FAUNA
of
AUSTRALIA

26. BIOGEOGRAPHY AND PHYLOGENY OF THE SQUAMATA

**Mark N. Hutchinson &
Stephen C. Donnellan**

This review summarises the current hypotheses of the origin, antiquity and history of the order Squamata, the dominant living reptile group which comprises the lizards, snakes and worm-lizards. The primary concern here is with the broad relationships and origins of the major taxa rather than with local distributional or phylogenetic patterns within Australia. In our review of the phylogenetic hypotheses, where possible we refer principally to data sets that have been analysed by cladistic methods. Analyses based on anatomical morphological data sets are integrated with the results of karyotypic and biochemical data sets.

A persistent theme of this chapter is that for most families there are few cladistically analysed morphological data, and karyotypic or biochemical data sets are limited or unavailable. Biogeographic study, especially historical biogeography, cannot proceed unless both phylogenetic data are available for the taxa and geological data are available for the physical environment. Again, the reader will find that geological data are very uncertain regarding the degree and timing of the isolation of the Australian continent from Asia and Antarctica. In most cases, therefore, conclusions should be regarded very cautiously.

The number of squamate families in Australia is low. Five of approximately fifteen lizard families and five or six of eleven snake families occur in the region; amphisbaenians are absent. Opinions vary concerning the actual number of families recognised in the Australian fauna, depending on whether the Pygopodidae are regarded as distinct from the Gekkonidae, and whether sea snakes, Hydrophiidae and Laticaudidae, are recognised as separate from the Elapidae. With the exception of the Pygopodidae, these families are represented in other parts of the world. However, several groups, such as the Scincidae, Typhlopidae and hydrophiine elapids, reach their greatest diversity, taxonomically and morphologically, in Australia (Figs 26.1, 26.2). In Table 26.1, the major groups of squamates in Australia are shown, listed by formal taxonomic name when widely accepted, but listed informally if relationships are controversial.

## CHARACTER SETS EMPLOYED IN ANALYSIS OF SYSTEMATIC RELATIONSHIPS

Comparative anatomy has provided the main source of phylogenetic data for squamates and Camp's (1923) treatise on lizard relationships is usually the starting point for modern analyses of squamate phylogeny. Camp relied mainly on osteological characters of the cranium, hyoid and vertebrae, but also showed that several characters of body and throat musculature were informative. Behavioural data have been used little in reptile systematics, compared with taxa such as frogs and birds. Workers since Camp (for example, McDowell & Bogert 1954; Underwood 1957; 1967; Rieppel 1980a) generally continued to use and refine his approach. Technical advances in the last two decades have made the analysis of morphological data sets more rigourous and have permitted the analysis of increasingly large data sets. Examples involving the Australian fauna include the squamates (Estes, de Queiroz & Gauthier 1988), the gekkonoids (Kluge 1987), pygopodids (Kluge 1974, 1976a), carphodactylines (Bauer 1990), scincomorphans (Presch 1988), iguanians (Frost & Etheridge 1989) and boids (Underwood & Stimson 1990). The most comprehensive recent review is that of Estes *et al*. (1988), which attempts to revise Camp's work by incorporating many new characters, scored across many more taxa, and analysing them in the light of recent advances in methods for reconstructing phylogeny.
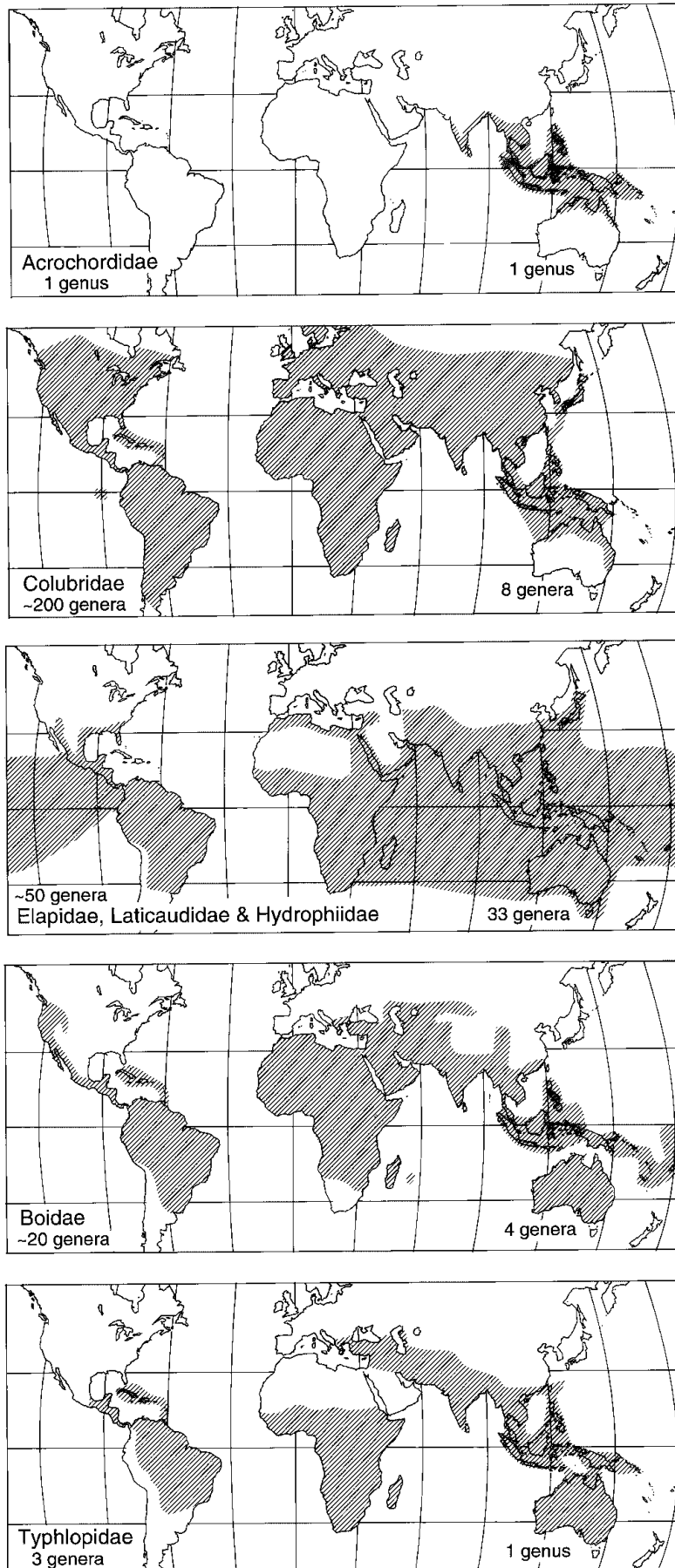
Figure 26.1 Worldwide distribution of snake families represented in Australia, and their taxonomic diversity based on numbers of genera. (After Shine 1991) [W. Mumford]
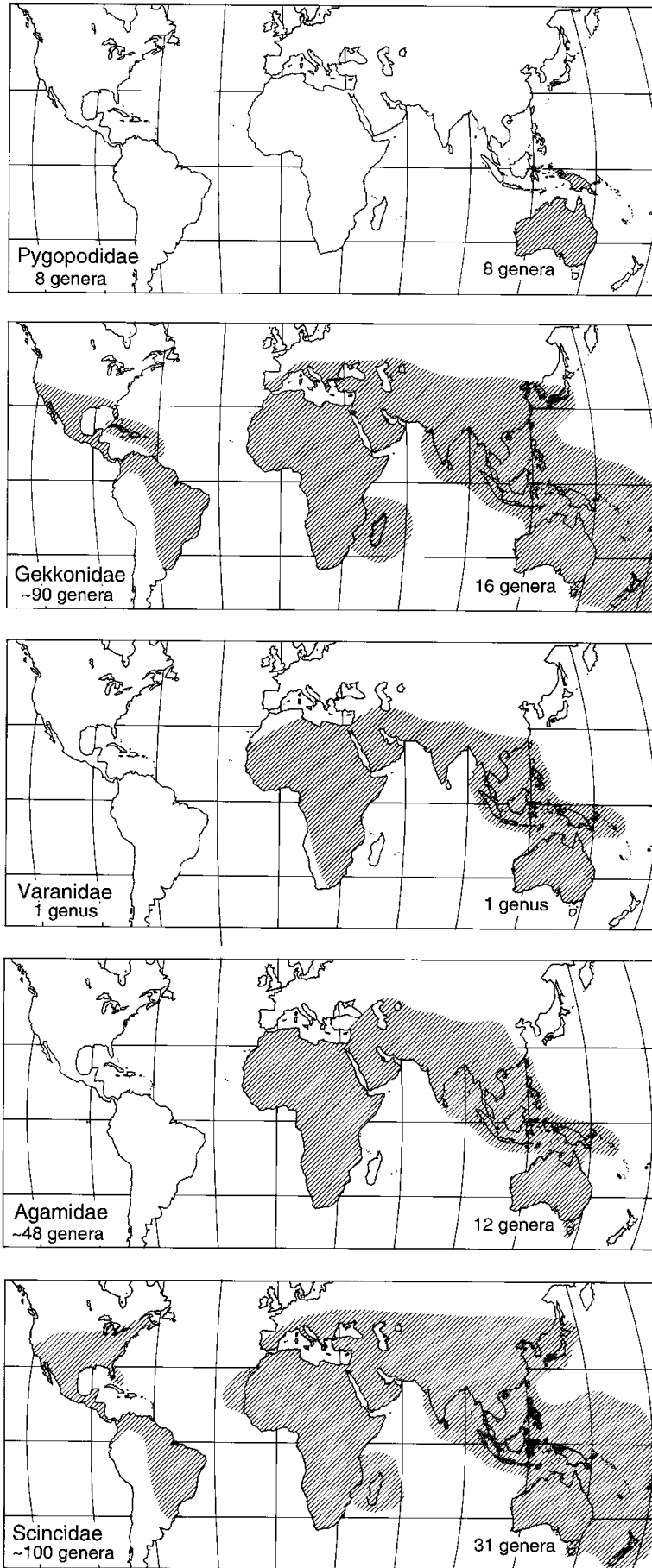
Figure 26.2 Worldwide distribution of lizard families represented in Australia and the taxonomic diversity based on numbers of genera. [W. Mumford]

Table 26.1 The major Australian squamate taxa. Numbers for both genera and species are approximate for most taxa.

Taxon	Number of genera	Number of species
IGUANIA		
Agamidae	12	65
GEKKOTA		
Gekkoninae	7	29
Diplodactylinae	9	68
Pygopods	8	33
SCINCOMORPHA		
Scincidae	31	320
ANGUIMORPHA		
Varanidae	1	25
SCOLECOPHIDIA		
Typhlopidae	1	35
BOOIDEA		
Pythoninae	4	15
COLUBROIDEA		
Acrochordidae	1	2
Colubridae	8	10
Elapids	20	80
Sea Snakes	13	33
TOTAL	114	715

In addition to the character sets provided by morphological analysis, systematists have available to them character sets derived from analysis of variation in chromosomes, proteins and nucleic acids (RNA and DNA). Chromosome studies of Australian squamates began in earnest with the work of King (1973) on skinks, and subsequent studies have included further work on skinks (Donnellan 1985; 1991a; 1991b) and considerable work on geckos (reviewed by King 1985; see also King 1987a, 1987b, 1987c, 1990; Moritz & King 1985), varanids (King & King 1975) and terrestrial elapids (Mengden 1985a, 1985b).

At the same time that computer programs have enabled more sophisticated analysis of morphological data, biochemical character sets have become more accessible and have improved in resolution. Recent reviews have dealt with methods for gathering, and analysis of, these latter types of character sets and the current controversies in each of these areas (King 1985; Baverstock & Schwaner 1985; Baverstock 1989; Hillis 1987; Hillis & Moritz 1990). Protein-based studies have included immunological comparisons of serum proteins of

several groups including boid and elapid snakes, skinks and dragons (Baverstock & Donnellan 1990; Hutchinson 1980; Hutchinson, Donnellan, Baverstock, Kreig, Sims *et al* 1990; Cadle & Gorman 1981; Minton & Da Costa 1975; Mao, Chen, Yin & Guo 1978; Schwaner & Dessauer 1981; Schwaner, Baverstock, Dessauer & Mengden 1985a), as well as other allozyme-based studies aimed mainly at problems of alpha taxonomy (for example, Donnellan & Hutchinson 1990; Harris & Johnston 1977; Hutchinson & Donnellan 1992; Hutchinson & Schwaner 1991; Mather 1990; Milton, Hughes & Mather 1983; Milton 1990).

Readers should note that when we use the term 'primitive' in relation to a taxon, this does not imply 'selective inferiority' but rather refers to the taxon as having diverged earlier in the history of the group. Early divergence does not imply complete retention of the ancestral phenotype; mosaic evolution generally ensures that all lineages develop some unique specialisations (autapomorphies).

PHYLOGENETIC RELATIONSHIPS OF THE SQUAMATE FAMILIES

Relationships of the Squamata

The Squamata is by far the larger of the two surviving lineages of diapsid reptiles belonging to the Lepidosauria (Gauthier, Estes & de Queiroz 1988), and is represented by over 6300 species (Halliday & Adler 1986). The second lineage, the Sphenodontida, encompasses the two living species of tuatara (Daugherty, Cree, Hay & Thompson 1990), which are both confined to New Zealand. Squamates preserve, in many respects, the general size and habitus of the earliest reptiles (Carroll & Baird 1972), but all living squamates possess many derived character states compared with early diapsids (Benton 1985; Gauthier *et al*. 1988; Laurin 1991). Character states which diagnose squamates are loss of the lower temporal bar, including the quadratojugal bone, a streptostylic (movable) quadrate bone, a transverse hinge between the frontal(s) and parietal(s), which has been lost secondarily within some squamate groups, loss of gastralia and the unique male copulatory organs, the paired hemipenes.

The limits of the Squamata are still being established, and vary according to the data set used, the interpretations put on some characters and the stringency with which particular workers adhere to cladistic systematic methods. Carroll (1975, 1988b) identified the Permo-Triassic Paliguanidae as the earliest known lizards, proposing that they had already diverged from the sphenodontid + squamate common ancestor. He also included the extinct, gliding kuehneosaurs of the Triassic (Robinson 1973) within the Squamata. Gauthier *et al*. (1988) rejected 'Paliguanidae' as a non-diagnosable assemblage and also excluded the kuehneosaurs from the Squamata. The divergence of these two rejected groups was placed prior to the divergence of sphenodontids and squamates. While there is still room for argument concerning the definition and composition of the Squamata, the scheme of relationships proposed by Gauthier *et al*. (1988), which effectively restricts the taxon to a group of lineages which still have living members, is accepted as a basis for this chapter.

Relationships within Squamata

The most exhaustive attempt to resolve interfamilial relationships among squamates was that of Estes *et al.* (1988), using a large data set which comprised 148 morphological characters. That study confirmed the existence of six monophyletic lineages within the Squamata: the Iguania (agamids, chameleons and iguanids), Gekkota (geckos and pygopods), Scincomorpha (cordylids, lacertids, scincids, teiids and xantusiids) and Anguimorpha (anguids,

helodermatids, lanthanotids, and varanids), traditionally regarded as infraorders of lizards, the Serpentes, and the Amphisbaenia (Fig. 26.3). Though the existence and content of major phylogenetic lineages was confirmed and refined, branching patterns among lineages were recovered with much less confidence. The relationships of one lizard family, the Dibamidae (Greer 1985; Rieppel 1984b) also remained unresolved.

A major reason for the failures, recognised and well documented by Estes *et al.* (1988), is the very large amount of homoplasy evident in the data set. Very few of the characters available could be shown to have undergone unique changes, and reversals and convergences/parallelisms were the rule rather than the exception. Alternative branching patterns, differing little from one another in such measures as consistency or tree length, are commonly found in broad scale phylogenetic studies. The 'best' tree often is scarcely better than several others suggesting alternative branching patterns. Such a situation does not inspire great confidence that the historically true branching pattern has been discovered. One response to finding weakly supported phylogenetic hypotheses is to search for additional characters to provide corroborating synapomorphies for one of the competing trees. However, as illustrated by the data of Estes *et al.* (1988) convergence, parallelism, reversal and conservatism are so common that increasing the number of characters surveyed appears inevitably to increase the number of homoplastic similarities as well as providing additional synapomorphies, and the impasse may remain. After reviewing that study, Kluge (1989) concluded that additional and, more importantly, alternative sources of data appeared to be necessary to better resolve relationships among the major squamate lineages.
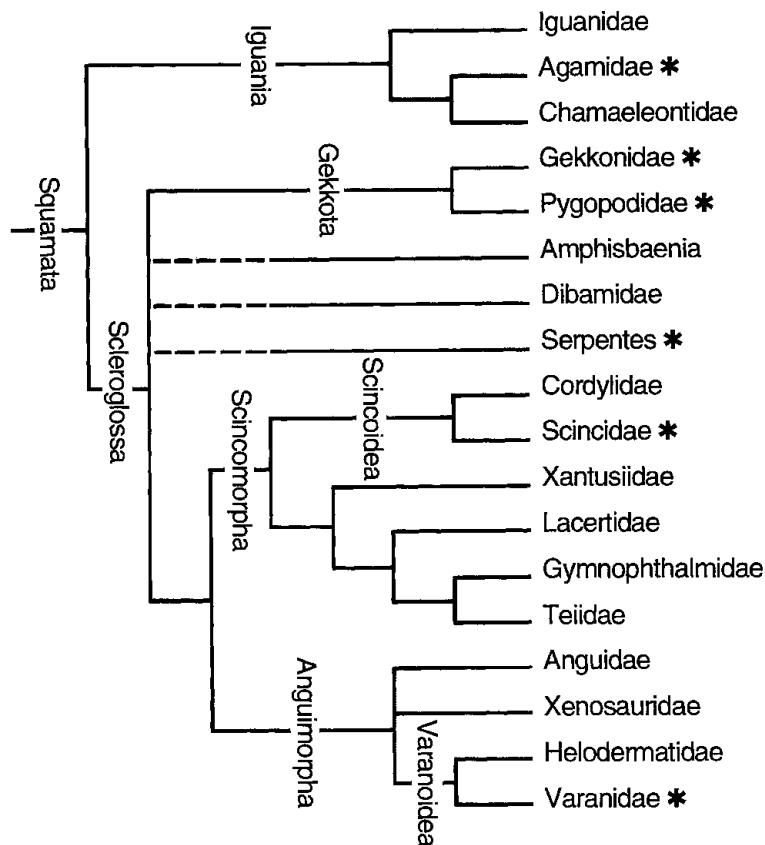
Figure 26.3 Interfamilial relationships within the Squamata. Australian taxa are indicated by *. (After Estes *et al.* 1988) [D. Wahl]

While well-corroborated hypotheses relating the major squamate lineages to one another are not available, some proposals on these relationships do exist and are moderately well-supported. The Iguania has been identified consistently as the sister taxon of all other squamates (Camp 1923; Estes *et al*. 1988). All other lizards, snakes and amphisbaenians are collectively termed the Scleroglossa (Estes *et al*. 1988 = Scincogekkonomorpha, Sukhanov 1961).

Morphological features such as a flattened and at least partly keratinised tongue, descending processes of the frontals and expanded septomaxillae which meet in a midline crest (indicating the importance of Jacobson's organ) are present primitively in other squamates (Estes *et al*. 1988), but are lacking in iguanians.

Other taxa have sometimes been considered as basal squamates, but based on one or a few character complexes. The retention in most geckos of persistently notochordal vertebrae has been a particular source of conflict—is this character a plesiomorphy or neotenic reversal? Similarities also have been noted in the cranial structures of fossil iguanians and teiids (Scincomorpha) (Estes & Price 1973), but these similarities may be symplesiomorphies. Based on shoulder anatomy only, Russell (1988) found that anguimorphans, not iguanians, were the sister group of all other squamates.

Even given the basal split of the Iguania, relationships among the three other lizard infraorders are still uncertain. Scincomorpha and Anguimorpha may be sister taxa (Estes *et al*. 1988), or Scincomorpha and Gekkota may be (Presch 1988; Schwenk 1988).

Relationships of the snake families, both to each other and to the several squamate lineages grouped as 'lizards', are a continuing source of debate. McDowell & Bogert (1954) presented a detailed case for a sister group relationship between snakes and varanoid lizards (helodermatids, lanthanotids, and varanids), that is, they saw snakes as arising within the Anguimorpha. By no means has this been universally accepted (Underwood 1967; Rieppel 1983; Rage 1984), but Estes *et al*. (1988) concluded that this general relationship probably was supported better than any other. However, the problems with the interpretation of some character state changes, and the significant support which could be found for alternative relationships, meant that the hypothesis of varanoid origin was not obviously better than other alternatives. Greer (1989) recently reviewed this problem and came to similar conclusions.

Three major grades of snakes are generally recognised, the blind snakes, 'primitive' snakes and the 'advanced' snakes. Blind snakes (Anomalepididae, Leptotyphlopidae, and Typhlopidae) are so extensively modified in relation to their fossorial, myrmecophagous (anteating) life that their anatomy leaves few clues regarding their relationships to other snakes. Recent authors (for example, McDowell 1987; Rage 1984; 1987) tend to place them as the sister group of all other Serpentes, as the Scolecophidia (an infraorder, or suborder if Serpentes is given ordinal status), and the remaining snakes form the Alethinophidia. Rage (1984), following in part the earlier work of Rieppel (1977; 1979), subdivided living alethinophidians into four superfamilies, the Anilioidea, Booidea, Acrochordoidea and Colubroidea, and suggested a phylogeny for these groups (Fig. 26.4). Relationships are uncertain among the anilioids and booids, either or both of which may be paraphyletic. An earlier, widely used scheme of higher taxonomy (Hoffstetter 1939) was certainly a grade classification, combining the acrochordoids and colubroids as the Caenophidia, and the anilioids and booids as Henophidia. McDowell (1987) used a more subdivided superfamilial scheme, which differed from that of Rage and Rieppel in the suggested affinities of some primitive snake taxa and elevated others (Tropidophiioidea and Bolyeroidea) to superfamilies of their own.
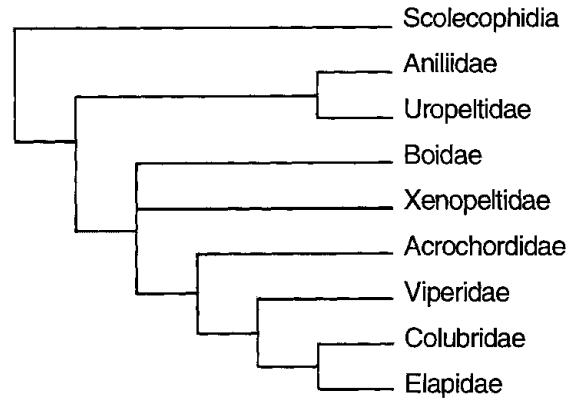
Figure 26.4 Summary of current views of the phylogeny of the major living snake taxa. (Modified after Rage 1984: fig. 37)   [D. Wahl]

Uncertainties regarding the position of some extinct snakes, such as *Dinilysia* and the madtsoiines (Rage 1984; Scanlon 1992), and of some living snakes, notably the acrochordids (Dowling, Highton, Maha & Maxson 1983; McDowell 1987; Rage 1984; Underwood 1967), mean that any phylogenetic schemes must be tentative. In addition, compared to the four lizard superfamilial groups, there is much less evidence that the four snake superfamilies are natural groups. Relationships among primitive snakes, the Anilioidea and Booidea, have been considered by McDowell (1975; 1987), Rieppel (1977) and Rage (1984). The composition of the families included has been unstable, several genera were switched from one family group to another, and no general consensus on the phylogeny of these snakes was reached. At best there is a consensus that aniliids (*Anilius* and *Cylindrophis*) are the most generally primitive living snakes, with boines and pythonines being more advanced and tropidophiines closest to the origin of the advanced 'caenophidian' (colubroid) snakes.

The great majority of living snakes are colubroids, and only a broad outline of relationships is available, notwithstanding the considerable body of literature on the subject. Family boundaries have been very difficult to establish, and subfamilial schemes much more so. Relationships between taxa have not been satisfactorily established. The most recent, primarily morphological review, is that of McDowell (1987) who recognises four families, Atractaspididae (an African group; see also Underwood & Kochva 1993), Elapidae (with six subfamilies), Viperidae (with three subfamilies) and Colubridae (with nine subfamilies).

As McDowell (1987) pointed out, morphological classifications have generally proven to be poor at predicting the outcomes of biochemical phylogenetic studies. Cadle (1987, 1988) summarised the literature on immunological data relating to interfamilial relationships of colubroid snakes. Cadle's (1988) own data on serum albumin divergences suggested that the viperids, atractaspidids and elapids (including hydrophiines) were each early monophyletic offshoots of the basic advanced snake stock, leaving an unresolved, highly diverse group of colubrids as a further monophyletic lineage. This study included relatively few colubrids in reciprocal comparisons, leaving some doubt as to the monophyly of the colubrid 'family' as a whole. Dowling *et al.* (1983), using similar immunological methods, showed that considerable heterogeneity existed within the traditional Colubridae, although both their data and Cadle's (see also Cadle 1984) suggest that several monophyletic units exist, including *Atractaspis*, homalopsines, colubrines, natricines, boaedontines (= lamprophiines) and two groups of xenodontines.

As there is no comprehensive, well-corroborated phylogeny available for the Squamata as a whole, the following discussions begin at the level of the identifiable monophyletic groups that include Australian taxa. These groups and their Australian representative families are: the Iguania (Agamidae), the Gekkota (Gekkonidae and pygopodids), the Scincomorpha (Scincidae), the Anguimorpha (Varanidae) and the Serpentes (Typhlopidae, Boidae, Colubridae and Elapidae).

Iguania

The Agamidae plus Chamaeleonidae are recognised as a monophyletic sublineage, the Acrodonta (Estes *et al*. 1988; Frost & Etheridge 1989), based on the distinctive dentition in which tooth replacement is lost (except for the anteriormost few tooth loci), and adjacent tooth bases become confluent. Frost & Etheridge (1989) concluded that their data best supported the chameleons as nested within the traditional 'Agamidae', and the older name, Chamaeleonidae, would therefore have to be applied to this taxon (agamids + chameleons) in order to produce a monophyletic taxonomy. Such a confusing nomenclatural change has not found immediate favour, partly because the evidence for relationships among acrodont iguanians is conflicting and because a nomenclatural alternative (recognition of an additional family, Leiolepididae) could preserve the traditional taxon Agamidae without sacrificing the goal of a monophyletic taxonomy. The closest iguanian sister taxon of the Acrodonta was not established clearly by the analysis of Frost & Etheridge (1989).

Relationships among Australian agamids have been studied using morphology by Cogger (1960) and Witten (1982), by Moody (1980) as part of a study on all agamids, and by Frost & Etheridge (1989) as part of a study of iguanian relationships. The recent consensus concerning Australian agamid relationships is that the fauna is highly endemic, consisting of three lineages, the amphiboluroids, *Hypsilurus* and *Physignathus*. The amphiboluroids comprise *Amphibolurus*, *Caimanops*, *Chelosania*, *Chlamydosaurus*, *Cryptagama*, *Ctenophorus*, *Diporiphora*, *Moloch*, *Pogona* and *Tympanocryptis* (Witten 1982). Character states supporting the monophyly of this group include great reduction or loss of the lachrymal bone and an apomorphic karyotype (2n=32, 10 pairs of microchromosomes, versus the plesiomorphic karyotype of 2n=36, 12 pairs of microchromosomes; Witten 1983).

The two remaining Australian genera, *Hypsilurus* (shared with New Guinea) and *Physignathus*, were thought to be more recent arrivals in Australia (Witten 1982), because of their phenetic similarity to some Asian taxa. However, Covacevich, Couper, Molnar, Witten & Young (1990b) have shown that *Physignathus*, at least, has been present in Australia for at least 20 million years, implying that the similarity between the living *P. lesueurii* of Australia and *P. cocincinus* of South-East Asia is the result of a lack of divergence rather than recency of origin. This view is supported by the immunological data (microcomplement fixation, or MC'F, of albumin) of Baverstock & Donnellan (1990), which suggests a closer relationship of *Physignathus* and *Hypsilurus* to the Australian radiation than to Asian *Gonocephalus* or other Asian genera (for example, *Calotes*). The data of Baverstock & Donnellan (1990) actually suggested a closer relationship of the Australian taxa to African *Agama* than to the Asian genera tested, although this conclusion needs corroboration from further generic comparisons.

Relationships within the amphiboluroid radiation are very poorly known, even though there have been recent major generic rearrangements (Storr 1982). Greer (1989) summarised the evidence put forward by Houston (1978) and Witten (1982) for two sublineages within the Australian radiation, which could be termed informally the *Amphibolurus* and *Ctenophorus* groups. The two are

defined on preanal pore characteristics and presacral vertebral counts, but relationships within these assemblages have not been analysed explicitly. The genus *Moloch* has caused difficulty, partly because of its highly autapomorphic morphology, but also because of the anomalous behaviour of its serum albumin in MC'F experiments (Baverstock & Donnellan 1990). Greer (1989) suggested that fundamentally this monotypic genus is a highly modified relative of *Tympanocryptis*, a member of the *Ctenophorus* group.

Gekkota

Ideas on gekkotan relationships have fluctuated considerably, based on conflicting interpretations of some characters, notably vertebrae. Some authors argue for either very primitive divergence of the group or great specialisation, although both views may be correct. In such apparently primitive features as notochordal vertebrae and paired, median skull bones, geckos may exhibit neotenic reversals to more embryonic stages of development rather than retained primitive features. In the great reduction of skull arch elements, living gekkotans are highly specialised.

The limbless Australian pygopod lizards feature strongly in the problems currently besetting a better understanding of relationships within the gekkotans. Three recent studies differ on pygopod relationships. Estes *et al.* (1988) indicated a sister group relationship between pygopods and all other gekkotans, recognising the traditional family Pygopodidae (Fig. 26.3). Kluge (1987) concluded that the pygopods were the sister group only of the Diplodactylinae, and advocated the transfer of the latter subfamily from the Gekkonidae to the Pygopodidae. King's (1990; King & Mengden 1990) karyotypic studies led him to conclude that pygopods share a common ancestor with some diplodactylines.

The conflict between the two morphological data sets appears to be reducible to interpretation of two characters. Kluge (1987) united pygopods and diplodactylines on the basis of their shared possession of an O-shaped muscle which closes the auditory meatus. Estes *et al.* (1988) did not identify the characters they used to reject Kluge's hypothesis, but inspection of their data reveals at least two characters (possibly not independent; Hutchinson pers. obs.) of the prootic which unite the geckos, but exclude the pygopods. They are the anterior closure of the trigeminal notch to form a foramen, and ventro-lateral prolongation of the crista alaris to form a projecting triangular flange (Fig. 26.5A, B). Biochemical data relevant to this problem are lacking.

Within the traditional family Gekkonidae, representatives of two lineages occur in Australia, the globally distributed Gekkoninae, and the Diplodactylinae, endemic to the Australian region. The most recent assessment of their relationships to each other and other gekkonoids is that of Kluge (1987) (Fig. 26.6). He concluded that the diplodactylines (plus pygopods) are the sister group of gekkonines (excluding eublepharines), but relationships of the several non-Australian gekkonine lineages (teratoscincines, sphaerodactylines, ptyodactylines, *etc.*) to one another are incompletely resolved.

Gekkonines show little generic endemism in Australia, although species endemism is almost complete (the only exceptions are some shared with New Guinea and some more widespread human commensals). The only endemic genus is *Heteronotia*, unless the Australian *Phyllodactylus* species are recognised as the endemic genus *Christinus*, but phylogenetic data supporting the latter are yet to be presented. No scheme of relationships has been proposed for the Australian gekkonines.

Most phylogenetic information available for Australian geckos concerns the diplodactylines. Kluge's (1987) evidence for diplodactyline monophyly is based on two synapomorphies, an O-shaped muscle closing the auditory meatus, and a thickening of the tectorial membrane of the auditory papilla. The latter character
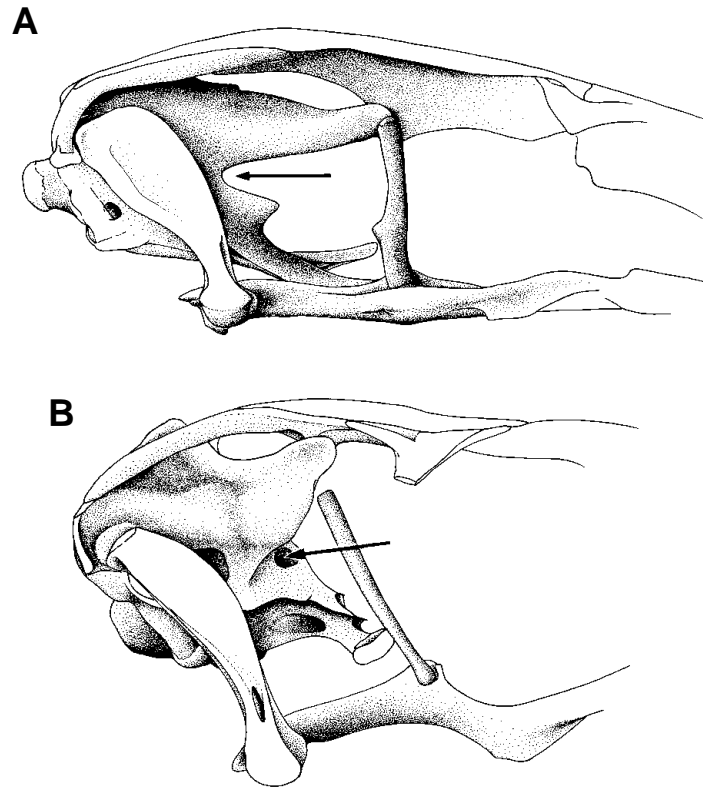
Figure 26.5 Lateral view of the trigeminal notch (marked with an arrow) on the anterior braincase of gekkotan lizards. **A**, a pygopodid, in which the notch remains open; **B**, a gekkonid, in which the notch closes to form a foramen.

[J. Thurmer]

is poorly surveyed in geckos and is known to be present in at least one gekkonine, *Thecadactylus* (Wever 1978). Two tribes have been proposed, the Diplodactylini and the Carphodactylini (Kluge 1967a), but only the latter has been subjected to a detailed phylogenetic study (Bauer 1990). Indeed, the monophyly of the two tribes has been taken for granted since Kluge's (1967a) pre-cladistic revision. King (1987a, 1987b) and King & Mengden (1990), on the basis of their karyotypic data, have suggested that *Oedura*, currently placed in the Diplodactylini, should be transferred to the Carphodactylini. Bauer (1990) provided a detailed phylogeny for the carphodactylines (he did not include *Oedura*). He placed *Carphodactylus* and *Phyllurus* as the sister group of *Nephrurus*, the latter expanded to include *Underwoodisaurus*. These three genera were placed as the sister group of *Pseudothecadactylus* and the remaining carphodactyline genera from New Zealand and New Caledonia, and the Australian endemic genus *Pseudothecadactylus* was placed as the sister taxon of some members of the New Caledonian genus *Rhacodactylus*. On karyotypic evidence, King (1987b) had already suggested a close relationship of *Pseudothecadactylus* and *Rhacodactylus*.

Within the pygopods, Kluge (1974) proposed a phylogenetic scheme (Fig. 28.8) which can be summarised as having a basal group of taxa, *Pygopus*, *Paradelma*, *Delma* and *Aclys*, between which relationships were poorly resolved, and four derived genera, *Lialis*, *Pletholax*, *Ophidiocephalus* and *Aprasia*, which form a monophyletic lineage. Problems among the basal genera, include the possible paraphyly of both *Pygopus* and *Delma* and the relationships of these forms to the more derived genera. *Pygopus* has been identified as the most generally plesiomorphic pygopodid (Kluge 1974), although *Delma* species are more primitive (=gecko-like) than *Pygopus* in the elongation of the body (Greer 1989) and the dentition (Hutchinson pers. obs.).
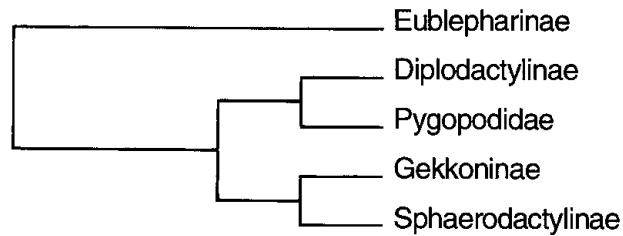
Figure 26.6 Major lineages of gekkonoid lizards. (After Kluge 1987)
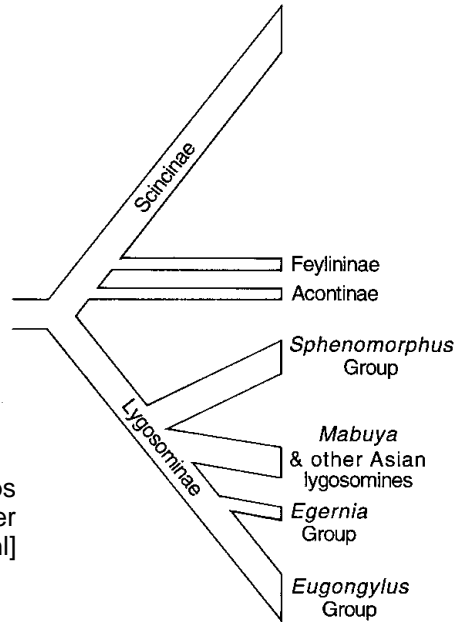
[D. Wahl]

Scincomorpha

Skinks have been the core group of the scincomorpha since its inception (Camp 1923), but their relationships to other scincomorphans are unclear. Recent workers have consistently regarded the African cordyliforms (Cordylidae and Gerrhosauridae; Lang 1991), especially the gerrhosaurs, as close relatives of the Scincidae, either alone (Greer 1979b; Estes *et al*. 1988), or together with the xantusiids (Estes 1983a; Presch 1988). It is noteworthy that the studies of Presch (1988) and Estes *et al*. (1988), based on large morphological data sets which overlapped significantly, agreed that the Cordylidae (including gerrhosaurs) and Xantusiidae are the nearest relatives of the Scincidae, but differed on whether the Cordylidae (Estes *et al*. 1988) or Xantusiidae (Presch) are the sister group of skinks. Lang's (1991) revision of cordyliform lizards supports Estes *et al.* (1988) in placing them as the sister group of skinks and he reported also that one possible (but not preferred) phylogenetic hypothesis placed Cordylidae as the sister group of Scincidae + Gerrhosauridae. Other unresolved issues include the relationships of the Dibamidae to the Scincidae (Greer 1985; Rieppel 1984b) and the monophyly of the plesiomorphic subfamily Scincinae (Chapter 31).

Scincid relationships are summarised in Figure 26.7. The subfamilial scheme of Greer (1970a) comprises three monophyletic groups: the African limbless, fossorial, Acontinae and Feylininae; the predominantly Australian-Asian Lygosominae; and the Scincinae. Rieppel (1981) queried the validity of Greer's family concept, but his doubts revolve around the dibamids, feylinids and acontines; no one has suggested that the core scincines and lygosomines (98% of living skinks) are not monophyletic.

The lygosomines are the only recognised Australian skinks. Three monophyletic lineages have been identified (Greer 1979b): the *Egernia* group, the *Eugongylus* group and the *Sphenomorphus* group (Fig. 31.1). Greer's (1979b) analysis of ten characters suggested an hypothesis of relationships between the groups in which the *Sphenomorphus* group is the sister of the other two. This relationship was supported by immunoelectrophoretic evidence (Hutchinson 1980).

The genera of the *Egernia* group, *Egernia*, *Cyclodomorphus*, *Tiliqua* and *Corucia* (a monotypic Solomon Islands endemic) constitute a radiation of relatively primitive lygosomines confined to the Australian region. Morphological (Mitchell 1950; Greer 1979b; Shea 1990), biochemical (Hutchinson 1980; Baverstock & Donnellan 1990) and karyotypic evidence (King 1973; Donnellan 1985, 1991a) all corroborate the monophyly of this lineage. Relationships within the group are not resolved yet beyond the sister group relationship suggested (Shea 1990) between *Cyclodomorphus* and *Tiliqua*. *Egernia* is a grade genus, possibly paraphyletic with respect to the rest of the group, while *Corucia* possesses a confusing mixture of numerous autapomorphies plus some very primitive character states, such as pterygoid teeth.

Figure 26.7 Phylogenetic relationships among the major skink lineages. (After Greer 1970, 1979a)   [D. Wahl]

The *Eugongylus* group is a diverse assemblage, and has undergone several distinctive geographic radiations, all centred in the Australian region. Thus, there is an Australian radiation, a New Guinean-Solomon Islands radiation, a New Caledonian radiation and a New Zealand radiation (Table 26.2). In each area, there are species with striking, superficial similarities to taxa in other areas, but accumulating evidence indicates that relationships are closest within, rather than between, the major geographic units (Sadlier 1987; 1990; Hutchinson *et al*. 1990).

Table 26.2 Endemic scincid genera of the Eugongylus group arranged by geographic unit.

Australian	Melanesian	New Caledonian	New Zealand
Bartleia	*Emoia*	*Caledoniscincus*	*Cyclodina*
Bassiana	*Eugongylus*	*Geoscincus*	*Oligosoma*
Carlia	*Geomyersia*	*Graciliscincus*	
Cautula		*Lioscincus*	
Cryptoblepharus		*Marmorosphax*	
Lygisaurus		*N. (Nannoscincus)*	
Menetia		*Phoboscincus*	
Morethia		*Sigaloseps*	
N. (Nannoseps)		*Tropidoscincus*	
Niveoscincus			
Proablepharus			
Pseudemoia			

The *Sphenomorphus* group is diverse in the Australian region, resembling the *Eugongylus* group in having independent radiations in Australia and Melanesia, but not including New Caledonia-New Zealand (Baverstock & Donnellan 1990). Relationships across the group, which is also diverse in South-East Asia, are very poorly understood. A major impediment to understanding the group is the very large grade genus *Sphenomorphus*, as it includes a wide variety of species from throughout the range of the group which lack diagnostic character states of other genera. Recent Australian usage has suggested dividing

Australian *Sphenomorphus* among two genera, *Eulamprus* and *Glaphyromorphus*, but neither, as currently defined (Greer 1990c, 1992; Cogger 1992) is readily distinguishable from extralimital *Sphenomorphus*. Within Australia, several clusters of taxa have been recognised as closely related, such as *Saiphos* and *Calyptotis* (Greer 1983b, *Hemiergis* and *Glaphyromorphus gracilipes* (Choquenot & Greer 1989), and *Lerista* and the *G. crassicaudus* species group (Greer 1979c). Greer (1990c) also proposed a monophyletic assemblage, the *Glaphyromorphus isolepis* species complex, members of which occur in both Australia and the Lesser Sunda Islands.

The skinks have been a notoriously difficult group for phylogenetic study and, in spite of the progress made so far, many aspects of the relationships of the Australian skinks are still unclear. Baverstock & Donnellan (1990) and Hutchinson *et al*. (1990) made MC'F comparisons of serum albumin to elucidate the phylogeny of the major lineages and relationships among the species formerly lumped as the grade genus, *Leiolopisma*. The divergences among the three Australian lygosomine groups were shown to be profound (Baverstock & Donnellan 1990), but so great that albumin MC'F could not reliably test Greer's (1979b) suggestion that the *Sphenomorphus* group is the sister of the other two. The magnitude of the divergences does, however, suggest strongly a considerable antiquity for these lineages, possibly as old as the early Tertiary. The study of *Leiolopisma* showed that the several Australian species groups were more closely related to other Australian genera than they were either to each other or to the type species of the genus (*L. telfairii* from Mauritius). Integration of morphological data permitted diagnosis of several new genera to accommodate the Australian '*Leiolopisma*' and preliminary data, plus subsequent unpublished MC'F comparisons of New Caledonian and New Zealand '*Leiolopisma*', also suggest that these regions support endemic genera, not disjunct congeners of *L. telfairii*.

Anguimorpha

Anguimorphs are regarded as a derived group of lizards, most authors placing them as the sister group of Scincomorphans. Indeed, some anguids (for example, diploglossines) are very similar externally and internally to skinks. The living Australian monitors (Varanidae) belong to a still more derived subgroup of the Anguimorpha, the superfamily Varanoidea (=Platynota), which also includes the Helodermatidae (now restricted to Mexico–southwestern North America, but known as fossils in Europe's early Tertiary) and the extinct, totally aquatic, Mosasauridae and Necrosauridae.

The interfamilial relationships of the Varanidae perhaps have been examined more rigorously than any other Australian squamate group. McDowell & Bogert (1954), Rieppel (1980a) and Estes *et al*. (1988) collectively provided a large morphological data set showing that the Varanidae (including Lanthanotidae, Estes *et al*. 1988) is probably most closely related to the extinct Mosasauridae, and the Helodermatidae are more remote (Fig. 26.3).

Relationships among the extant members of the widespread genus *Varanus* have been investigated with morphological (Branch 1982; Böhme 1988; Becker, Böhme & Perry 1989), karyotypic (King & King 1975; King 1990) and microcomplement fixation of albumin data sets (Baverstock, King, King, Birrell & Kreig 1993) (Fig. 26.8). Australia's varanids have been placed traditionally in two subgenera, *Varanus* and *Odatria* (Mertens 1963). King *et al*. (1991) suggest that neither of Merten's subgenera is monophyletic. However, they identified two monophyletic clusters among the varanids that are largely confined to Australia. The first of these is a diverse group of small species confined to arid and northern Australia, which essentially represents Merten's *Odatria* minus the

New Guinean *V. prasinus*. The second cluster of large species is the core of Merten's subgenus *Varanus*, but without several South-East Asian and New Guinean endemics (*V. indicus*, *V. karlschmidti*, *V. salvator*).

Serpentes

The Australian snakes belong to three major assemblages, the Scolecophidia (typhlopid blind snakes), the Booidea (pythons) and Colubroidea (acrochordid file snakes, elapids and colubrids). As noted earlier, relationships between the three major groups are poorly established, but divergences date back to the early Tertiary or before (Rage 1982; Cadle 1988).

The phylogeny of typhlopid snakes has attracted little attention. At present, the allocation of the members of the family to just three genera—*Ramphotyphlops* in the Australian region, *Typhlops* throughout the Old World except for Australia, and *Rhinotyphlops* in Africa (Roux-Estève 1974)—implies a distinctive, monophyletic origin for the Australian typhlopids. No work has been done on phylogenetic relationships within the Australian Typhlopidae.
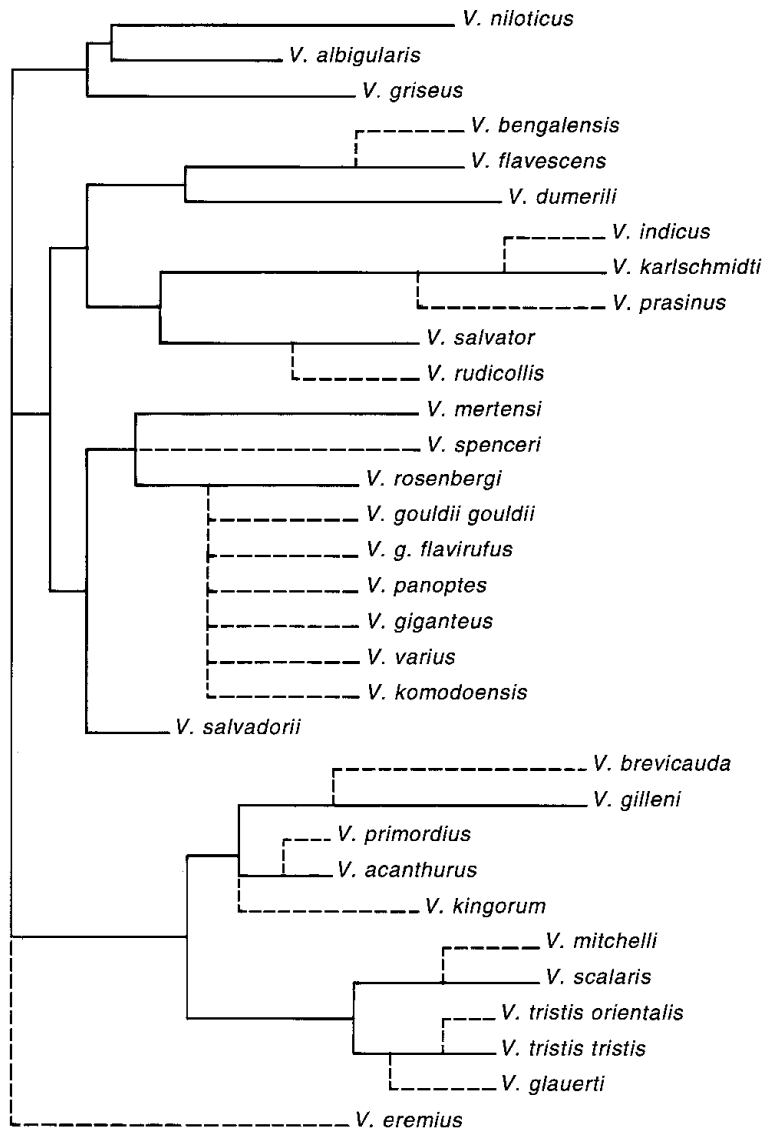
Figure 26.8 Possible relationships among the major species groups of the genus *Varanus*. (After King, King & Baverstock *et al*. 1991) [D. Wahl]

The pythons and boas have attracted much more study, but this has yet to result in a clear consensus regarding the relationships of the Australian pythons with each other, or with pythons elsewhere. A long period of taxonomic inactivity ended with McDowell's (1975) revision of the pythonines of the Australian region, which allocated some species to the Afro-Asian genus *Python*. Schwaner & Dessauer (1981), based on immunological comparisons of transferrins, disagreed with McDowell's scheme, and indicated instead that the Australian species were closer to one another than to any non-Australian species. Underwood & Stimson (1990) also concluded, from a multi-character cladistic study, that Australian pythons are monophyletic. Further, they suggested that the conventional taxonomy (for example, Cogger 1992) over-split the group. They recommended synonymising *Liasis* and *Chondropython* with *Morelia*, leaving only this genus, plus *Aspidites* which differs from other pythonines in lacking heat-sensitive labial pits. Underwood & Stimson (1990) interpreted this as a reversal, but Kluge (1991) identified the Australian pythonines as generally primitive, implying that the lack of pits could represent a primitive character state. If so, Australia supports not only the most structurally diverse, but also the most primitive pythonine radiation. Further studies by Kluge (in press) may shed more light on Australian boid relationships. Within Australia, Underwood & Stimson (1990) found that their concept of *Morelia* comprised several groups: the small *M. childreni* species complex (Smith 1985; conventionally *Liasis childreni*), the elongate, slender *M. amethistina* and *M. oenpelliensis*; the large *M. fuscus* and *M. olivaceus* (both conventionally *Liasis*) and the heavily built *M. spilota*, *M. carinata* and *M. viridis* (conventionally *Chondropython viridis*).

The state of knowledge regarding phylogenetic relationships among the advanced colubroid snakes is chaotic. The following are among many unresolved questions. Are the acrochordid file snakes primitive colubroids or advanced booids? Should the Elapidae include hydrophiine and/or laticaudine sea snakes or not? Are all proteroglyphs monophyletic? What are the limits of the enormous assemblage still conventionally referred to as the family Colubridae? This last problem is one which mostly concerns areas elsewhere, as the 'family' is poorly represented in Australia, and shows practically no endemism (Shine 1991c). Australian colubrids represent three subfamilial units, the Colubrinae (*Boiga*, *Dendrelaphis*), the Natricinae (*Stegonotus*, *Tropidonophis*) and Homalopsinae (*Cerberus*, *Fordonia*, *Myron*). Preliminary MC'F comparisons of representatives of these three subfamilies (Dowling *et al*. 1983) suggest a possible sister group relationship between the first two, but a very remote relationship between them and the homalopsines.

Within the Elapidae in its broadest sense, the sea snakes share craniomuscular and biochemical similarities with the Australian elapids (McDowell 1969a; 1969b; 1970), although these similarities have not been analysed rigourously in terms of shared-derived character states. Immunological studies by Mao *et al*. (1978), Cadle & Gorman (1981) and Schwaner *et al*. (1985a) strongly support a close relationship between the Australian terrestrial elapids and the sea snakes, especially the large hydrophiine radiation. Afro-Asian and Neotropical elapids are much more distantly related. Schwaner *et al.* (1985a) showed that biochemical divergence across the Australian elapid/sea snake group is relatively low, implying a recent origin (since mid-Tertiary). It appears, therefore, that if the Hydrophiidae or Hydrophiinae is to be recognised as a distinct taxon, it must also include the Australian terrestrial elapids.

A major attempt to resolve relationships among the Australian terrestrial elapids is represented by the articles drawn together in a volume edited by Grigg, Shine & Ehmann (1985). Articles based on biochemistry (Schwaner *et al*. 1985a), karyology (Mengden 1985a), and morphology (Wallach 1985) provided some consensus, although considerable disagreement remained. Several major themes are supported by the separate studies. The earliest diverging groups are the large,

surface dwelling, oviparous forms (*Demansia*, *Pseudonaja*, *Pseudechis* and *Oxyuranus*). A monophyletic origin for the large radiation of viviparous species with entire subcaudals was supported, but it is within this apparently relatively recent radiation that the greatest uncertainty exists regarding relationships. Hutchinson (1990b) attempted a consensus generic classification based on the data in Grigg *et al*. (1985).

BIOGEOGRAPHY

As is becoming clearer for more and more groups, the Australian members of a particular squamate family appear to be monophyletic to the exclusion of non-Australian members of the same family. Biogeographic inferences therefore depend on how much is known of the relationships of the Australian clade with these extra-Australian lineages. The details of these relationships are poorly known, if at all, for most Australian families.

Most discussions regarding the origins of major taxa in Australia reduce to choosing between an Asian and a Gondwanan origin; origin within Australia has seldom been considered (see King 1990). This has depended on a relatively simple palaeogeographic interpretation of Australia. Recent advances in understanding past geology of Australia and Asia (Audley-Charles 1987; 1991; Burrett, Duhig, Berry & Varne 1991) show that the picture has probably been much more complicated, and geology is not likely to provide rigid constraints on biogeographic hypotheses. The reverse is almost closer to the truth, as knowledge of the relationships among living taxa guides geologists to the discovery of terranes (Veevers 1991).

The orthodoxy of static continents clouded attempts to explain Australian squamate biogeography until about 1970. Thus Keast (1959), Storr (1964a) and Kluge (1967a) all explained the patterns they observed against a modern Indo-Malaysian archipelago which acted as a filter bridge for Asian immigrants. This seemingly continuous distribution, plus the prevailing taxonomy which included many widely dispersed grade taxa, tended to diminish both the perceived uniqueness of the Australian fauna and its antiquity. For example, Rawlinson (1974b) could write of the 'genus' *Leiolopisma* as being a widespread, Australian-Asian group which had 'radiated widely during the Quaternary'.

The acceptance of continental drift changed this viewpoint, but only partially. Several elements of the herpetofauna, with obvious South American affinities, (chelid turtles; hylid and leptodactyloid frogs) became accepted as Gondwanan relicts (Maxson, Sarich & Wilson 1975; Tyler 1979). The rest of the fauna was regarded as being more closely related to Asian taxa, but the initial palaeogeographic maps (for example, Colbert 1973) showed an extremely wide ocean gap between northern Australia and South-East Asia with no archipelagic connection until the Miocene or later. As a consequence, a northern origin for the fauna continued to be equated with a recent origin (for example, the review by Cogger & Heatwole 1981).

During the 1980s, revisions have been made of the origins and movements of plates and smaller continental fragments (terranes) between Australia and Asia. It is now becoming accepted that there has been a continuous rifting away of terranes from the leading, northern, edge of the Australian plate, so that much of the Indo-Malayan Archipelago and mainland South-East Asia is Gondwanan in origin. This implies that for Australian taxa showing 'Asian' connections, the common origin may be potentially much earlier than mid-Tertiary. It raises also the possibility that the relationship is not necessarily with Laurasian fauna, but may merely be with other Gondwanan elements that were isolated vicariantly on the rifted terranes.

The timing of the rifting of the various terranes is not yet well established (Fig. 26.9). For example, Audley-Charles (1987) suggested that the terrane now forming part of Thailand and the Malay Peninsula rifted during the Cretaceous, whereas Burrett *et al*. (1991) concluded that this terrane had already accreted onto the Asian landmass by the end of the Triassic. Also in doubt is the degree to which these terranes were actually exposed above sea level during their crossing of the Australia-Asia gap. As Burrett *et al*. (1991) pointed out, this exposure is absolutely crucial to terrestrial biogeographic reconstructions, but evidence for it may be very hard to detect during routine geological mapping. The area between Australia and Laurasian Asia thus may have been linked by a wide ocean gap or by various landmasses, although their composition and relative positions along the route would have changed constantly. The trend for land to leave Australia and join Asia invites the speculation that Australian fauna could have reached Asia via vicariance or dispersal, while Asian fauna could only disperse via island hopping to Australia.

It is hard to avoid the feeling that geology places few constraints on zoogeographic explanations and that a wide range of possible times, vicariant events and dispersal routes are possible. Rather, a strongly corroborated hypothesis of relationships for a group is likely to constrain the geologic setting. As pointed out above, such hypotheses are not generally available at present. Greer (1989) provided a pungent critique of the history of biogeographic speculation regarding Australian reptiles.

The following discussion summarises knowledge on the age of taxa in Australia, its likely nearest extralimital relatives and probable geographic origin. A common theme through this discussion is that Australian taxa, represented in recent fossil finds and/or subjected to molecular 'clock' studies, are now suggested to have originated or arrived in Australia by at least the early Tertiary.

Squamates in General

A supposed Permo-Triassic 'lizard', *Kudnu*, was described by Bartholomai (1979) from the *Lystrosaurus* Zone Rewan Formation of Queensland. This fragmentary specimen is probably not a paliguanid as originally proposed, and in any case, paliguanids, as discussed above, are not necessarily squamates. However, the find does show that primitive, possibly lepidosaurian diapsids, were present in Australia at a very early stage (Molnar 1985). The oldest undoubted squamate fossils in Australian are Cretaceous mosasaur fragments from Western Australia (Molnar 1985).

Outside Australia, the earliest fossil lizards (for example, bavarisaurs, paramacellodids; Estes 1983b) in the strict sense are Jurassic and Laurasian, while the oldest snake, *Lapparentophis* (Lapparentophiidae), from the Lower Cretaceous of Algeria, is Gondwanan (Rage 1984). Evidently squamates were potentially worldwide in distribution well before the end of the Mesozoic.

Agamidae

The oldest Australian fossil records are from the Early Miocene of Queensland (Covacevich *et al*. 1990b), where the living genus *Physignathus* has been identified, along with an extinct genus, *Sulcatidens*, and numerous indeterminate fragments. Early fossils have yet to be associated explicitly with the amphiboluroid radiation. Apart from *Physignathus cocincinus* from South-East Asia, it is uncertain which extralimital taxa are the closest relatives of the Australian agamids. The profound biochemical divergence between Asian and Australian taxa (Baverstock & Donnellan 1990) implies that if any Asian-Australian exchange occurred it was probably long ago. The possibility raised by the MC'F data of an Australian-African relationship needs further evidence.

The three agamid lineages differ in distribution within Australia. *Physignathus* and *Hypsilurus* inhabit tropical and warm temperate, forested habitats along Australia's east coast, while the amphiboluroids inhabit virtually all environments except these wet forests, being particularly diverse in arid and wet-dry tropical environments. The diversity of the amphiboluroids could be a late Tertiary phenomenon, correlated with the recent development of widespread aridity in Australia (Bowler, Hope, Jennings, Singh & Walker 1976).
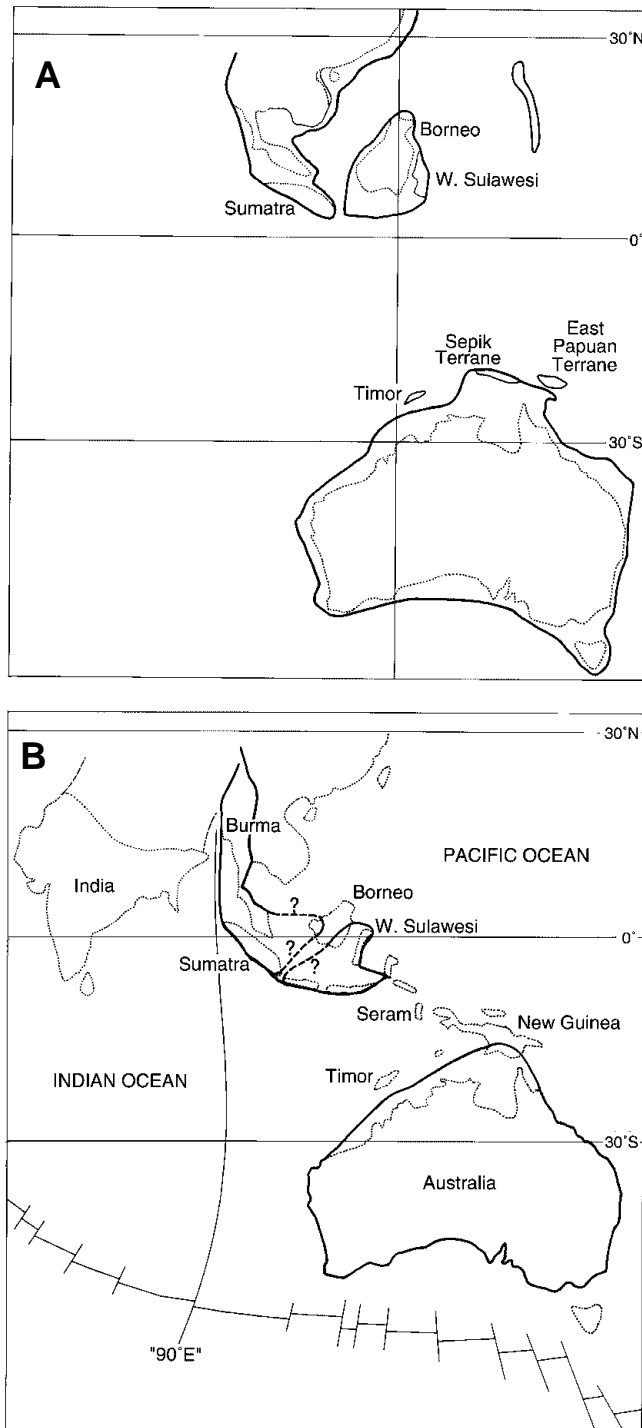
Figure 26.9 Two recent views on the presence of insular 'stepping stones' between Australia and Asia during the early Tertiary (Oligocene). Uncertainty regarding the geological history of this area is a major barrier to understanding the origins of Australia's reptile fauna. **A**, presence of a broad ocean gap; **B**, gap filled by Indonesian-Malaysian archipelago. (A, after Burrett *et al.* 1991; B, after Audley-Charles 1987)   [W. Mumford]

Gekkonidae

Gekkotan lizards are among the first, undoubted squamates known in the fossil record. The extinct families Ardeosauridae and Bavarisauridae from the Late Jurassic of Eurasia have been assigned to the Gekkota, based on general skull proportions and the presence of persistent intercentra and notochordal vertebrae (Estes 1983b). Kluge (1987) believed that the bavarisaurs are reasonably interpreted as gekkonoids, but that the evidence for ardeosaur relationships is more ambiguous. Diplodactyline fossils are known from the Early Miocene of Queensland (Hutchinson pers. obs.), but Australian gekkonines are not known as fossils for certain.

Diplodactylines are known only from the Australian region, while gekkonines are worldwide, implying a local origin for the former, but suggesting no obvious pattern for the latter subfamily. Bauer's (1990) analysis simply posits the existence of diplodactylines (and pygopods) in Australia by the mid-Cretaceous; earlier authors assumed an Australian origin for both taxa. Subsequent differentiation within the Diplodactylinae was linked by Bauer to vicariant isolation of lineages on Australia, New Zealand and New Caledonia during the past 60 million years. Both subfamilies are widespread in Australia, although the much greater range of morphological variation and the greater taxonomic diversity of the diplodactylines, suggests a longer stay in Australia. Both taxa also show significant radiations in tropical and arid regions of Australia; temperate regions support lower diversity, due probably to the low nocturnal temperatures.

Pygopodidae

Pygopodids are known from the Early Miocene of Queensland (Hutchinson pers. obs.). The nearest relatives are the diplodactylines (Kluge 1987; King 1990) or all other gekkonids (Estes *et al*. 1988). If the former view is correct an Australian origin is very likely.

Within Australia, pygopods are most diverse in the southern third of the continent, especially in semi-arid to warm temperate heath and grass habitats. The north-west and tropical far north are relatively depauperate, with no endemic genera and only a few species. Densely forested and cool habitats in the east and south tend to lack pygopods altogether. This pattern contrasts with that of the elapid snakes, which are most numerous and diverse in the east and north. It has been suggested (Storr 1964a; Bustard 1970b) that elapids have displaced pygopods, but the two groups, at least today, seem to complement one another ecologically rather than compete.

Scincidae

Earliest Australian records are from the Oligo-Miocene of South Australia (Estes 1984) and Early Miocene of Queensland (Hutchinson 1992). These early records indicate that the fauna at that time was Australian in character, pushing the origin and differentiation of the Australian scincid lineages further back in time. Two of the three Australian skink lineages, the *Egernia* group and the *Eugongylus* group, are almost entirely confined to the Australian region (see above), implying possible origin here. The *Sphenomorphus* group is more widespread through Asia. South-East Asia supports a diverse but largely distinct lygosomine fauna, as well as relictual scincines, but apart from the identification of the Asian *Mabuya* as an ancestral form for lygosomines in general (for example, Greer 1974, 1979b, 1989), no relationship of any of the three Australian lineages to a particular extralimital taxon has yet been established.

Within Australia, all three lineages are found throughout the continent, but with no clear biogeographic bias, emphasising their likely long period of evolution here.

Skinks occur throughout the Australian mainland and on virtually all adjacent islands. Greatest generic diversity is reached along the east coast, but all parts of Australia show significant local diversity and endemism.

Varanidae

The earliest definite Australian record is from the Oligo-Miocene of South Australia, as *Varanus* sp. (Estes 1984). Older varanid remains, of the extinct genus *Saniwa*, are known from the Early Tertiary of North America (Estes 1983b). The new evidence from immunology and chromosomal analysis (King *et al*. 1991) emphasises the Australian nature of our varanid lizards. Merten's (1963) two Australian subgenera, *Odatria* and *Varanus*, can only be maintained if non-Australian species (*V. komodoensis* is a notable exception) are excluded. Even though the family is widespread across the Old World tropics, there is a distinct changeover from an Australian to a New Guinean to an Asian fauna north-west of the Australian mainland. In this, the varanid pattern of endemism matches the pattern seen in skinks and dragons and, to a lesser extent, in geckos and elapids.

The study of King *et al*. (1991) suggests that the species excluded from Merten's Australian subgenera (*V. salvator*, *V. indicus*, *V. carlschmidti* and *V. prasinus*), together with other more specialised South-East Asian genera, form a cluster of Asian-New Guinean species which are the sister group of the Australian species. The profound immunological divergence among Australian varanids and the generally primitive morphology of the Australian subgenus *Varanus* could be interpreted to mean that Australia was the point of origin not only of its own varanid fauna but also the New Guinean and Asian radiations.

Typhlopidae

Fossil typhlopids have been found in the Early Miocene of Queensland (Scanlon, cited in Archer, Godthelp, Hand & Merigan 1989). These are the oldest typhlopids, the next record being from the Middle Miocene of France (Rage 1984). There are no phylogenetic data on the relationships of Australian typhlopids, and no soundly based speculations on the origins of this globally distributed group.

Boidae (Pythoninae and Madtsoinae)

The pythonines *Montypythonoides riversleighensis* and *Morelia antiqua* have been described from the Miocene of Queensland and the Northern Territory, respectively (Smith & Plane 1985). *Montypythonoides* is close to, if not identical with *Morelia* (Scanlon, pers. comm.). *Morelia*, a distinctively Australian genus, was thus established by this time, but the relationship to extralimital pythonines (basically the genus *Python*) is rather distant (Schwaner & Dessauer 1981). Evidently the group has been in Australia since the early Tertiary, and its precise origins remain obscure.

Until Pleistocene times, Australia supported a second group of large snakes, the madtsoiines, first recorded when *Wonambi* was described from the Naracoorte Caves of southeastern South Australia (Smith 1976b). Recent finds (for example, *Yurlungurr*, Scanlon 1992) and restudy of *Wonambi* (Barrie 1990) have expanded the knowledge of these snakes, showing that they have been in Australia since the Eocene. McDowell (1985) and Scanlon (1992) suggested that the group deserves familial status. The oldest fossil regarded by Rage (1984) as a booid is *Madtsoia madagascariensis* from the Late Cretaceous of

Madagascar. The primitive nature of Australian region boids, plus the presence of a second major lineage of boid-like madtsoiines, suggest that the entire booid group could be seen as having had a primarily Gondwanan, if not Australian, origin and differentiation, with only small scale invasions of the northern continents.

Acrochordidae

The living genus *Acrochordus* has been identified as a fossil from the Middle Miocene of Pakistan but the family is unknown in the Australian fossil record. Acrochordid relationships to other snakes are not well established. The three living species are found from tropical Asia to northern Australia and the family could have originated anywhere within its present range and subsequently dispersed readily because of its obligate aquatic, including littoral, habits. The two Australian species are confined to tropical freshwater and mangrove environments.

Elapidae (including Hydrophiidae)

The nearest relatives of Australia's elapids are Asian, but this relationship is not close (Cadle & Sarich 1981; McDowell 1967). The prevailing conclusion is that probably both groups of sea snakes, hydrophiines and *Laticauda*, share a common ancestry with or within the Australian proteroglyphs (McDowell 1969a; Mao *et al*. 1978; Cadle & Gorman 1981). This suggests a reasonably long period of evolution in Australia, especially in view of the wide dispersal and diversification undergone by hydrophiines.

Elapids are known from the Early Miocene of Queensland (Scanlon, cited in Archer *et al*. 1989), where cranial remains indicate species of Australian type (Scanlon pers. comm.). The oldest elapid fossils elsewhere in the world are from the Middle Miocene (*Palaeonaja*) of Europe. Immunological data (Schwaner *et al.* 1985a) suggested a Miocene origin for the Australian elapid–sea snake radiation. Fossil and biochemical data therefore provide a minimum age for the Australian elapid radiation (15 to 20 million years), but whether this represents the first arrival of the group in Australia, or simply the origin of the surviving lineages, remains to be seen.

Terrestrial elapids are most diverse in eastern tropical and warm temperate habitats, but nevertheless show significant diversity and endemism in cool temperate, semi-arid and arid environments. Elapids are one of only three reptile families to occur in Tasmania, possibly aided by the viviparity which characterises a major elapid lineage (Shine 1985c).

Colubridae

The oldest caenophidian, presumably colubrid, fossils are from the Late Eocene Quercy limestones of France (Rage 1984). The family is unknown in the Australian fossil record. As all Australian species are congeneric with Asiopapuan populations, their arrival in Australia was evidently from the north and very recent. Colubrids have successfully invaded arboreal and semiaquatic ecological niches only marginally exploited by elapids (Shine 1991c).

Concluding Remarks

The squamate fauna of Australia, with the single exception of the recently dispersed Colubridae, consists of families that probably have been present and differentiating within Australia through most of the Tertiary. Sister taxa of the Australian radiations are largely uncertain, apart from a general trend for an Asian relationship, and agamids are possibly exceptional in having African

affinities. Australia is the centre of diversity for, and therefore possibly the point of origin of, diplodactylines, pygopodids, *Egernia* group and *Eugongylus* group scincids, the varanid subgenera *Varanus* and *Odatria*, pythonine boids, *Ramphotyphlops* blind snakes and hydrophiine sea snakes. All of these groups have dispersed to varying extents through the Australian region, but in most instances have made limited incursions into the Oriental region.

Future research on the evolutionary relationships of the Australian squamates should concentrate on the basal dichotomies and relationships between Australian and extralimital members of the same taxa. Reworking of existing morphological data sets, replacing intuitive or phenetic conclusions with cladistic analysis, must continue, as well as the development of new morphological data sets to augment the often analysed osteological and scutellation data sets (Kluge 1989). In the near future it will become increasingly easy to incorporate nucleotide sequence data sets in such analyses. Whether such molecular studies are used to test morphological hypotheses or included in 'total evidence' style studies, they should help considerably in clarifying phylogenetic relationships. Only then will biogeographic studies be likely to produce useful and soundly based scenarios explaining the origins and distributional patterns of Australia's squamate fauna.