Secondary habitats may serve as refugia if the primary habitat becomes reduced or disappears altogether. The role of heathlands and mangroves as refugia for rainforest species during past arid pulses has already been discussed.

Wet habitats have a lower species diversity of birds than do drier ones (Brereton & Kikkawa, 1963; Kikkawa, 1974). Perhaps there was extinction of more wet-adapted species during arid expansions than of dry-adapted ones at any time. Birds from the wetter habitats had stronger associations of species, suggesting that they occur in discrete assemblages that have a real discontinuity with the more loosely structured assemblages from arid regions (Fig. 5.11; Kikkawa, 1974).

Although moist habitats have served most often as refugia, this has not been exclusively the case. For example, grass-wrens (*Amytornis*) are inhabitants of the arid zone where they occupy primarily *Triodia* habitats. Isolation of populations, leading to speciation, appears to have resulted at least in part from dissecting of *Triodia* habitat by invading savannah grassland, *i.e.* leaving the populations of grass-wrens in semi-arid refugia (Keast, 1958a).

In conclusion, refugia in Australia have more often been moist areas surrounded by aridity rather than the reverse. At the present time, mountain tops or other locally moist areas are serving as refugia for some species.

## Barriers

Animals vary in the ease with which they can cross barriers; what may constitute a barrier for certain species may not hinder the movement of others. For this reason, geographic subregions based on one group may not be applicable to other taxa. Yet, as noted above, many taxa have similarities in distributional patterns that relate to physical and climatic features deemed to be barriers. There are certain features that commonly prevent or reduce the movement of many kinds of animals. Some of these have been mentioned briefly in connection with delimitation of the boundaries of zoogeographic subregions. They will be discussed in general terms now and applied later to the interpretation of speciation. Barriers may be physical, climatic or biotic.

**Physical Barriers.** For terrestrial animals, these include topographic features such as mountain ranges, steep rift valleys and bodies of water (Keast, 1981b). The sea, of course, is a major barrier to the movement of terrestrial animals and its role in the isolation of Australia during its northward drift has been discussed. The ability of animals to cross open sea water varies greatly. Obviously, flying animals such as birds, bats and insects generally are better able to cross sea barriers than are more sedentary species such as earthworms or frogs. The relative ineffectiveness of sea barriers for the former groups is evident from the many records of land birds found as solitary, "accidental" individuals on islands far afield from their usual range. At least four species of Australian birds are known to have reached and become established in New Zealand since 1830 and stragglers of others are common there and in various other Pacific islands (Keast, 1981a). Heatwole *et al.* (1981) record 18 species of Australian mainland birds reaching One Tree Island, Great Barrier Reef, over a five-year period. Migratory birds are the prime example of indifference to oceanic barriers; some species cross long stretches of sea water on an annual basis.

Many flying insects readily cross extensive sea water barriers, either by actually flying or by passive dispersal by wind currents. The number of species and individuals reaching remote islands in this way is astounding. Farrow (1984) found that at Willis Island in the Coral Sea at least 13 influxes of airborne insects from Queensland (minimum distance 450 km) and possibly one influx from New Guinea (minimum distance 600 km) occurred during winds from the mainland in less than one year. At least 51 species were involved. Heatwole *et al.* (1981) note that minimal rates at
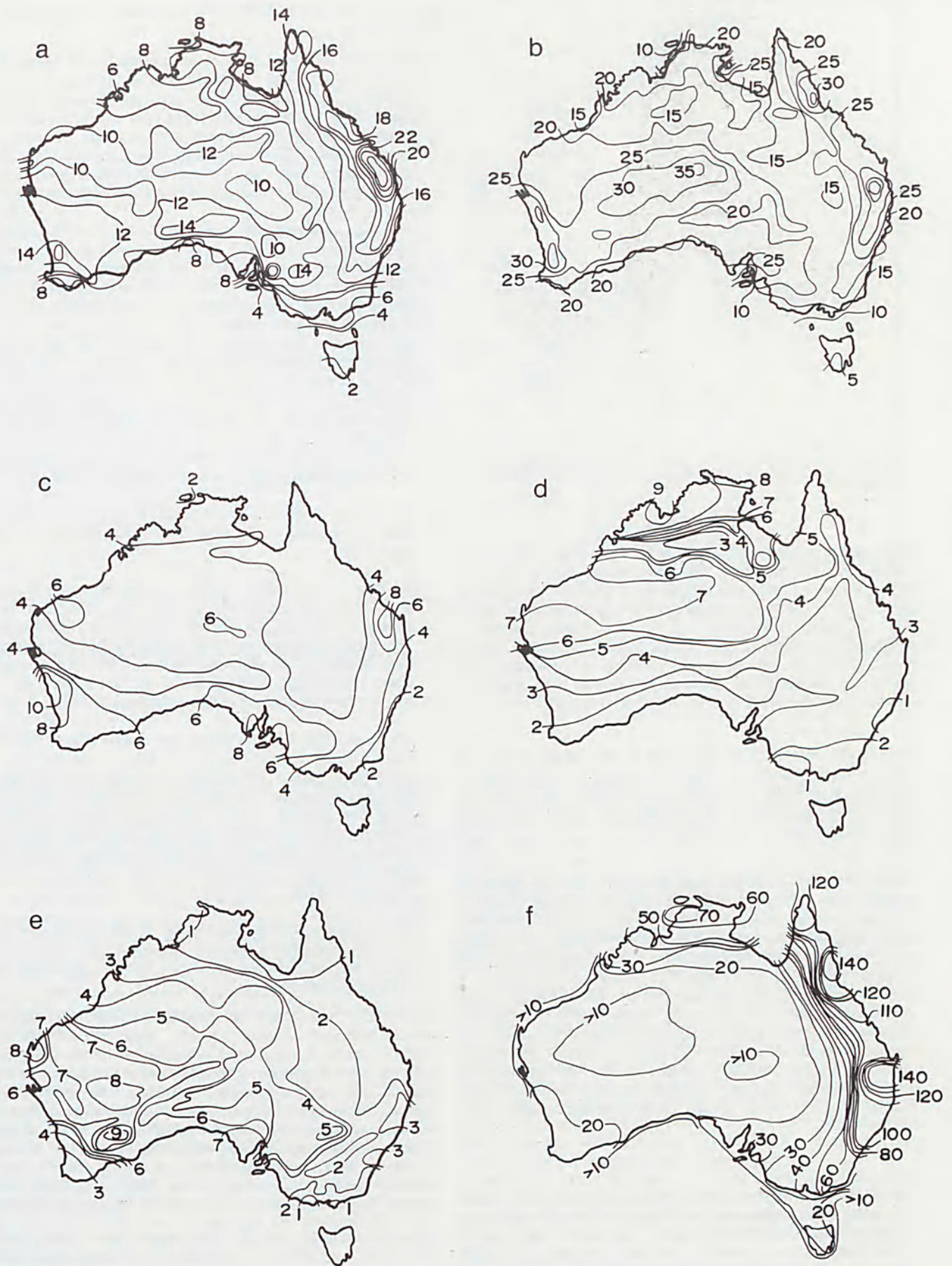
Figure 5.10 Isoclines of species density of some reptiles and butterflies in Australia. (After Cogger & Heatwole, 1981, Pianka, 1981; Kitching, 1981): a. Elapid snakes; b. Scincid lizards; c. Pygopodid lizards; d. Lizards of the genus *Varanus*; e. Lizards of the genus *Amphibolurus*; f. Papilionoid butterflies.

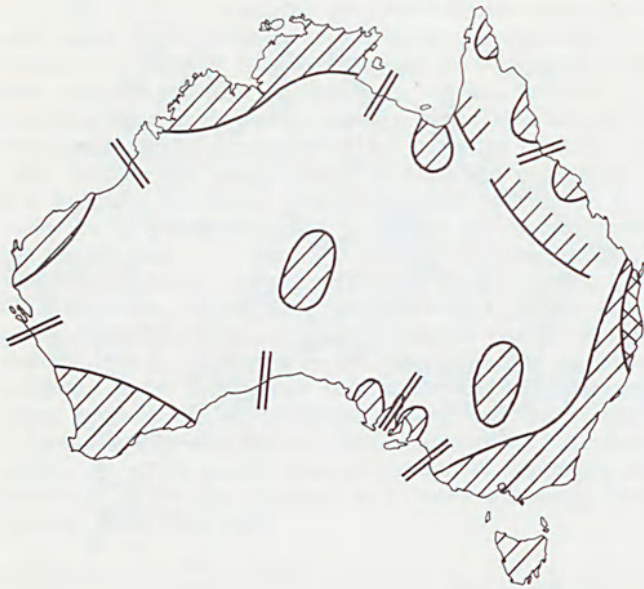[L. Bridges]

# 5. TERRESTRIAL COMPONENTS AND DISTRIBUTION



Figure 5.11  Refuges (hatched areas) and barriers (parallel lines) proposed to account for bird speciation in Australia. (After Horton, 1984)

which above-ground arthropods arrived on One Tree Island varied from 20 to more than 50 species per two-month period. Traps on ships and aircraft have revealed that even at great heights and over mid-ocean there are significant numbers of small arthropods of various kinds dispersing (Holzapfel & Harrell, 1968). Not all of these are flying forms. Some are young spiders floating on gossamer and others are minute forms, such as mites, that were probably blown upward by wind into the upper airstreams.

Some small animals take advantage of the volant powers of other animals and "hitch-hike". For example, snails may be transported in mud on birds' feet (Malone, 1965) and, of course, internal parasites and ectoparasites such as lice, ticks and fleas accompany their flying hosts.

Aerial transport is not the only method of crossing saltwater barriers. Sea currents themselves can be dispersal agents. Flotsam such as floating logs, coconuts or other terrestrial debris may harbour animals and transport them. This method is probably more frequent than is usually supposed. For example, Heatwole & Levins (1972) dissected 59 pieces of flotsam in the Caribbean and found that 25% of them contained at least one live terrestrial invertebrate and often there were many. Pseudoscorpions, snails, spiders, mites, millipedes, isopods, worms and 19 families of insects were represented. There is difficulty accounting for the presence of relatively large, flightless animals such as centipedes, spiders and lizards on remote islands other than by flotsam transport.

The ease with which a taxon crosses sea barriers by flotsam transport is dependent upon tolerances to the physical rigours of temperature, desiccation, salinity and food and water deprivation experienced during the voyage and whether special reproductive adaptations exist that improve chances of establishment once in a new location. An example of the latter is parthenogenesis, the ability of females to reproduce via unfertilized eggs and in the complete absence of males. Thus, a minimum of only one female individual, not a pair, has to survive the voyage.

Sea water barriers have been of significance in Australia in certain ways:

(1) Gondwana was, not likely an unbroken land mass. The Antarctic part was probably an archipelago (Archer, 1984a). If so, Antarctic water gaps may have acted as a faunal filter, selectively permitting easy access to Australia by alien taxa that crossed such barriers easily, but denying access to other, less vagile forms. One may speculate that this explains why only the microbiotheriids among the ancient marsupial stock seem to have made the journey.

(2) Large epicontinental seas covered much of the central part of Australia in the early Cretaceous and separated the continent into a series of islands (Fig. 5.12), among which faunal exchange would have been reduced. This early separation may account for the distribution of some of the older faunal elements. For example, some spiders, the morabine grasshoppers and some of the geotrupine scarabs have distributional patterns centring on the larger of these Cretaceous islands (Main, 1981a; Howden, 1981). Speculatively, the barriers formed by those continental seas could explain the restriction of relicts like the chelid turtle *Pseudemydura umbrina* to southwestern Australia (Burbidge *et al.*, 1974) or the origin of pygopodid lizards in the southwest, when it was a Cretaceous island.

(3) During much of the Tertiary, the continent was isolated by oceans, a situation that has persisted to the present day.

(4) Marine incursions at various places along the periphery of Australia during the Tertiary (Fig. 5.13) may have served as barriers, fragmenting peripheral distributions. The most important one was in the Nullarbor from the Late Eocene to the Miocene (Nelson, 1981). Others were along the western coast and in the lower part of the Murray-Darling basin (Galloway & Kemp, 1981).

(5) Even after the Australian and Asian Plates collided, there were water gaps separating the emergent parts of those land masses. These acted as faunal filters, much as described above for the Antarctic archipelago. Bats and birds, for example, were more successful in colonizing Australia from Asia than were the non-volant placental mammals. The faunas of Australia's offshore islands are influenced today by the varying ability of different taxa to cross sea barriers.

(6) Alternate opening and closing of sea barriers between Australia and New Guinea in the north and Tasmania in the south has had an effect on faunal exchanges and speciation patterns.

In the late Tertiary and the Pleistocene, there were marked eustatic changes. During glacials, large portions of the world's supply of water were locked as ice on the polar caps and sea level dropped accordingly. Conversely, during interglacials when the caps melted, sea level rose again. Levels reached 200 m below current sea level and rose more than 40 m higher than at present (Galloway & Kemp, 1981). During periods of lowered sea level, when land connections between Australia, New Guinea and Tasmania existed, there could be interchange of fauna across Torres Strait and Bass Strait, limited only by whatever habitat barriers might have existed.

As sea level rose and the land connections were severed, followed by progressive widening of the water gap, faunal exchange would have diminished with the degree of reduction varying among taxa. At present, the proportion of New Guinean elements decreases and that of Australian ones increases in the Torres Strait's insular faunas from north to south (Cameron *et al.*, 1978).
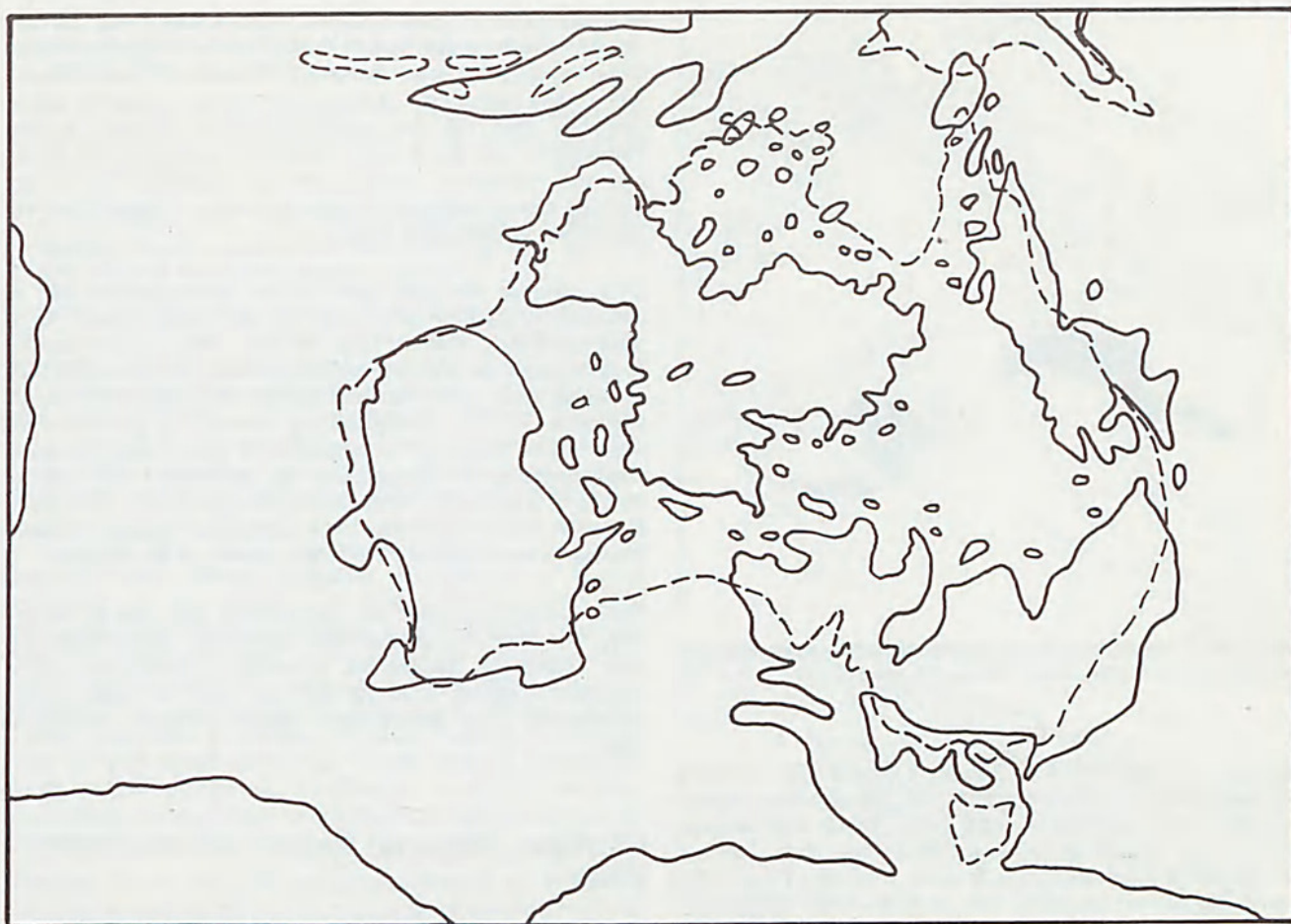
Figure 5.12 Land and epicontinental areas of Australia in the Early Cretaceous. Present day coastlines in dashed lines. Cretaceous coastlines in solid lines. (After Howden, 1981) [L. Bridges]

Bodies of freshwater such as lakes and rivers can also serve as barriers for the less vagile terrestrial animals. Australia is one of the poorest continents in terms of bodies of freshwater and there are few present-day freshwater barriers of any significance. In the past, however, there were extensive freshwater systems that may have influenced animal distribution. A number of large inland lakes and marshes replaced the withdrawing Cretaceous marine seas and persisted for some time. These could have acted as barriers for terrestrial animals. Later, during moist Pleistocene periods (see below), freshwater lakes in the interior combined with mountain ranges would have formed barriers (Fig. 5.14) separating previously continuous ranges of widespread dry-adapted species (Kluge, 1967a).

Mountain ranges are effective barriers for some taxa. Australia is relatively flat and most mountain ranges are of limited geographic extent or are very low. There are, however, elevated segments and dissected plateaus in the central deserts, Arnhem Land, the Kimberleys and the southwestern corner (Keast, 1981b). The Great Dividing Range, with its altitudinal zonation of climate and vegetation, separates many taxa on an east-west basis and seemingly poses a barrier to faunal movement. The Flinders Ranges and the Hammersley Plateau may have been barriers to east-west and north-south movement, respectively (Fig. 5.14).

**Climatic and Habitat Barriers.** Allusion to climatic differences as barriers forming some of the boundaries of zoogeographic subregions has already been made.

An important consideration is the nature of previous climatic barriers in the Torres Strait region. An older view was that during Pleistocene glacials, when sea level was lowest and land connections broadest with New Guinea, the climate tended to be cool and moist. Conversely, interglacials with high sea level and severed land connections were believed to be relatively warm and dry (Horton, 1972). This view prompted the belief that wet-adapted fauna could easily cross land connections during glacials. More recent evidence suggests a different climatic pattern, with glacials being cool but dry and interglacials warm and moist (Bowler et al., 1976; Flenley, 1979; Galloway & Kemp, 1981; Kershaw, 1981; Keast, 1981b). If so, then at times when climate was most conducive for transit, land connections would have been closed. When there were broad land connections, arid barriers would have prevented passage of the predominantly wet-adapted New Guinean species into Australia. Indeed, Kikkawa et al. (1981) show that the dry-adapted Australian taxa were able to colonize the dry savannah areas of southern New Guinea better than the New Guinean rainforest ones were able to colonize Australian rainforest on Cape York.

Neither of the above generalizations cover all cases. Then, as now, there were significant local and regional differences in climate and there were north-south shifts in climatic belts, such that at times the centre of aridity was further north than at others (Keast, 1981b). Nix & Kalma (1972) indicate that at 14,000 years ago, when sea-level was 120 m below present levels, the broad land connection between Australia and New Guinea was covered by xeric to sclerophyllous vegetation, with New Guinean rainforest contracted and re-

Figure 5.13  Marine incursions (black areas) onto the Australian continent in the Tertiary. (After Galloway & Kemp, 1981)

mote from similar habitat in Australia (Fig. 5.15). At 8,000 years ago, however, when sea level was 30 m below present level and a land connection with New Guinea still existed, though narrowed, the climate was wetter and New Guinean and Australian rainforests were in close proximity (Fig. 5.15). Clearly, there were at least some periods when sufficiently moist conditions prevailed during lowered sea level to permit migration of wet-adapted fauna from New Guinea into Australia. Such conditions probably did not occur in every glacial cycle. Horton (1984) estimates that three of the Pleistocene cycles would have been suitable.

**Biotic Barriers.** Several kinds of distributional patterns of one species relative to another have been recognized. Species that do not overlap in geographic range are said to be allopatric. A special case is when such species have mutually exclusive ranges, but which are contiguous along a broad zone. Such species are said to be parapatric. Where their geographic ranges broadly overlap, the species are said to be sympatric. If within the general region of overlap, species also occupy the same localities and habitats they are additionally considered to be syntopic.

A species of animal may pose a barrier to another species. Much has been made of interspecific competition as a determinant of distributional patterns. Closely related species often are allopatric or parapatric. Allopatry may result from the parent population being fragmented by some non-biotic barrier and the two isolated populations then diverging. Their spatial isolation is imposed by the non-biotic barrier, not by whether or not they are potential competitors. In the case of parapatric species, however, there is no physical separation and a common interpretation is that in one region one species has a competitive advantage and eliminates the other, the reverse being true elsewhere. Thus, if conditions change along an environmental gradient, the point where the competitive advantage shifts from one species to another is where the boundary between the two occurs, with each species competitively displacing its opposite number from its own range. Empirical demonstration of competitive exclusion is difficult and involves detailed ecological study. Often circumstantial evidence was accepted, circular reasoning employed, and competitive exclusion uncritically invoked as an explanation of parapatric distributional patterns. As a result,

this answer has become suspect even though very careful, detailed studies unequivocally have demonstrated competition to be operative in some instances. The role of competition is one of the most hotly debated of current ecological issues. The best that can be concluded at the moment is that competition can be a very important zoogeographic factor and that parapatric distributions are suggestive of it, but warrant closer examination and assessment of alternative explanations in individual cases.

Less attention has been paid to the zoogeographic role of competition between species that are not closely related. Even phylogenetically distant taxa, however, may share similar requirements and compete with each other for resources. For example, some birds, bees and hawkmoths compete for nectar (Carpenter, 1979). Seed-gathering ants and granivorous rodents show reciprocal abundances in some desert habitats and experimental manipulation of populations has demonstrated a competitive interaction (Brown et al., 1979). The extent to which such taxa limit geographic ranges of others through competition is a field that remains to be explored.

Biotic interactions other than competition also may be important. For example, interspecific aggression, territoriality, intense predation, disease or parasitism theoretically could eliminate a species from an area and limit its range. These interactions, like competition, require detailed ecological study.

## Corridors, Dispersal Routes And Points Of Entry

Corridors are the opposite of barriers. They permit rather than block movement. They are narrow regions of favourable habitat extending into an otherwise harsh environment. Often corridors connect two parts of an animal's range and permit migration between areas. They can take different forms, such as a narrow land connection across bodies of water (sometimes called land bridges), narrow bands of favourable habitat along river banks, the floors of valleys or gorges or merely bands of vegetation related to local peculiarities of



Figure 5.14  Principal physical barriers for xeric animals during Pleistocene wet periods. (After Heatwole, 1976)    [L. Bridges]

soil, topography or climate. Like barriers, corridors may not be permanent, but may be broken and reformed with changing climate. They may affect speciation patterns in two ways:

1) they may reduce isolation by facilitating faunal exchange between otherwise isolated areas and in this way inhibit speciation;

2) conversely, they may promote speciation by allowing passage of taxa to otherwise inaccessible areas which are then isolated when the corridor is broken.

Corridors probably have played a significant role in speciation in the Eyrean Subregion. The central deserts seem relatively uniform in topography and few physical barriers are evident. Yet, the distributional patterns of animals indicate that there has been considerable isolation. Isolation may arise from differences in substrate and vegetation. Pianka (1981) identifies three major different habitat types: sandplains, sandridges and mulga. These are interdigitated in complex ways and although there are species that span two or more of them, there are others that are restricted to particular ones. Pianka postulates that shifting of habitat boundaries and the opening and closing of corridors between fragmented areas of similar habitat account for the recurrent cycles of isolation followed by movement to new areas which is requisite for proliferation of species. He identifies a number of corridors in central Australia (Fig. 5.16). Similarly, Keast (1958a) postulates a corridor of desert "spinifex" (*Triodia*) from the arid centre to the base of the Gulf of Carpentaria during periods of climatic deterioration to explain the close relationship between two geographically distinct species of grass-wrens.

Dispersal routes may be ecological corridors or isthmuses which have contributed to the movement of species from one region to another. On a longer-term basis, dispersal routes may reflect the gradual movement of a higher-level taxon outward from its centre of origin through different types of habitat, not by following corridors of the original habitat, but



Figure 5.16 Vegetation of the land connection between Australia and New Guinea at two different times in the Quaternary. Upper: sea level at 120 m below present level, about 14,000 years ago. Lower: sea level at 30 m below the present level, about 8,000 years ago. Rainforest is stippled. Short-dashed lines represent present coastlines; solid lines paleocoastlines; long-dashed lines approximate limits of vegetation types. (After Kikkawa *et al.*, 1981) [L. Bridges]
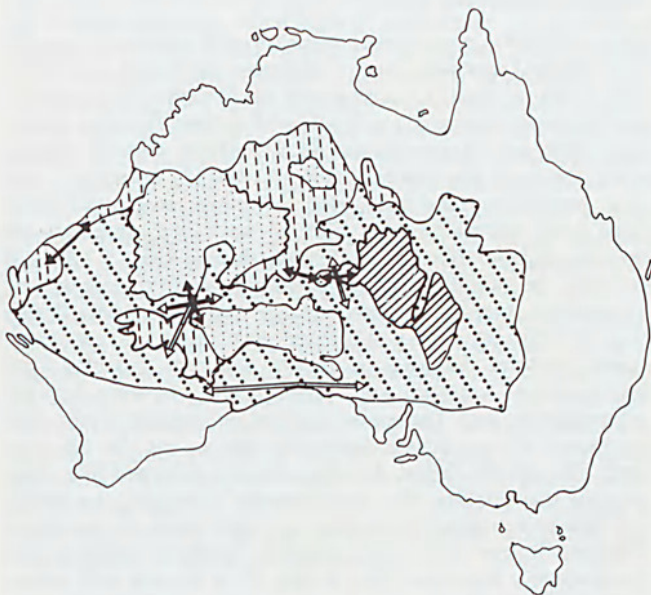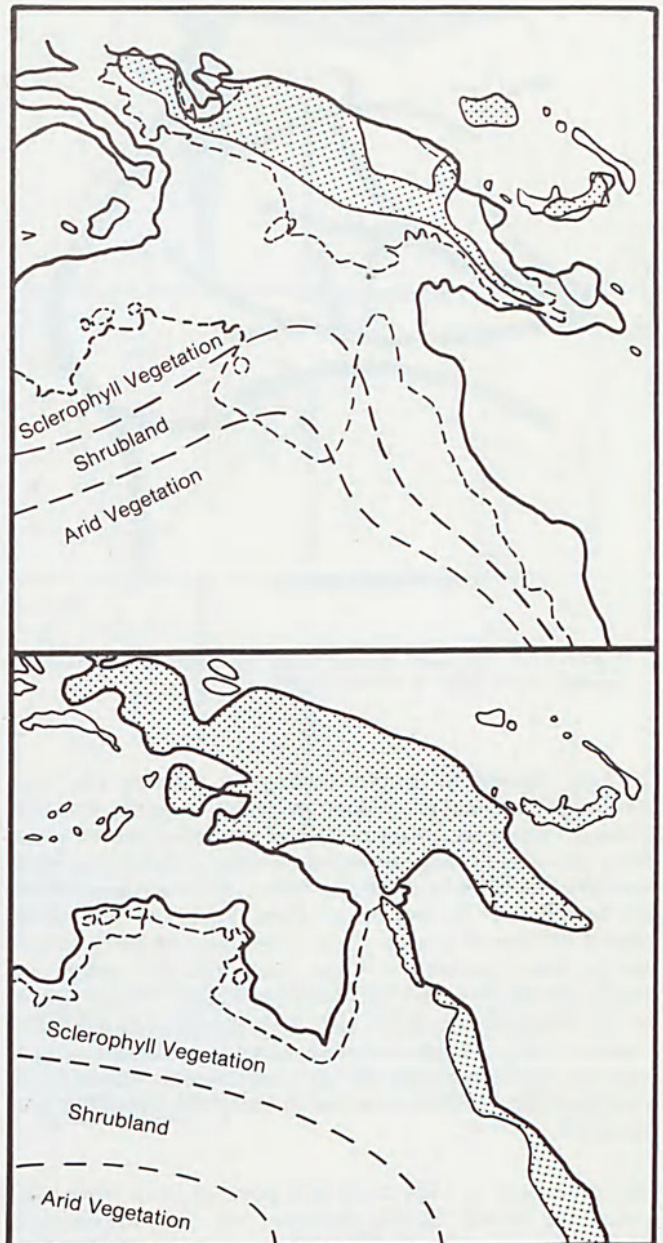


Figure 5.15 The major arid habitats and dispersal corridors of Australia. Arrows indicate probable location of corridors between regions of sandy habitat (black) or mulga habitats (white) arising from Quaternary habitat shifts in areas of interdigitation. Finely stippled areas represent sandplains, coarsely stippled areas (two types) represent sandridges, and hatched areas represent mulga habitat. (After Pianka, 1981) [H. Hunt]

by adaptive radiation into new kinds of habitat, that is, by crossing barriers through adapting to the environments of the barrier. Species density maps again are useful in identifying such dispersal routes. The highest species densities are in the centre of dispersal with declining numbers outward along the route of dispersal. Figure 5.17 shows those identified by Cogger & Heatwole (1981; 1984) as important to reptiles. They probably are applicable to other taxa as well, *e.g.* birds (Serventy & Whittell, 1976).

Of particular significance are the patterns of geographic distribution and species density that identify the point of entry of a taxon into Australia. Taxa that have been resident for long periods (the old Gondwanan Elements and the earliest of the Tertiary Asian Elements) may have radiated from one

Figure 5.17 The major disperal routes postulated for Australian reptiles. (After Cogger & Heatwole, 1981)

Given that the tip of Cape York is a common point of entry for taxa of New Guinean origin, Cape York, not surprisingly, is an important southward dispersal route for immigrants. Kikkawa *et al.* (1981) review the zoogeographical importance of Cape York for insects and terrestrial vertebrates. The most important of their findings can be summarized as follows: (1) the Cape, although a region of important faunal exchange, has been a filter varying in effectiveness according to the adaptations and habitat specializations of the taxa concerned; (2) southward dispersal of New Guinean rainforest forms was impeded partly because rainforests on the cape are disjunct (separated by drier barriers) with the larger and older isolates towards the south; (3) colonization rates have varied with climatic fluctuation; (4) faunal attenuation in both directions is marked (Fig. 5.18), but because of the mosaic of dry habitats and rainforest, is the result of interdigitation as well as intergradation; (5) for the least vagile group (frogs) only one species colonized and survived in the Australian post-Pleistocene rainforest while for birds, which are more vagile, 14 species established themselves in the northern part of the Cape in addition to those that expanded their range southward and speciated since colonization. New Guinean butterflies frequently colonize localities in Cape York and persist for a few years without becoming permanently established.

## Speciation In The Pleistocene

The Pleistocene was a time of enormous change in a variety of the categories discussed above (Keast, 1981b). There were drastic changes in climate with accompanying expansion and contraction of the arid zone and alternating fragmentation and coalescence of peripheral refugia. Sea level lowered and raised, forming and breaking land connections. The scene is one of shifting barriers, boundaries and corridors and of repeated cycles of isolation and renewed contact of populations. These are conditions which favour accelerated rates of speciation.

Whereas divergence at the higher categories probably reflect events from the Tertiary back into extreme antiquity, many modern species and perhaps even genera, may have had their origin in Pleistocene times.

Horton (1984) incorporates climatic and sea level changes and physical barriers into a dynamic model of speciation (Fig. 5.19). A slight expansion and modification of it includes the following stages: (1) migration of a New Guinean ancestral stock into Australia during a suitable climatic period when sea level was lowered (Fig. 5.19a); (2) severing of the land connection and expansion of range southward from Cape York during a moist part of the cycle, separately on the two sides of the Great Dividing Range (Fig. 5.19b); (3) isolation of populations by expanding aridity, assisted by topographic barriers imposed by the Great Dividing Range (Fig. 5.19c); (4) during a second wet phase, the southern coastal species followed a moist, southern corridor into southwestern Australia and, when sea levels were lowered appropriately, into Tasmania (there to be isolated by the next severance of land connections); the species on the drier inland side of the Great Dividing Range followed the drier edge of the corridor into southwestern Australia; the northern isolate expanded southward on both sides of the Great Dividing Range and across a moist northern corridor into northwestern Australia (Fig. 5.19d); (5) a second arid expansion reformed the previous aridity barriers and isolated populations in each of the two northern corners of the continent, two in each of the southern corners, one on either side of the Great Dividing Range in the east and one in Tasmania (Fig. 5.19e). Each of these could form a species, and thus, just from this single sequence of events nine species (counting the New Guinean one) could be generated. During these changes, however, a second speciation cycle could begin by another

or more secondary centres leading to patterns that may obscure the original entry point or centre of origin. For later arrivals without secondary centres of speciation and dispersal, however, present day distributions may indicate the route whereby they entered Australia. Many of the modern arrivals are found only on the tip of Cape York and are closely related to Papuan species. Clearly, the point of entry of such species into Australia is Cape York and the source was Papua. There are other taxa that have most of their species in northwestern Australia and their closest non-Australian relatives are in Timor or other Indonesian islands. Again, both the source and point of entry are obvious. These are the two most common recent points of entry into Australia from the north.

The prevalence of Cape York as a point of entry is probably related to several factors, including its close proximity to New Guinea, its frequent land connections with that land mass during Pleistocene glacials and the presence of "stepping stone" islands in the Torres Strait. Indeed, for many terrestrial taxa the Torres Strait has not constituted a serious barrier; rather, ecological differences between areas on either side have been of critical importance (Kikkawa *et al.*, 1981).

In this regard, the faunal patterns of the islands in Torres Strait are of importance. The western islands are extensions of the Great Dividing Range of Australia and are of Carboniferous igneous rock. In contrast, the eastern islands are of Pleistocene volcanic origin (Jennings, 1972) and are more similar to New Guinean than to Australian habitats. Scattered throughout are coral cays which originated from local reefs. The herpetofauna of the western islands has greater affinities with Australia, whereas that of the eastern ones is allied more closely to the New Guinean fauna (Cogger & Heatwole, 1981; Cogger & Heatwole, in prep.). The fauna of the coral cays contain mainly elements of the widely dispersed Indo-Pacific atoll fauna. This mixture indicates three dispersal routes: one from Australia toward New Guinea via the western islands, another from New Guinea toward Australia via the eastern islands and "sweepstakes" dispersal throughout the area. In each case, the distributions and routes of movement reflect the availability of appropriate habitat.

invasion from New Guinea during low sea-level. Superimposed cycles are not shown in Fig 5.19 in order to prevent confusion.

Successive speciation cycles, like the above, could lead to a concentric pattern of species distributions. The more inland population would be the most dry-adapted (Fig. 5.19) and in wet periods would move further inland, following its drier habitat, to be replaced on the periphery by wet-adapted species. Several species cycles would generate a sequence of east-west pairs of increasing age and dry-adaptedness from the coast toward the inland. Eventually, the most dry-adapted ones might be spread widely in the centre to form an Eyrean distribution. The range of such species could be fragmented by watercourses during wet periods (Fig. 5.14) or by shifts in habitat boundaries.

Horton (1984) bases his model on the skink genus *Egernia*, but it probably has wider applicability as similar distributional patterns occur in such diverse groups as lizards, tabanid flies, birds and plants (Keast, 1981b). Clearly, events would not proceed exactly the same for all taxa. There would be differences in timing, in dispersal rate and sensitivity to moisture. Some isolates might become extinct, thereby eliminating part of the sequence. One would predict, however, that speciation patterns of a variety of taxa of New Guinean origin could be interpreted in this framework.

The timing of such events is not indisputable. Horton (1984) and many other zoogeographers consider them as Pleistocene; they may have been. There were, however, climatic fluctuations and land connections between Australia and New Guinea before the Pleistocene (Doutch, 1972). The possibility exists that Horton's (1984) sequence of events may be correct, but that they occurred earlier than he proposes.

Speciation, regardless of when it occurs, is dependent not only on changes in climate, vegetation and sea level, but upon certain attributes of the organisms themselves. Especially important are vagility, habitat selection and reproductive system. Keast's (1958b) demonstration of this phenomenon in the Australian chats is a good example. *Epthianura crocea*, the Yellow Chat, is sedentary and is found in marshy habitats of several widely separated river systems. Its specialized habitat and lack of movement means that the population in each river system has diverged as a distinct morphological isolate (incipient species) with the potential for producing a new species as long as conditions do not change and cause a coalescence of presently isolated habitats. At the other extreme, *E. tricolor* (the Crimson Chat) inhabits inland plains and savannahs (over a large, relatively continuous area), but shows no regional morphological divergence. This species exhibits nomadism and seasonal movements as an adaptive response to dry, unpredictable environments. Movements are continent-wide and multi-directional and serve to mix individuals from different localities. There are no regular breeding areas or times; the species is opportunistic in these regards. Unless pair bonds are maintained during non-breeding periods or the same ones re-established whenever and wherever conditions again are favourable, such opportunistic breeding would contribute further to mixing of individuals from different geographic origins. The above life history traits probably account for the fact that *E. crocea* is beginning to differentiate into morphological isolates and *E. tricolor* is not. Other species of chats are intermediate.

## ACCOUNT BY TAXA

In the above Sections, the role of refugia, barriers, corridors, biotic interaction, present and past climate and vegetation were assessed in terms of their effect on animal distributions and speciation. Although examples have been supplied for each of these as appropriate, no overall assessment of how
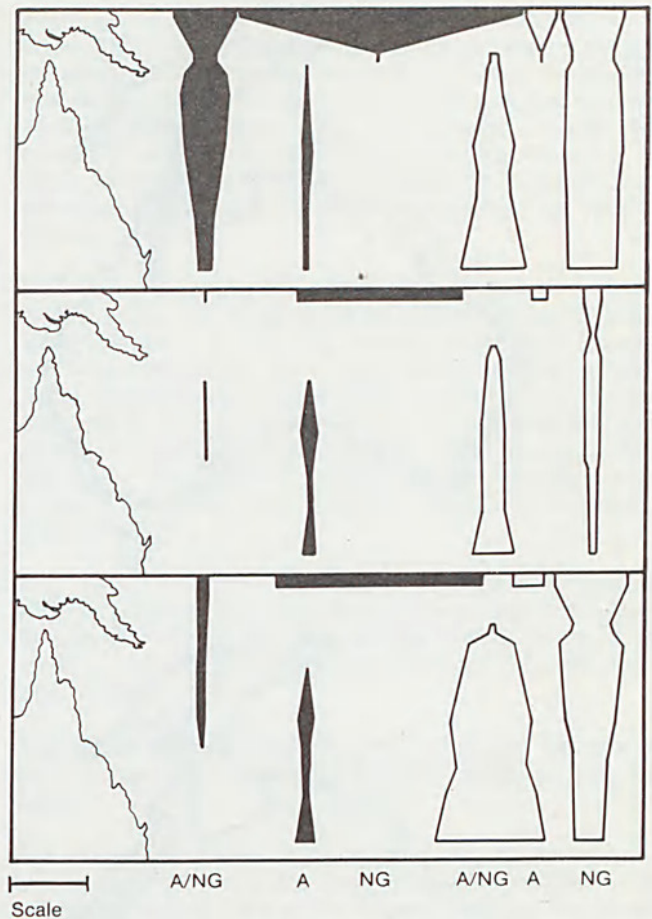


Figure 5.18 Diagramatic representation of the transition in species richness from New Guinea to northeastern Australia of different components of the butterfly (upper), frog (centre) and reptilian (lower) faunas; A = Australian endemic species; NG = New Guinean endemic species; A/NG = species shared between Australian and New Guinea; black figures are rainforest species; white figures are open forest                                      [L. Bridges]

particular taxa have responded to the totality of their environment was made. In this Section, a general synopsis of the major taxa of Australian animals and the factors believed to have influenced their evolution and distribution are presented. Not all instances of the way palaeoclimates and changes in barriers have affected distributional patterns can be given in a brief review such as the present one and to do so in detail would usurp much of the content of the volumes to follow.

## Mammals

The native, terrestrial mammals are of three groups. The marsupials and monotremes collectively account for about 56% of the species, rodents for about 22% and bats for the remaining 22% (Baverstock, 1984).

The monotremes occur in Australia and New Guinea today and are known as fossils only from Australia as forms that resemble the Platypus more than the Echidna (Archer, 1981; Augee, 1984; Murray, 1984).

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Figure 5.19  Postulated sequence of events in the immigration, dispersal and speciation of Australian terrestrial animals originating in New Guinea. Outer narrow line indicates boundary of land masses when sea level was low and New Guinea and Tasmania were connected to Australia. Parallel lines indicate barriers to dispersal. Different symbols indicate populations at different stages of divergence. For further explanation, see text. (After Heatwole, 1976)                                              [D. Horton and L. Bridges]

A recent find of a fossil one from the Early Cretaceous (Archer *et al.*, 1985) is the oldest mammalian fossil from Australia and indicates that monotremes were in Australia well before separation from the rest of Gondwana.

Various views on the origins, phylogeny and migrations of marsupials have been expressed (see reviews by Archer, 1981; Archer 1984b; Kirsch, 1984).

The account by Archer (1984c) is the most comprehensive and evaluative one available and is the basis of the following summary. Marsupials originated in the Cretaceous, either in North America or South America. A diverse radiation in South America produced an array of different forms that invaded many niches and adopted different life styles. Among these were the microbiotheriids, the only South American group of marsupials belonging directly to the lineage giving rise to all known fossil and living Australian marsupials. Microbiotheriids probably dispersed southward into Antarctica and then to Australia in the Late Cretaceous or early Tertiary times, where they radiated into a great diversity of animals rivalling that of placental mammals in other continents and showing a number of convergences (sometimes previously mistaken for evidence of relationship) with the South American radiation. Among the extinct and living Australian forms are the equivalents of placental lions, cats, tapirs, rodents, wolves, marmots, moles, flying squirrels, as well as many types not directly comparable with any non-marsupial. The extinct species included giant, spectacular beasts, some of which lasted up through the Pleistocene and were contemporaries of Aboriginal man.

The microbiotheriid diversification probably began in Antarctica-Australia prior to the separation of Australia, with establishment soon thereafter of the three major Australian lineages: the Dasyuroidea, the Perameloidea and the Diprotodonta (Archer, 1984c).

The dasyuroids comprise three living (or recently extinct) families of 42 carnivorous or insectivorous species. The family Dasyuridae includes the genera of small mouse-like, rat-like or possum-like marsupials known as antechinuses (*Antechinus*, *Parantechinus*, *Pseudantechinus*), phascogales (*Phascogale*), dunnarts (*Sminthopsis*), planigales (*Planigale*), mulgaras (*Dasycercus*), kowaris (*Dasyuroides*), ningauis (*Ningaui*) and kulltarrs (*Antechinomys*), as well as medium sized quolls or native cats (*Dasyurus*) and the larger Tasmanian Devil (*Sarcophilus harrisii*) (Strahan, 1983). The other two families have only one species each. The Myrmecobiidae, represented only by the Numbat (*Myrmecobius fasciatus*) is now restricted to southwestern Australia and is endangered. The Thylacine or Tasmanian Wolf (*Thylacinus cynocephalus*) probably became extinct in the 1930's (see Chapter 20). It had become restricted to Tasmania, possibly eliminated on the Australian mainland by the Dingo.

The omnivorous Perameloidea include the bandicoots (Peramelidae, four genera and nine species) and the bilbies (Thylacomyidae, one genus, two species).

The herbivorous Diprotodonta has the greatest richness of living species (75), the most diversity of form and habit of any of the Australian marsupials and includes most of the spectacular, now extinct forms. There are three main lineages of living ones, (1) the Vombatoidea which includes wombats (Vombatidae, two genera, three species) and the Koala (Phascolarctidae, *Phascolarctos cinereus*), (2) the Phalangeroidea (possums) which includes the ringtails and large gliders (Petauridae, five genera, 11 species), the brushtails and cuscuses (Phalangeridae, three genera, six species) and the pygmy possums and feathertail gliders (Burramyidae, three genera, six species) and (3) the Macropodoidea which contains the potoroos, bettongs and rat-kangaroos (Potoroidae, five genera, nine species) and the kangaroos and wallabies (Macropodidae, nine genera, 39 species).

There are two groups which have not been included in the above scheme because their relationships to other marsupials are problematical. One is the monotypic family Tarsipedidae (the Honey-possum, *Tarsipes rostratus*); it may belong to the Phalangeroidea (Archer, 1984c; see Chapter 33, this Volume). The other are the marsupial moles (*Notoryctes*) of the family Notoryctidae. They have become so morphologically specialized as burrowing animals that phylogenetic relationships are not clear.

This amazing marsupial radiation has produced, probably from a single microbiotheriid stock, nearly the entire gamut of mammalian types known, including arboreal, terrestrial and burrowing forms. They have become adapted to stark desert, tropical rainforest and cold alpine heath and all environments in between. There are carnivores, insectivores, omnivores, herbivores and nectar feeders. They hop, run, climb and glide. The adaptive radiation of the Australian marsupials is one of the most fascinating chapters in the book of evolution.

The fossil record in Australia is inadequate to indicate whether placental mammals of Gondwanan age ever existed in Australia. If they did, they became extinct. None of the modern Australian placental fauna belongs to the old Gondwanan Element.

Australia's native terrestrial placental mammals are only of three groups, rodents of the family Muridae, bats and humans.

The rodents originated in Asia, probably in the Miocene (about 25 mybp) and dispersed southward, probably first reaching Australia only in the Pliocene (four to five mybp) (Hand, 1984). Divergence at the subfamilial and tribal level probably took place outside the region with entry into Australia by different stocks taking place in three different waves.

The tribe Conilurini contains eight genera and 40 species of hopping mice (*Notomys*), tree-rats (*Conilurus*), rabbit-rats (*Mesembriomys*), stick-nest rats (*Leporillus*), rock rats (*Zygomys*) and some other rat-like taxa (Baverstock, 1984). They have diversified primarily in the semi-arid regions. There are two distantly related species of water rats (tribe Hydromyini). One (*Hydromys chrysogaster*) occurs in waterways throughout Australia and the other (*Xeromys myoides*) usually is found in mangroves. The genera *Uromys* and *Melomys* (tribe Uromyini) are tropical to subtropical rats occurring in forests and grasslands in the north; they are closely related to New Guinean taxa. Finally, the true rats (genus *Rattus*; subfamily Murinae) occur throughout Australia, but with the greatest species richness in coastal Queensland.

Both suborders of bats are well represented in Australia (Hall, 1984). The Megachiroptera or fruit bats are represented by one family (Pteropodidae) with five genera and eight species. They feed on fruit and/or nectar. Generally, they are confined to the northern and eastern parts of the continent. The Microchiroptera includes the insect-eating bats and are represented in Australia by five families, 16 genera and 51 species. Bats evolved from a small nocturnal insectivore in the Late Cretaceous or Early Eocene. Their early radiation occurred in the Old World and they entered Australia from the north prior to the Miocene (Hall, 1984). They are most abundant in the north; 57% of all Australian species occur on Cape York with decreasing numbers southward (17% in Tasmania). The eastern coast has a greater species density than other parts of the continent at equivalent latitudes. Availability of roosts seems to be one of the important local factors influencing distribution.

Humans reached Australia and became established as part of the native fauna certainly more than 30,000 years ago as evidenced by fossil remains. Some estimates would place it as much as 120,000 years ago (Archer & Aplin, 1984). There probably was more than one early entry.

## Birds

Some birds cross water gaps relatively easily and hence Australia was never so isolated from them as it was from many other taxa. As a result, the origin and time of arrival of some groups of birds in Australia is shrouded in mystery (Keast, 1981a; 1984). There are some groups, however, whose history is less in doubt. Some of the higher taxa, such as the ratites (emus and cassowaries), penguines, megapodes and parrots are almost certainly of Gondwanan origin. The kingfishers (Alcedinidae) have been in Australia a long time and have undergone extensive radiation within the continent and produced some distinctive endemics. Whether they were present prior to separation of Australia from Antarctica or were merely an early group to cross the still extensive water gap during northward movement cannot be ascertained from available data.

In contrast to previous views (Keast, 1981a; 1984), more recent evidence from Sibley & Ahlquist (1985) indicates that the Australian oscine passerine birds are in two major groups, each with a different history. The Corvi (three super-families and ten families in Australia and New Guinea, including the lyrebirds, Menuridae, and scrub-birds, Atrichornithidae, in the classification of Sibley & Ahlquist) is an old group which began its radiation 55 to 60 mybp, *i.e.*, while Australia was still connected to Antarctica. It probably originated in that part of Gondwana that is now Australia rather than having diverged from a South American group. The other oscine group (Muscicapidae) originated either in Africa or Asia. As Australia approached Asia during the Tertiary, two types of movement occurred. Members of the Corvi dispersed from Australia to Asia and radiated there and in other parts of the world; members of the Muscicapidae colonized Australia from Asia. The suboscines, as redefined by Sibley & Ahlquist (1985), are represented in Australia only by the pittas (Pittidae) which are recent arrivals from the north.

## Reptiles

Among the extant reptiles of Australia, none is of certain Pangaean origin. The ancient and diverse reptilian fauna included dinosaurs of various types as well as a wide variety of other forms. These groups became extinct without leaving any derivative modern forms.

One of the curious features of the history of reptiles in Australia is that the most diverse and successful modern taxon, the Lacertilia, may have originated in Australia in Pangaean times. There are fossils of the very earliest lizards from the lower Triassic of Australia (Molnar, 1983b; 1984a). Estes (1983) postulates Australia to have participated in a Pangaean origin for the modern families Gekkonidae, Agamidae and Scincidae. One view is that many of the present day representatives of these families in Australia can trace a continuous lineage there from Pangaean times. All three families have radiated extensively in Australia. The more common view, however, is that except for the geckos, these lizards thrived and radiated elsewhere in the world, but disappeared from Australia until their re-invasion upon contact of the Australian and Asian Plates millions of years later (Tyler, 1979a; Heatwole & Taylor, in press). Although a firm decision on this matter cannot be made because of the incompleteness of the fossil record in Australia, the latter view is the one tentatively followed in this Chapter.

The turtle family Chelidae (side-necked tortoises) is certainly a Gondwanan taxon. The only places other than Australia in which it occurs is South America and New Guinea. By contrast, other families of turtles (except sea turtles and one recent immigrant from New Guinea, see below) are now absent from Australia.

The gekkonid subfamily Diplodactylinae is another likely reptilian candidate for a Gondwanan origin (Tyler, 1979a). It has radiated extensively in Australia. The suggestion by Kluge (1967b) that diplodactylines had a southwestern Asian origin no longer seems tenable (Tyler, 1979a). The family Pygopodidae (scaly-foots) is derived from geckos within Australia and attests to the antiquity of the gekkonid lineage there.

Most Australian reptiles probably belong to the Asian Tertiary Element. Many have radiated extensively and were probably among the first groups to enter the continent as it approached the Asian Plate.

The skinks are diverse and have the largest number of species in Australia (nearly 300) of any reptilian family. They have radiated into a variety of arid and mesic habitats and obviously have a long history on the continent. Cogger & Heatwole (1981; 1984) consider that they probably arrived on a number of occasions and that separate histories would have to be traced for different subfamilies or even genera, before their history could be understood fully. That task is hampered by an imperfect knowledge of their taxonomy.

The successive invasions of varanids and agamids already have been discussed. Most of them probably first entered in the Tertiary, but a few invasions may have occurred in the Pleistocene.

The terrestrial Elapidae (front-fanged venomous snakes) probably originated in Asia and reached Australia when more primitive colubrids (their ancestors) were waning in Asia and before the modern colubrid radiation began (Cogger & Heatwole, 1981). They show extensive radiation in Australia and are the dominant family of snakes. The Typhlopidae (blind snakes) and Boidae (pythons) have radiated in Australia, presumably from ancestors arriving from Asia in the Tertiary.

The geckos of the subfamily Gekkoninae are pantropical and are remarkable for their powers of transoceanic dispersal. They probably entered Australia several different times and their origins are obscure. Some of them, like the genera *Heteronotia* and *Phyllodactylus*, have speciated in Australia and probably arrived in the Pleistocene or perhaps Tertiary. Species of the genera *Cyrtodactylus*, *Hemidactylus* and *Lepidodactylus* are not restricted to Australia, but are widespread on islands, beaches and strands. They probably invaded repeatedly from a variety of sources, up to the present time (Cogger & Heatwole, 1981).

By the Pleistocene, many modern genera of Australian reptiles were present and even a number of extant species were represented as fossils (see review by Heatwole & Taylor, in press). These genera had become widespread in Australia and had undergone a certain amount of adaptive radiation. Speciation and further adaptive radiation within Australia was influenced greatly by Pleistocene events (see below), but few new, higher taxa made their appearance in Australia after the Tertiary. The Quaternary was short in comparison to the Tertiary and the rate of immigration per unit time may not have changed. Alternatively, most niches may have become filled or the pool of potential dispersers had become exhausted.

A probable Pleistocene entry has been postulated for the *indicus* group of varanids (goannas), the gekkonine geckos, the Pitted-shelled Turtle *Carettochelys*, the agamids *Gonocephalus* spp. and *Physignathus lesueurii* and the terrestrial colubrid snakes (Cogger & Heatwole, 1981). The latter group is worldwide in distribution and has radiated extensively in all continents but Australia. They account for most of the species of snakes in the world. Yet, only three terrestrial genera (containing five species) occur in Australia. Cogger & Heatwole (1981; 1984) suggest that they probably arrived late in New Guinea and entered Australia from there during a Pleistocene regression of Torres Strait or by fortuitous seawater dispersal.

A note of caution regarding the above interpretation of reptilian history should be sounded. Although the consensus view (and that of the author) is reported in this account, there are some that would consider certain elements, indicated as Asian Tertiary ones in this Chapter, to be Gondwanan. For example, Schuster (1980) suggests a Cretaceous, Gondwanan age for some scincid lineages in Australia. Witten (pers. comm.) considers some of the Australian agamids as part of the Gondwanan Element. An open mind should be maintained regarding the age of some of the more extensive of the reptilian adaptive radiations; they may be older than currently believed.

## Frogs

Ancient amphibians or labyrinthodonts were present in Australia and reached their greatest diversity there in the early Triassic (Warren, 1983). They subsequently became extinct worldwide, are not known in Australia after the Early Jurassic (before the fragmentation of Gondwana) and have no significance for the modern Australian amphibian fauna.

All modern Australian amphibians are anurans (frogs), most of which are clearly of Gondwanan origin (Tyler *et al.*, 1981). Although there are no frog fossils from Australia prior to the mid-Miocene (Tyler, 1983), the combined circumstantial evidence of South American affinities and extensive adaptive radiation into many habitats throughout Australia, indicate a Gondwanan origin for the two major families, the Hylidae and the Myobatrachidae (Tyler, 1979a; White, 1984), which account for 94% of the total frog species of Australia.

Speciation within these old families has been traditionally interpreted along the same lines as Horton's (1984) model, discussed above. That is, expanding and contracting aridity and rising and lowering sea levels in the Pleistocene alternately isolated populations in southwestern Australia and Tasmania and permitted their expansion and reinvasion. Speciation was postulated to have occurred during periods of isolation. Series of sibling species of different degrees of affinity with southeastern taxa were considered to represent sequential episodes of immigration and isolation. This pattern seems to occur in various taxa of Gondwanan origin (Main *et al.*, 1958; Littlejohn, 1961; 1981; Watson & Littlejohn, 1985). It corresponds closely with known Pleistocene events. Migration is viewed as having taken place primarily from southeastern Australia into southwestern Australia during moist periods, with much less movement in the reverse direction. Some movement is postulated in both directions between southeastern Australia and Tasmania during sea level lowering (Watson & Littlejohn, 1985).

Some of these interpretations are contested by Roberts & Maxson (1985) on the basis of immunological and electrophoretic studies. They suggest *in situ* speciation in southwestern Australian frogs rather than multiple invasion from the east. The taxa studied were *Crinia* and *Heleioporus*, genera previously viewed as providing support for the multiple invasion hypothesis.

The research of Robert & Maxson (1985) also calls into question the timing of the separation of southeastern and southwestern taxa. Whereas the multiple invasion hypothesis places it as occurring in the Pleistocene, Roberts & Maxson suggest, on the basis of molecular clocks, that it took place in the Tertiary. That molecular clocks keep constant time and run at the same speed in all organisms seems to be an article of faith among the devotees of this approach, but is disputed by some biochemists (Tamiya, pers. comm.). The multiple invasion hypothesis, however, does not provide an adequate explanation of frog speciation in southwestern Australia and the timing of separation of eastern and western frog faunas must be reconsidered carefully.

Essentially, the controversy is whether the biogeography and speciation of these frogs conforms to a Pleistocene dispersal model or to a Tertiary vicariance one. Regarding these two explanations as mutually exclusive alternatives, however, restricts heuristic thinking. Observed biogeographic patterns likely arose as a result of vicariant processes in combination with dispersal. The task is to separate the relative importance of the two. Two separate aspects of the problem must be distinguished. The timing is a different problem from that of whether dispersal or vicariance played a major role. Linking these two aspects may lead to unrealistic polarization in interpretation.

In light of the above, a reassessment of the origins of Tasmanian frogs and other groups, such as lizards, may be warranted. Does the older taxon (frogs) display a Tertiary separation with *in situ* speciation patterns that superficially track Pleistocene events? Has the more recently arrived taxon (lizards) actually undergone speciation in the Pleistocene? Or, do Australian lizards parallel the situation proposed by Roberts & Maxson (1985) for frogs and have they an earlier arrival time in Australia than usually postulated? Clearly more research is required. The biogeography and speciation of Australian hylid and myobatrachid frogs will be an important part of that research.

In contrast to the Gondwanan families Hylidae and Myobatrachidae, the Microhylidae is part of the Tertiary Asian Element. This family is widespread throughout the world, but poorly represented in Australia (two genera with eight species, all on Cape York Peninsula or in Arnhem Land). Tyler (1979a) suggests that they occurred on the outlying Asian islands which became incorporated in the mid-Miocene into the island of New Guinea. They were able to radiate into the newly forming moist montane environments of New Guinea by virtue of having direct development on land (no free-living tadpole stage, but hatching as miniature froglets). Direct development has arisen independently in other groups of frogs in various moist mountainous regions (Goin & Goin, 1962), but is absent in other Asian microhylids. This mode of development avoids the hazards to aquatic larvae posed by fast-flowing montane streams. The Australian microhylids represent an extension of this peculiar New Guinean radiation, but in a different ecological context. In Australia their radiation is associated, not with steep mountainous regions, but with habitats where there is a shortage of suitable aquatic breeding sites. The migration from New Guinea to Australia may have been a Pleistocene event (Tyler *et al.*, 1981).

The only other amphibians in Australia are a species of Ranidae, a very recent invader from New Guinea, and *Bufo marinus*, a toad introduced by man.

## Arachnids

The Australian arachnids include scorpions, spiders and mites as well as four minor groups, the Opiliones (harvestmen), Pseudoscorpionida (false scorpions), Amblypygi

(whip scorpions) and Schizomida. The Australian harvestmen occur in three suborders, six families and about 35 genera. Most occupy temperate, humid forests with low foliage and abundant litter, although there are species from semi-arid regions or caves. Main (1981c) lists their origin as mostly Gondwanan but with some of northern, including New Guinean, affinities. Pseudoscorpions are represented in Australia by seven families, 24 genera and over 50 species. They are found primarily in temperate humid forests and sclerophyll forests where they are cryptozoic; one occurs in arid regions. Most are of Gondwanan origin although some have northern affinities (Main, 1981c). The Amblypygi and Schizomida are ancient arachnids primarily found in the humid tropics. They are represented in Australia only by a few species in the north which are probably tropical relicts (Main, 1981c). Scorpions are not diverse in Australia, comprising only three families, six genera and 29 species (Koch, 1977; 1981). The family Bothriuridae (only two Australian species) is of Gondwanan origin, the Australian genera having South American affinities. The others (Buthidae and Scorpionidae) have northern affinities and evolved from Asian stock since Australia moved northward in the Tertiary (Koch, 1981).

The Australian native spider fauna is diverse, containing 46 families and 338 genera of which 62 genera are in the family Salticidae (jumping spiders). There are three introduced families (Main, 1981c). The spiders constitute an ancient, persistent and relatively immutable group of animals. The more generalized and widespread extant families probably go back to the early Mesozoic and perhaps some of the modern genera do; some gnaphosid genera derive from the Early Jurassic.

The kinds of vertebrates that shared the terrestrial environment with some of the older genera of spiders have long since disappeared entirely or are represented today by descendants that depart so widely from their Jurassic ancestors that the relationship is evident only by virtue of the continuity of the fossil record. The significance of the great antiquity of the lower taxa of spiders is that some events influencing their modern distributional patterns may be identifiable further back in time than those affecting terrestrial vertebrates at the same taxonomic level.

Main (1981a) considers the global distribution of Australian spiders to fall into five categories, each with its own historical interpretations. They are: (1) widespread, including cosmopolitan, circumtropical and circumtemperate; (2) on southern continents; (3) Asian and/or Melanesian-Polynesian-Australian; (4) common to Australia and New Zealand; and (5) Australian only. The majority (55%) of the families are in the cosmopolitan category and most families are considered to be ultimately of northern origin (probably Pangaean). Though this classification applies primarily to families, generic examples also are given.

The Australian spider fauna has multiple origins. Taxa may be widespread for two very different reasons. Some were once continuously distributed over a large land mass which subsequently fragmented, leaving far-flung faunal relicts on the various continents, often with local ranges restricted through climatic change. Others are widespread because they disperse readily across oceanic gaps.

Many orb-weaving spiders of several families, and even some terrestrial ones, practise aerial dispersal of young spiderlings by ballooning on gossamer. In some cases, they may be carried for thousands of kilometres and intercontinental dispersal would seem to be a possible explanation of extensive distributions. Even such a cosmopolitan family as the Araneidae, however, renowned for aerial dispersal of young, has many genera with restricted distribution. Habitat and climate often may have a greater affect on distribution than dispersal

abilities. Main (1981a) concludes that only a few individual species such as *Argiopa fuscata*, *Latrodectus mactans* (the Red-back) and some sparassids maintain an intercontinental distribution by aerial dispersal. Although the separation of dispersal factors from historical ones is not always possible, ballooning does not appear to adequately explain the global distribution of the widespread Australian families. Many of these widespread families (and genera) probably attained cosmopolitan distribution on Pangaea and survived in Australia throughout the subsequent fragmentation and movement of continents (Main, 1981a).

The taxa with more restricted distributions probably had a different history. About 19% of the Australian spider families have an exclusively southern distribution. Certain families and lower taxa have affinities only with other Gondwanan regions, such as South America, New Zealand, New Caledonia, New Guinea or some combination of these (Main, 1981a;b). It is tempting to speculate that these are taxa which developed in Gondwana after it split from Pangaea. Not all southern distributions, however, necessarily reflect a Gondwanan origin; some taxa, presumed to be of Gondwanan origin, were later found to be remnants of a wider Pangaean range (for example, *Hickmania* and the Symptognathidae) (Main, 1981a). Although most families of spiders appear to have an ultimate northern (Pangaean?) origin, the Migidae, Actinopodidae, Hexathelinae and families with obvious New Zealand origin are probably Gondwanan relicts. Taxa of northern origin which have entered Australia relatively recently include the family Theraphosidae and various ctenizid genera, some of which are restricted to Queensland (Main, 1981a;b;c)

Within Australia, the distribution of particular species depends on their ecological amplitude. Main (1981a) classifies the major patterns of distribution of spiders within Australia as: (1) widespread (southern continental, tropical or throughout the continent); (2) eastern Australia; (3) temperate and subtropical wet forest habitats (southeastern Australia, southwestern Australia, refugia in central Australia, isolated montane areas and riverine situations); (4) caves; (5) disjunct east-west distributions; and (6) offshore islands. Some of these patterns seem to be related primarily to present day habitat and climate. Many species are dispersed so easily that their main restriction may be presence or absence of suitable habitat.

Although particular species may have very specific requirements, as a group, spiders occupy most habitats in Australia, from the tropics to cool alpine regions, from rainforest to desert. There are cavernicolous species and others that inhabit such inhospitable places as the high tide splash zone of seashores. Their adaptive radiation is reviewed at length by Main (1981a).

Spiders have reacted to changing conditions by both kinds of responses discussed above; some remain restricted to wet refugia like rainforests and others have adaptively radiated into arid and semi-arid habitats.

## Insects

Hexapods are first known from the Middle Devonian and true insects from the Late Devonian (over 350 mybp); they are an ancient terrestrial group. The Australian fossil record includes material from about 350 species of 19 orders stretching from the upper Carboniferous (about 300 mybp) to about the Pliocene (Riek, 1970a; 1974).

There are three classes of non-insectan hexapods and 26 orders, 585 families and about 54,000 species of true insects known in Australia (CSIRO, 1970) (Table 5.1). There are

many species yet to be described. Clearly, only the briefest of summaries can be given here for such a large and diverse group.

Mackerras (1970), in a review of the zoogeography of Australian insects, points out that the Archaic Element mostly consists of groups that have changed little since the Paleozoic or Mesozoic. Some are patchily distributed relicts such as the mecopteran family Meropeidae (North America, Australia), the dipteran genus *Nemopalpus* (Neotropics, Canary Islands, South Africa, Malaysia, Australia, New Zealand; fossils in Baltic amber) or the beetle genera *Cupes* and *Rhysodes* (Howden, 1981). Whether patchy distributions reflect ability to cross barriers and colonize new areas or are cases of extinction of once widespread taxa may not always be possible to ascertain. Others are not relicts, but are widespread and currently successful. Examples are the Blattodea (roaches), the lepidopteran family Hepialidae (found worldwide but with greatest development in Australia and dating back to the Cretaceous; Tindale, 1981) and many worldwide beetle genera from various families (Howden, 1981).

The Gondwanan Element has undergone extensive radiation and forms a significant faunal component of most orders of insects from Ephemeroptera to Coleoptera (Kuschel, 1960; Mackerras, 1970). This element often represents a rather early level in the evolution of those orders, for example in the more primitive sections of nearly all of the Nematocera and Orthorrhapha (Diptera). Tindale (1981) gives the lepidopterans of the superfamily Dastnioidea and Howden (1981) the scarabs of the subfamily Dynastinae and the lucanid beetles as other examples. The Old Northern Element also can be recognized among the insects as relatively old taxa that have northern affinities or affinities with India or Africa via Asia (Mackerras, 1974). Extensions of this element into Australia are mostly small, although in some cases, the extent of diversification suggests a relatively long occupancy of the continent.

The Oriental Element forms the most highly evolved and conspicuous part of almost every insect order. It has undergone considerable speciation within Australia, but comparatively little diversification at the higher taxonomic levels.

The Modern Element contains a variety of taxa characterized more by their powers of dispersal than by their geologic history. For example, some very primitive hexapods such as collembolans as well as more advanced insects like aphids and chironomid flies, because of their small size, are carried widely by air currents (Mackerras, 1970). In addition to this "aerial plankton", there are larger insects with good powers of flight that disperse widely either under their own power, such as some Odonata and Lepidoptera, or by unusual weather conditions. There is a number of cases of migration between Australia and New Zealand of butterflies (Tindale, 1981) and beetles (Howden, 1981).

## Land Molluscs

The fossil record of terrestrial molluscs in Australia only goes back to the Miocene and interpretation of their early history is difficult. Bishop (1981), however, tentatively indicates the probable origins of the 24 families known from Australia. He lists six of them as widespread and probably present in Australia by the Tertiary (Pangaean?), two as very old Asian-Pacific families, seven as Gondwanan and nine as probably mid-Tertiary invaders from Asia.

The present distributional patterns are determined to a great extent by climate, vegetation and nutrients. Although there are some snail taxa that are remarkably adapted to prolonged drought, including some found in desert habitats in Australia, most land molluscs are highly sensitive to moisture loss and

Table 5.1 The taxa and geographic affinities of the known Australian hexapod fauna. Data primarily from CSIRO (1970); numbers of known species have increased since 1970 and many more remain to be described; *plus 2 superfamilies.

| CLASS OR ORDER | FAMILIES FOUND ELSEWHERE BUT NOT IN AUSTRALIA | NO. OF AUSTRALIAN Families | Species |
|---|---|---|---|
| COLLEMBOLA | 0 | 5 | 215 |
| PROTURA | 0 | 3 | 30 |
| DIPLURA | 1 | 3 | 32 |
| INSECTA | | | |
| Archeognatha | 1 | 1 | 3 |
| Thysanura | 2 | 3 | 23 |
| Ephemeroptera | 7 | 4 | 124 |
| Odonata | 8 | 16 | 248 |
| Blattodea | 1 | 4 | 439 |
| Isoptera | 1 | 5 | 182 |
| Mantodea | 6 | 2 | 118 |
| Dermaptera | 2 | 5 | 60 |
| Plecoptera | 3 | 4 | 84 |
| Orthoptera | 13 | 13 | 1 513 |
| Phasmatodea | 0 | 2 | 132 |
| Embioptera | 5 | 3 | 65 |
| Psocoptera | 6* | 21 | 120 |
| Phthiraptera | 5 | 10 | 208 |
| Hemiptera | 16 | 88 | 3 661 |
| Thysanoptera | 2 | 3 | 287 |
| Megaloptera | 0 | 2 | 16 |
| Neuroptera | 2 | 15 | 396 |
| Coleoptera | 38 | 114 | 19 219 |
| Strepsiptera | 0 | 5 | 93 |
| Mecoptera | 2 | 5 | 20 |
| Siphonaptera | 8 | 9 | 68 |
| Diptera | 28 | 87 | 6 256 |
| Trichoptera | 6 | 18 | 260 |
| Lepidoptera | 29 | 76 | 11 221 |
| Hymenoptera | 14 | 59 | 8 834 |
| TOTAL | 206* | 585 | 53 927 |

are found in relatively wet, shady environments. Much of the Australian environment is inhospitable and numbers of species in any given area are not high by world standards (Bishop, 1981). The deficiency of Australian soils in nutrients such as nitrogen, phosphorous and calcium (see Chapter 4, this Volume) affects snails and may limit their distribution. Shell formation, for example, requires considerable calcium. The eastern coast of Australia has the most eutrophic soils and provides forest habitat with adequate moisture and shelter. This area, not surprisingly, is the most favourable in Australia for terrestrial molluscan life (Bishop, 1981).

## Oligochaetes

Oligochaetes are in three orders, the Lumbriculida and Tubificida (microdriles) and the Haplotaxida (earthworms). Collectively, they are represented in Australia by 10 of the 25 worldwide families. The native terrestrial oligochaetes, however, involve only two families, the Enchytraeidae (Tubificida) and the Megascolecidae (Haplotaxida). The remainder are either widespread anthropochorous species or are aquatic and hence outside the scope of this Chapter.

The enchytraeids are known so poorly in Australia that little can be deduced of their history, affinities or distributions.

Both Australian subfamilies of megascolecids, the Acanthodrilinae and Megascolecinae, have nearly worldwide distributions (though largely excluding the Palaearctic) which

may reflect a former Pangaean distribution. The lower taxa of both subfamilies, however, in Australia have strong affinities with other southern areas and particularly so with New Zealand and New Caledonia. Affinity with India is especially interesting. The non-pheretimoid part of the tribe Megascolecini occurs both in India and Australia. Since India was the first major land mass to separate from Gondwana, the taxon must be ancient. Yet, this group is absent from Africa and South America which separated from Gondwana later. These earthworms may have had a restricted distribution on Gondwana that included the Australian-Indian segment, but not the African-South American one (Jamieson, 1981).

Other than general Pangaean relationships, the affinities with northern regions are slight. A post-Miocene inflow of pheretimoids (tribe Megascolecini) from Asia is still in progress. Movement has been greater in the opposite direction, as two tribes, the Dichogastrini and Megascolecini, have representatives that invaded the Oriental Region from Australia (and India) in the Cainozoic and spread as far as China and Japan (Jamieson, 1981).

In summary, some Pangaean earthworm elements reached Australia via Gondwana where they diverged in isolation; later there was a small two-way exchange with Asia in the Cainozoic.

## Other Taxa

There are some terrestrial groups that have not been discussed, either in the above Section treating individual taxa or in the general discussions of the various faunal elements. Some of these have been mentioned briefly by Main (1981c) who notes that some of the centipedes are of Gondwanan origin, some of Old Northern and some of more recent northern derivation.

Others, including terrestrial flatworms, leeches, mites, tardigrades, protozoans and many insect groups have not been reviewed in the context of modern ideas of plate tectonics. Their taxonomy and distribution is inadequately known.

# THE AUSTRALIAN TERRESTRIAL FAUNA IN A GLOBAL PERSPECTIVE

The virtual isolation of Australia from other continents during its northward movement between the Late Paleocene and the Miocene and its partial isolation from the Miocene to the present time has resulted in a terrestrial fauna that is unique in several ways.

The taxonomic composition of the Australian fauna differs from that of other continents. In many cases, a taxon of a comparatively low level has radiated adaptively in Australia in much the same way as another taxon of the same Class has radiated elsewhere. For example, marsupial mammals take the place of eutherians, elapids the place of colubrids and so on. Such replacement may even occur at higher taxonomic levels. The significance of these taxonomic "imbalances" is discussed below.

## Missing Or Poorly Represented Taxa

There are two scenarios that may be invoked to account for a missing or depauperate taxon in Australia. One is that the taxon originated elsewhere after the fragmentation of Australia from Gondwana and either has not reached Australia subsequently (missing taxon) or has only done so recently and has not had sufficient time to spread, adaptively radiate and diversify (depauperate taxon). The second is that the group was present at the time of separation, but subsequently became extinct in Australia and has not (missing taxa) or has only recently (depauperate taxa) reinvaded the continent.

Whether missing taxa have been unable to reach Australia or whether they have arrived (or do arrive periodically) but fail to establish may not always be clear. In the latter case, the physical environment may be different from that of the place of origin and to which they are adapted or they may find a favourable physical environment, but be unable to compete successfully with already established species. Clearly, detailed ecological studies would be required to resolve such hypotheses.

Taxa that clearly belong to Scenario 1 would be those whose fossil record indicates they did not originate until after Australia separated from Antarctica and whose pattern of distribution in Australia would suggest recent entry. There are a number of examples that fit this combination of characteristics, including most of the modern and some of the Asian Tertiary Elements.

The frog genus *Rana* (family Ranidae), for example, is known first from the Miocene of Europe and Asia and the Miocene, Pliocene and Pleistocene of North America (Dowling & Duellman, 1974–78). Extant members of the genus are nearly cosmopolitan although they are represented poorly in South America and do not occur at all in the southern part of that continent. The sole Australian species, *Rana daemeli* (closely aligned with the New Guinean *R. papua*), occurs only on Cape York Peninsula (Cogger, 1979). This genus (and probably the subfamily Raninae) thus originated after Australia had separated from the rest of Gondwana. Only one species succeeded in reaching Australia and then only recently, having scarcely diverged from the New Guinean form.

The turtle family Carettochelydidae now consists of only one species, *Carettochelys insculpta*, found in the rivers of the southern coast of New Guinea and in a few rivers in the Northern Territory. The fossil record of this family goes back to the upper Cretaceous to Oligocene of Europe and North America and to the Miocene in New Guinea. This suggests that the family originated in the north but did not reach Gondwana, but rather, arrived in New Guinea from the north by the Miocene and only recently reached Australia from New Guinea (Scenario 1). It is probable that previous post-Tertiary invasions may have occurred as there are fossils that may be *Carettochelys* from the Pleistocene of Windjana Gorge, Western Australia (Molnar, 1983a).

Some old groups seem to belong to Scenario 1. Several widespread groups of earthworms are absent in Australia. All of the families of the Lumbricoidea (except for introduced species) are absent, even though the group probably originated in the Triassic or earlier. Similarly, the family Ocnerodrilidae, supposedly Pangaean and with probable origin in South America-Africa is not in Australia. Jamieson (1981) suggests that Australia may not have been warm enough in the Mesozoic to support this heat-loving group. The lack of a fossil record ensures that much of this remains speculation; why these worms are not part of the Australian fauna is a mystery.

Eutherians are very depauperate in Australia. Of the world's terrestrial orders, 11 are missing from Australia, though most are distributed widely elsewhere. They probably never reached Australia, not surprising in light of the fact that only one stock of marsupials (the microbiotheriids) did. Gondwana, perhaps because of its archipelagic nature, does not seem to have been a continent easily crossed by mammals. The three orders of eutherians that did reach Australia came in the Tertiary or later, have not radiated extensively and are depauperate by world standards.

Amphibians are represented poorly in Australia at the higher taxonomic levels. Of the four extant orders, three, Gymnophiona (caecilians), Caudata (salamanders) and Meantes (sirens) are absent and probably were never there. Even the Anura, the only order present, is represented by only two families with extensive radiations and two depauperate ones which are relatively recent arrivals.

The softshell turtles (family Trionychidae) do not occur now in Australia although they are widespread in Asia, Africa and North America (Bellairs, 1969; Dowling & Duellman, 1974–78) and are known as fossils from South America. Their fossil record dates back to the Jurassic (Molnar, 1983a). Hence, they antedate the breakup of Gondwana and were distributed in southern continents. Trionychids are known from the Pliocene of Queensland (Molnar, 1983a; Molnar, 1984b), that is, well after Australia had separated from Antarctica. Softshell turtles probably were part of the Gondwanan fauna that persisted in Australia after it became isolated, but became extinct and have not succeeded in re-establishing in Australia in modern times. They provide a clear example of Scenario 2. Because of the poor fossil record, other taxa whose absence may be accountable by Scenario 2 are difficult to identify. Indeed, if the few fossils of trionychid turtles had not been found in Australia, that family would probably be allocated to Scenario 1 rather than Scenario 2.

Examples of missing fauna which cannot be assigned confidently to either Scenario are: two orders of insects, Zoraptera (Smithers, 1970) and Grylloblatoidea (Key, 1970), the stonefly suborder Setipalpi (Riek, 1970b), flies of the ancient and widespread family Ptychopteridae (Colless & McAlpine, 1970), several otherwise worldwide groups of Hymenoptera (Riek, 1970c), a number of spiders, the arachnid orders Solpugida (sun spiders), Uropygi (whipscorpions) and Ricinulei (Main, 1981c) and the reptilian order Rynchocephalia (Tuatara).

Adaptive radiation is apt to produce endemic lower taxa within any continent. The absence of taxa at the familial or lower level is not remarkable unless they occur on most other continents except Australia.

# Endemism

On any continent, or even smaller geographic unit, one would expect a high degree of endemism at the specific and generic levels and that such is also the case for Australia is of little intrinsic interest. The taxa that are endemic at the familial level or above are of most interest and emphasized here.

In considering the topic of endemism, sometimes Australia and New Guinea may be usefully linked because these two regions have been connected by land repeatedly in the Pleistocene, most recently only a few thousand years ago. There has been insufficient time since the most recent separation for extensive divergence of populations isolated on opposite sides of the Torres Strait.

There are two processes whereby endemism can occur. One is the failure of an autochthonous taxon to reach other areas. The second is extinction of a taxon in parts of its geographic range, leaving it extant only in one area as a geographical relict (Darlington, 1963). The area in which it is endemic is not necessarily the one in which it had its origin (it may be either autochthonous or allochthonous). These two kinds of endemism are designated Originative Endemism and Extinctive Endemism, respectively.

Extinctive Endemism: Extinctive endemism probably is much less common on a continental basis than originative endemism, particularly for a relatively isolated continent. If monotremes originated outside Australia, which is doubtful, they would be examples of extinctive endemism.

Originative Endemism: The long period of relative isolation of Australia during its northerly movement provided an opportunity for the old Gondwanan fauna trapped on it to diverge from their relatives on other fragments. In some cases, that divergence was relatively slow and only reached the generic level. The turtle family Chelidae occurs both in Australia and South America, but the two continents have different genera (Dowling & Duellman, 1974–78).

The marsupials are perhaps the best vertebrate examples of endemism at the familial level. All 14 of the Australian marsupial families are indigenous in Australia or to Australo-New Guinea and none has ever been found as fossils on any other continent. They are true endemics, having originated in the Australian Region and (except for a few introductions of them by man elsewhere) have never been established on other continents.

The avian families Menuridae (lyrebirds) and Atrichornithidae (scrub-birds) clearly originated in Australia and have never dispersed elsewhere.

The reptilian family Pygopodidae is found only in Australo-New Guinea. It is believed to have evolved from geckos in southwestern Australia, where the greatest number of genera occur and species density is greatest (Fig. 5.10; Cogger & Heatwole, 1981).

Whether Australo-New Guinea has any endemic families of amphibians depends on which side of current taxonomic debate one elects to support. Clearly, the two major radiations of frogs took place *in situ* and represent either endemic families or subfamilies, according to one's taxonomic taste.

Table 5.2 indicates the endemism of various taxa of Australian animals at different levels. The taxonomy is not sufficiently known for many groups. Other than the expected increase in proportional endemism from higher to lower taxa, the main point to be made is that endemism at the generic and specific levels is high and that non-eutherian mammals have high endemism, even at the familial level.

## Community Structure

Australian communities differ in structure from one locality to another. They may be analysed in terms of the environmental factors influencing such structuring and compared with equivalent communities elsewhere.

**Geographic Variation.** Communities change geographically. The number of organisms tends to decrease from low latitudes toward higher ones and from moist habitats toward drier ones. For example, the total number of species in a tropical rainforest is far higher than in the same hectarage of alpine heath or stark desert. This pattern holds true in a general way for some individual taxa as well, but regional peculiarities in climate, soil, vegetation or other conditions may impose modifications.

For certain taxa, geographic trends in species richness may be just the opposite, with the greatest number of species being found in deserts or at high latitudes or altitudes. In Australia, some groups, like reptiles, have the greatest numbers of species in the tropics, but species richness of birds and mammals of various taxa either have the reverse trend, exhibit no relation to latitude or have lowest values at intermediate latitudes. Individual taxa within a Class differ in

# 5. TERRESTRIAL COMPONENTS AND DISTRIBUTION

Table 5.2 Endemism of the Australian terrestrial fauna. Groups selected on the basis of the completeness with which they have been studied and on the availability of summaries in the literature. (Data from CSIRO, 1970; Cogger, 1975; Keast, 1981; Strahan, 1983; Archer & Clayton, 1984; Jarman, pers. comm; van Dyke, pers. comm.)

| TAXON | PERCENTAGE OF AUSTRALIAN ANIMALS THAT ARE ENDEMIC AT THE LEVEL OF: | | | REMARKS |
|---|---|---|---|---|
| | Family | Genus | Species | |
| **MAMMALS** | | | | |
| Monotremes | 50 | 50 | 50 | all non-endemic taxa shared only with New Guinea |
| Marsupials | 53 | 46 | 89 | all non-endemic species shared only with New Guinea |
| Placentals | 0 | 33 | 73 | mainly bats that aren't endemic |
| **BIRDS** | 11 | 37 | 71 | many more taxa are endemic to Australia and New Guinea combined |
| **REPTILES** | 0 | 55 | 88 | not including sea-snakes and sea-turtles; two families endemic to Australia and New Guinea combined |
| **AMPHIBIANS** | 0 | 79 | 94 | |
| **INSECTS** | | | | |
| ORTHOPTERA | | | | |
| Acridoidea | – | 90 | – | |
| Grylloidea | – | 25 | – | |
| Other superfamilies | – | 50–60 | – | |
| PHASMATODEA | | | | |
| Phasmatidae | – | > 50 | nearly all | |
| LEPIDOPTERA | | | | |
| Papilionidae | – | 17 | 24 | |
| Pieridae | | | | |
| Coliadinae | – | 0 | 64 | |
| Pierinae | – | 0 | 25 | |
| Nymphalidae | | | | |
| Danainae | – | – | 6 | |
| Satyrinae | – | 50 | 83 | |
| Nymphalinae | – | – | 4 | |
| Lycaenidae | | | | |
| Theclinae | – | 28 | 61 | |
| Polyommatinae | – | 14 | 37 | |
| All other families and subfamilies | – | 0 | 0 | |
| COLEOPTERA | 0 | 75 | – | |
| **ARACHNIDS** | | | | |
| Spiders | 2 | 26 | – | |
| Scorpions | 0 | 75 | 79 | |
| **LAND SNAILS** | 4 | – | – | |
| **EARTHWORMS** | | | | |
| Megascolecini | – | 71 | – | |

pattern. In some cases, there is an overriding relation to moisture: numbers of species of birds and frogs have a positive correlation with rainfall, for example. When tropical and temperate areas of equivalent rainfall are compared, there is still a greater richness of some reptiles in the tropics, but the reverse is true for mammals and frogs; some groups of lizards show no difference. Certain lizard groups increase in species richness with increasing mean annual hours of sunshine (Pianka & Schall, 1984). Hall (1984) shows that numbers of species of bats decrease in Australia with increasing latitude and at a given latitude is lower in the drier regions than in humid ones.

Vegetation complexity may be involved for some taxa. Species richness of birds is greater in habitats with a larger number of horizontal layers of vegetation (Keast, 1981b).

Other biotic factors may be significant in either a positive or a negative way. There is a tendency for certain species to associate, even over a range of environmental conditions (Kikkawa et al., 1981) and they may be responding to each other as well as other environmental factors. Conversely, some taxa have inverse relationships. In various deserts, including those of Australia, numbers of birds and numbers of lizards are inversely related and may reflect competition between members of these two groups (Pianka & Schall, 1984).

Because different taxa have different patterns of species density, clearly not only are there going to be geographic changes in numbers of species, but also in the relative proportions with which various taxa are represented in regional communities. That is, taxonomic composition of communities varies from place to place. One of the most important and controversial issues in modern ecology is the extent to which difference in species composition affect the way communities function.

**Ecological Equivalence.** Given that in different geographic regions similar climates exert the same kinds of selective pressures, adaptive radiation may follow similar trends, with convergent evolution resulting in genetically different species with similar morphological, ecological and physiological adaptations. Unrelated taxa which share common adaptive attributes through parallel evolution are called ecological equivalents. Sometimes the parallels are striking, both at the level of the individual taxon and the whole biotic community. A number of examples of ecological equivalence between taxa from Australia and other continents has been outlined (see Heatwole, 1970; Pianka & Pianka, 1970, for reptilian examples). At the level of the entire biotic community, tropical rainforests, for example, have a similar appearance and structure (several canopy layers, vines, lianas, vascular epiphytes) in all continents, although the structural units are made up of different families or genera in the different areas. Wherever certain conditions of temperature and moisture prevail, unless limited by soil conditions, tropical rainforest develops in time. The various structural elements evolve from whatever taxonomic units are at hand.

Comparisons of communities of the same biome (e.g. tropical rainforest, desert) from different continents permit assessment of the role of evolution in community structure. The few faunal comparisons that have been carried out have produced the surprising conclusion that most continents are similar to each other, with the exception of Australia which is unique in some respects. Lizard assemblages have been subjected to intercontinental comparisons (reviewed by Heatwole, 1976; Heatwole, 1982; Pianka, 1981). Australian deserts have a greater number of species of lizards per locality than does either the Kalahari or American deserts, the latter two being nearly the same. Part of the explanation is that habitats such as sandridges, mulga and sand plains interdigitate more in Australia and a given locality may encompass several habi-

tats. Also, within a habitat, Australian species show more specialization for particular microhabitats and a greater number of species can be accommodated (for example, 10 species in Australian sandridges compared to only one in the Kalahari). The more constant climate of Australian deserts may permit the species to divide up the day into a greater number of suitable activity periods and accommodate more species in that way. Finally, lizards seem to have usurped the ecological roles played by some worms, insects, snakes, birds or mammals in other deserts. There are fewer species of ground-nesting insectivorous birds in Australian deserts than in the Kalahari and their numbers seem to have been replaced by species of lizards. When different localities within Australia are compared, there is an inverse relationship between numbers of species of lizards and ground-nesting insectivorous birds. There must be a balance between these two ecologically similar groups; if there are more species of one, there must be fewer of the other.

In contrast to deserts, the rainforest fauna has fewer reptilian species in Australia than in other continents (Heatwole, 1981). Perhaps wet-adapted species suffered greater extinction rates in the past when moist refugia were restricted or eliminated by expanding aridity.

Morton (1979) compared Australian and North American deserts and found that the latter had more species of mammals (109) than the former (73) despite the area of desert being greater in Australia. The difference lay mainly in the greater abundance of granivorous mammals (mostly rodents) in North American deserts. In Australia, there is a preponderance of seed-gathering ants and granivorous birds.

By contrast, there are more species of insectivorous mammals, birds and lizards in Australian deserts than in North American deserts, perhaps because of the abundance of ants for food.

With a paucity of small mammal species to serve as prey, there are relatively few mammalian carnivores in Australian deserts. The role of predation upon the rich lizard fauna is performed by carnivorous lizards, especially varanids, rather than by mammals.

Ants play a particularly important role in Australia, where they are responsible for the dispersal of about 1,500 species of vascular plants, as opposed to $\approx 300$ species in all the rest of the world (Berg, 1975). Ants often control the composition of much of the rest of the insect fauna. A quantitative assessment of the structuring of Australian ant assemblages and comparison with that of other continents would be extremely valuable.

There also are differences in the trophic structure of avian assemblages on different continents. In this respect, Australia is like most continents in having bird species specialized as nectar feeders and pollinators. Europe differs and is depauperate in flower-visiting birds compared to similar climatic regions in Australia. Ford (1985) advances the hypothesis that in Europe, nectarivorous birds were pre-empted by social bees. There is a greater propensity for frugivory among birds from wet habitats and a stronger tendency toward granivory among those from dry ones.

Eventually some species fills each of the niches characteristic of a given biome, even if the taxa which are modified vary from one locality to another. Ecological equivalents, thus formed, are often from the same high level taxon, say Class or Order, but with parallel evolution occurring between different families (e.g. ecological equivalence in the Class Reptilia between the family Agamidae in Australia and the family Iguanidae in America). If taxa from the group are not available, however, quite different genetic entities may become ecological equivalents (e.g. seed-collecting ants and

grain-eating rodents; insectivorous birds and lizards). Ecological equivalence seemingly develops more easily among related taxa, but does occur in genetically very different ones.

## HUMAN INFLUENCE

Extermination by direct methods is often difficult to achieve. Population densities of target organisms are reduced, but complete extinction is nearly impossible for many species. Unsuccessful attempts to exterminate many "pest" species in Australia through shooting, trapping, poisoning and other methods have resulted in temporary control but not complete extermination. The largest kangaroos continue to thrive despite heavy shooting pressure in many areas. These eurytopic species are among the most difficult to eradicate and are problems partly because they are ecologically flexible and succeed in invading human habitats. Other species are much more sensitive.

Australian vertebrates probably exterminated by direct means by Europeans are *Thylacinus cynocephalus*, which was hunted for bounty (but see Chapter 20, this Volume), the Toolache Wallaby (*Macropus greyi*), also hunted for bounty (Calaby, 1984), and three insular forms of small emus (Archer, 1984f). Improved legislation and increased public awareness may prevent any further instances of this kind (see Chapter 11, this Volume).

There has been speculation that early Aborigines may have been responsible for the extinction of many of the larger Australian native mammals at the close of the Pleistocene (but see Chapter 10, this Volume) .

In contrast to direct methods, introduction of exotic fauna and habitat destruction have been very important in eliminating species from the Australian fauna and in endangering the survival of others. The traditional use of fire by Aborigines for many millennia altered vegetation and may have contributed to the extinction of some animals (Archer & Aplin, 1984).

A great proportion of the Australian continent has been affected by human activity (Adamson & Fox, 1982). European-style agriculture and pastoralism have, in a few cases, led to improved conditions, at least temporarily, for a variety of native mammals that flourished and became sufficient pests in crops and pastures to attract bounties. They included various kangaroos, wallabies, rat-kangaroos and (briefly) wombats and bandicoots. In most cases, they became extremely abundant following human modification of the landscape, then, like the introduced species, suffered a decline to a lower level around which populations have since fluctuated (Jarman & Johnson, 1977). The Ord River scheme provided greater food resources for corellas and magpie geese which became a nuisance (Beeton, 1977). Birds that inhabit open areas (*e.g.* Willie Wagtail) probably benefited from human activities. Construction of artificial bodies of water by humans has created breeding sites for some frogs (Tyler, 1979b). Usually, however, pastoralism and agriculture have led to a degradation of habitat. Clearing of habitat leads to local extinction of all but the most eurytopic species and when drastic modification occurs over extensive areas, as it has in Australia, entire species are lost. For some species, offshore islands still unmodified by agriculture, are the only remaining refuges.

Calaby (1984) estimates that 15 vertebrate species (one bird, seven marsupials and seven native rodents) have become extinct in Australia since European settlement; many more are on the endangered list. Archer & Aplin (1984) note that 16 species of marsupials have become extinct, at least locally, in the State of New South Wales. The greatest extinction occurred on the open plains, where 43% of the species were lost. Less devastation occurred in woodland savannah (13%) and sclerophyll forest (8%) and no species are lost from rainforest. These different intensities of extinction may be related to the relative degree to which these habitats have been modified by man, his domestic animals and inadvertently introduced exotics. Those species that have survived extreme habitat alteration are probably able to cope with the modified conditions and now are relatively safe. Paradoxically, the rainforest species are now at greater risk than those of the more open habitats; they cannot survive habitat alteration and many of their rainforest refuges are at risk.

Habitat destruction may occur in ways that are not as obvious as direct clearing. Forests and woodlands in many parts of Australia are declining alarmingly and the phenomenon is referred to as "dieback". There is debate as to whether this is a "natural" phenomenon or induced by human activities; the causes are probably different in different regions. Such diverse factors as intensity and nature of land use, root pathogens, insect defoliation and attack on roots, drought, salinity, senescence and nutrients, variously or in combination, can be associated with the malady (see review by Heatwole & Lowman, 1986). Whatever the cause, the significant habitat alteration affects birds (Ford & Bell, 1981) and reptiles (Crome, pers. comm.) at least.

A more insidious threat to the Australian fauna than habitat destruction is pollution. In contrast to clearance or drastic modification of habitat, the effects of pollution are not as readily visible, but are potentially as destructive. The same scientific procedures that produced the technology necessary to support burgeoning human populations in the first place, must be applied to the solving of this and related problems. If that is successful, perhaps the animal diversity of Australia can be maintained.

## OVERVIEW

The different elements of the fauna may show different distributional patterns. The old Gondwanan fauna 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. As past climates changed, some Gondwanan taxa were able to adapt gradually to those changes. A combination of radiation into new habitats and adaptation to changing conditions led to diversification. The marsupials constitute a prime Australian example. Other taxa of Gondwanan origin lacked flexibility in adapting to changing conditions and became relicts, whose ranges became progressively more restricted as their habitats shrank. Relict taxa became widely separated in ever-dwindling refugia.

Between these two extremes lies a continuum of intermediate conditions. One feature that all of them show, in contrast to many of the newer elements, is that their distributions do not reflect their point of entry into Australia. They have been there so long that their Gondwanan distributions have been blurred by later geological and climatic events and adaptive radiations.

The Asian Tertiary Element may share some of these characteristics. Adaptive radiation does not proceed uniformly in time or among taxa. Rather, particular taxa in certain periods seem to expand into new habitats and lifestyles with remarkable rapidity. In other cases, only slight change occurs over many millions of years. The interactions of changing ecological conditions and genetic factors probably account for these differences. Whatever the reason, rapid adaptive radiation by an Asian Tertiary Element could lead to diversification within a taxon and a collective widespread distribution of its derivatives. Tertiary incursion into Australia could have produced distributional patterns similar to those mentioned

for successful Gondwanan elements. Secondary centres of speciation and adaptive radiation could mask the effect of the entry point, especially in the older of the Tertiary elements. They, too, have been in Australia long enough to radiate into new habitats and have experienced a kaleidoscope of changing conditions that alternately caused isolation and permitted migration. The newer Tertiary elements and especially the Quaternary ones, however, have not had time to spread far from their point of entry into Australia. They have experienced fewer oscillations of climate. Consequently, there have been fewer occasions of unusually favourable conditions that might have permitted them to cross areas currently acting as dispersal barriers; nor have they had sufficient time to adapt to the conditions of such barriers and radiate into new habitats. As one proceeds from the older to the newer elements, distributional patterns increasingly reflect the points of entry into Australia and the present day climate and vegetation, but decreasingly reflect past climatic changes and the opening and closing of barriers within the continent.

In a very general way, the older elements have a greater diversity than equivalent taxa among the newer elements. There are, of course, variations imposed by different rates of adaptive radiation among taxa and relict or declining taxa do not conform to the trend.

Climate, habitat and history are not the only determinants of distributional patterns. Various interactions with other species may have an effect. A species may be eliminated by predation, parasites or competition.

Humans have had a great effect on distributional patterns, directly through introduction of species and indirectly through the effect these species have had on native fauna. Humans also limited distributions or caused extinction through overexploitation, habitat destruction and pollution.

Important in a study of the fauna of a continent such as Australia is to list what kinds of animals are present, where they come from, when they came and where they now occur. Also important is the assessment of the relative roles of climate and vegetation (past and present), geological history, palaeogeography, biotic interactions and human interference as determinants of observed distributions. This Chapter has broadly outlined some of the historical and ecological factors influencing the distribution of the terrestrial fauna of Australia. Further volumes in this series will treat these topics in depth and in reference to individual taxa.

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