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A PHYLOGENETIC SUBDIVISION OF AUSTRALIAN SKINKS

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Skinks are the largest and most diverse of the five families of lizards in Australia. The most recent review of the lizard fauna, for example, recognizes 193 species (54 percent of the total; Cogger 1975), but as a result of recent work by several collectors, we now know of at least 242 species. Furthermore, new species are being discovered at a faster rate than in any other family of Australian reptiles (pers. obs.).

Quite justifiably, Australian skinks are receiving considerable attention from researchers whose interests range from cytogenetics (e.g., King 1973 a and b and Donnellan 1977) and ecology (e.g., Barwick 1965, Bustard 1970, Pengilley 1972, Pianka 1969, Robertson 1976, Smyth 1968, Smyth and Smith 1968 and Spellerberg 1972 a-d) to systematics (e.g., the many papers of Storr cited at the end of this paper) and zoogeography (e.g., Horton 1972, Pianka 1972 and Rawlinson 1974 a).

Given the numbers and diversity of Australian skinks and the interest in them, it may be useful to present a subdivision of this fauna that reflects major phylogenetic lineages. Hopefully, such a subdivision will provide a broad conceptual framework for synthesizing both old and new information about these animals.

MATERIALS AND METHODS

All the skinks in Australia, and indeed in the Australian Region, are members of the subfamily Lygosominae, the largest, most diverse and most widespread of the four subfamilies currently recognised (Greer 1970 a)¹. Several distinct groups are recognisable within lygosomines (Greer 1970 b, 1974 and 1977) and three of these occur in Australia. In this paper these groups will be called the *Egernia*, *Eugongylus* and *Sphenomorphus* groups. They can be diagnosed by the means of eight characters: two of osteology, four of squamation, one of colour and one of internal soft anatomy.

A list of the specimens examined for this paper would be very long, hence it may be more realistic to give only a general account of the material examined. The first osteological character, the total number of premaxillary teeth, has been surveyed for a large number of specimens of most Australian species (Table 1) but only a few specimens, often only one, in a variety of non-Australian species. This disparity is due to the availability of large series of Australian skinks which have been preserved with their mouths open as opposed to, generally, only single dried skulls of non-Australian species.

The other osteological character, the condition of Meckel's groove, has been surveyed in at least a single species of each genus or major species group with the exception of the following very rare taxa: *Phoboscincus* and *Tachygyia*.

1. Rawlinson (1974 a) has suggested that *Egernia* and *Tiliqua* are representatives of the subfamily Scincinae (sensu Greer 1970 a), a primitive and now somewhat relictual subfamily that was almost certainly ancestral to the lygosomines. I do not believe that the evidence supports this suggestion but defer discussion of it to another paper.

The four characters of squamation have been surveyed in most of the species in the three groups due to the general availability of alcoholic specimens.

The colour character, the colour of the iris, has been examined in most of the Australian species and in at least a single specimen of the following non-Australian species: *Corucia zebrata*, *Lipinia noctua*, *Prasinohaema virens* (Kodachrome only) and *Tribolonotus schmidtii*.

The character of soft anatomy, the morphology of the everted hemipenis, has been examined in at least a single specimen of all Australian genera and in single specimens of the following non-Australian species: *Lipinia noctua* and *Tribolonotus schmidtii*. It would, of course, be most useful if workers with access to live specimens of the non-Australian taxa in the three groups outlined here would check their animals for these last two characters.

The primitive and advanced character states of each of the characters have been inferred by considering the state of the character in three different taxa: (1.) the gerrhosaurine cordylids (as represented by *Gerrhosaurus*,) the group that appears to encompass the closest living relatives of skinks (pers. obs.); (2.) *Eumeces*, the genus that seems to comprise the most generally structurally primitive species in the most primitive subfamily of skinks, i.e., the Scincinae (see the Appendix of this paper), and (3.) *Mabuya*, the genus that seems to comprise the most generally structurally primitive species among the lygosomines as determined on characters other than those used in this analysis (see the Appendix).

Most lygosomines belong to one of the three groups outlined here and hence the diagnosis and discussion of relationships of these groups will serve as an introduction to the place of these skinks in the radiation of the lygosomines as a whole. Discussions of the relationships of the remaining skinks in this radiation will be found in Greer 1967 b, 1970 b, 1976 a and 1977.

Finally, it may be mentioned that although this paper emphasizes morphology, a popular account of the ecology and behaviour of the Australian representatives of the three groups discussed here will be found in Greer 1976 b.

ANALYSIS OF CHARACTERS

(A.) *Premaxillary tooth number*. The total number of teeth on the two premaxillary bones appears to be resolvable into three modal conditions, at least in surface dwelling forms: (A) nine, (a) eight or fewer (almost invariably seven), and (a') 11 or more (generally 13) (Table 1).

The number of premaxillary teeth is significantly variable only in the *Sphenomorphus* group. The more surface dwelling members of this group, e.g., *Sphenomorphus* and *Eremiascincus*, generally have nine premaxillary teeth whereas the many burrowers in the group often have fewer, e.g., *Anomalopus* (9-5), *Hemiergis* (8) and *Lerista* (7-5). It seems likely, however, that the fewer number of premaxillary teeth in these burrowers is a reduction from the primitive number of nine. There are three reasons for believing this. First, nine is probably the primitive number of premaxillary teeth for lygosomines in general (see below). Second, in any group of skinks, burrowing habits are more likely to be derived than surface dwelling habits and hence any associated aspect of a burrower's morphology that may otherwise be difficult to interpret in phylogenetic terms (e.g., tooth

number) is more likely to be derived than primitive. And third, the burrowing genera with fewer than nine premaxillary teeth all appear, on the basis of characters whose phylogenetic polarity is not difficult to infer without recourse to secondary associations such as habitat, to be derived from *Sphenomorphus* (Greer 1967 a, 1973 and work in progress) which has a modal number of nine premaxillary teeth (Table 1).

Although burrowing habits may account for the reduced number of premaxillary teeth in the burrowing members of the *Sphenomorphus* group, they cannot account for the fewer premaxillary teeth in the numerically large, surface dwelling genus *Ctenotus* in which the modal number is seven (Table 1). On most other characters, however, *Ctenotus* appears to be allied to the *Sphenomorphus* group. Most *Ctenotus* have a slightly conical snout which appears to have been brought about by a narrowing of the premaxillary region, and this may have been responsible for the loss of two teeth.

Notoscincus, which is also in the *Sphenomorphus* group, has a modal number of 8 (range 9-7) premaxillary teeth (Table 1). I have no explanation for this apparent reduction.

Finally, it may be noted from the data given in Table 1 that premaxillary tooth number is often a useful systematic character at the specific and generic level.

Although gerrhosaurines, or at least *Gerrhosaurus*, and *Eumeces* have a total of seven premaxillary teeth, I believe that a total of nine premaxillary teeth is probably primitive for lygosomines (A) and that both a lower (a) and higher (a') number are independently derived. The reason for this is that nine seems to be the most frequent number in the lygosomines that seem generally primitive on other grounds, and it is also the number that seems to occur most frequently in different lygosomine lineages.

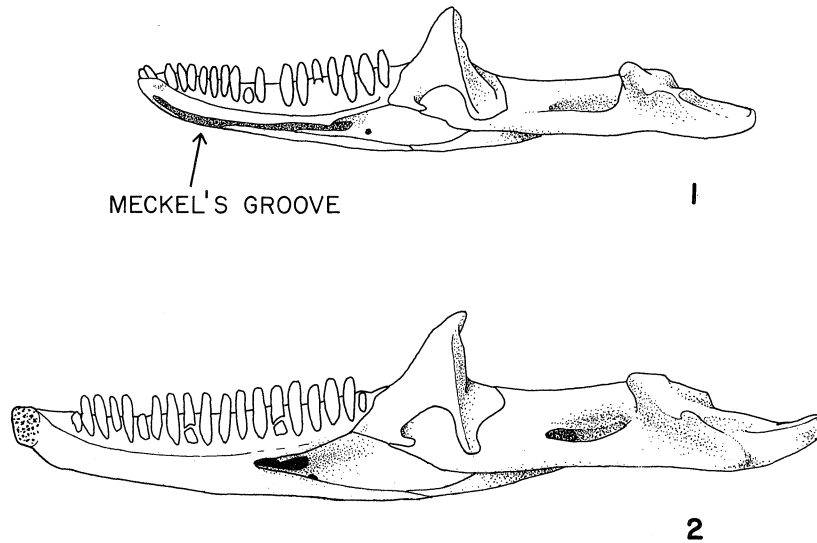
(B.) *Meckel's groove*. Meckel's groove may be either (B) open on the lower lingual side of the dentary or at the very least represented by a longitudinal suture in the overlapping dentary (Fig. 1 this paper and Fig. 32 in Greer 1974) or (b) completely obliterated by the overlapping and fusion of the dentary (Fig. 2 this paper and Fig. 33 in Greer 1974).

Most *Ctenotus* have the open condition typical of the *Sphenomorphus* group, but at least one of the small species, i.e., *schomburgki*, has the groove obliterated for all but a short distance anteriorly. *Notoscincus* appears to be the only taxon in the *Sphenomorphus* group which has the groove completely obliterated over its entire length.

In an earlier paper, I suggested that the open condition of Meckel's groove in lygosomines was perhaps secondarily derived from the closed condition (Greer 1974). My reason for this was that *Mabuya* seems remarkably primitive in a large number of characters whose phylogenetic polarity seems clear, and I was therefore willing to let this association guide my inferences in other characters. I now think, however, that this association of primitive characters cannot quite match the evidence from gerrhosaurines, *Eumeces* and the fossil record of reptiles in general (Romer 1956) that the open condition is primitive (B) and the closed condition derived (b).

(C.) *Interparietal and parietal scales*. The parietals may either be (C) completely separated by the interparietal or (c) meet behind the interparietal (Figs. 3 and 4).

There is little variation in this character within the major groups. In most members of the *Sphenomorphus* group the parietals meet behind the interparietal but in some individuals of the *Sphenomorphus quoyii* complex the parietals are completely separated by the interparietal.



Figs. 1 and 2. Lingual aspect of the lower jaw: 1, Meckel's groove open as in the *Sphenomorphus* group (*Sphenomorphus douglasi*); 2, Meckel's groove obliterated by the overlapping and fusion of the dentary as in the *Egernia* and *Eugongylus* groups (*Egernia striata*).

Although gerrhosaurines have the parietals meeting broadly behind the very small interparietal, *Eumeces* and *Mabuza* generally have the parietals separated by the interparietal (C) and for this reason, this condition is taken as primitive in lygosomines and the condition in which the parietals meet behind the interparietal is taken as derived (c).

(D.) Scales along the posterolateral edge of the parietal scale. Each parietal scale may be bordered along its posterolateral edge by either (D) two or more temporals and a medial nuchal which is often transversely enlarged and generally oriented obliquely to the parietal (Fig. 3 this paper and Figs. 18-21 in Greer 1974), or (d) only one temporal and a nuchal which is almost always enlarged and generally oriented flush with the parietal (Fig. 4 this paper and Figs. 22-27 in Greer 1974).

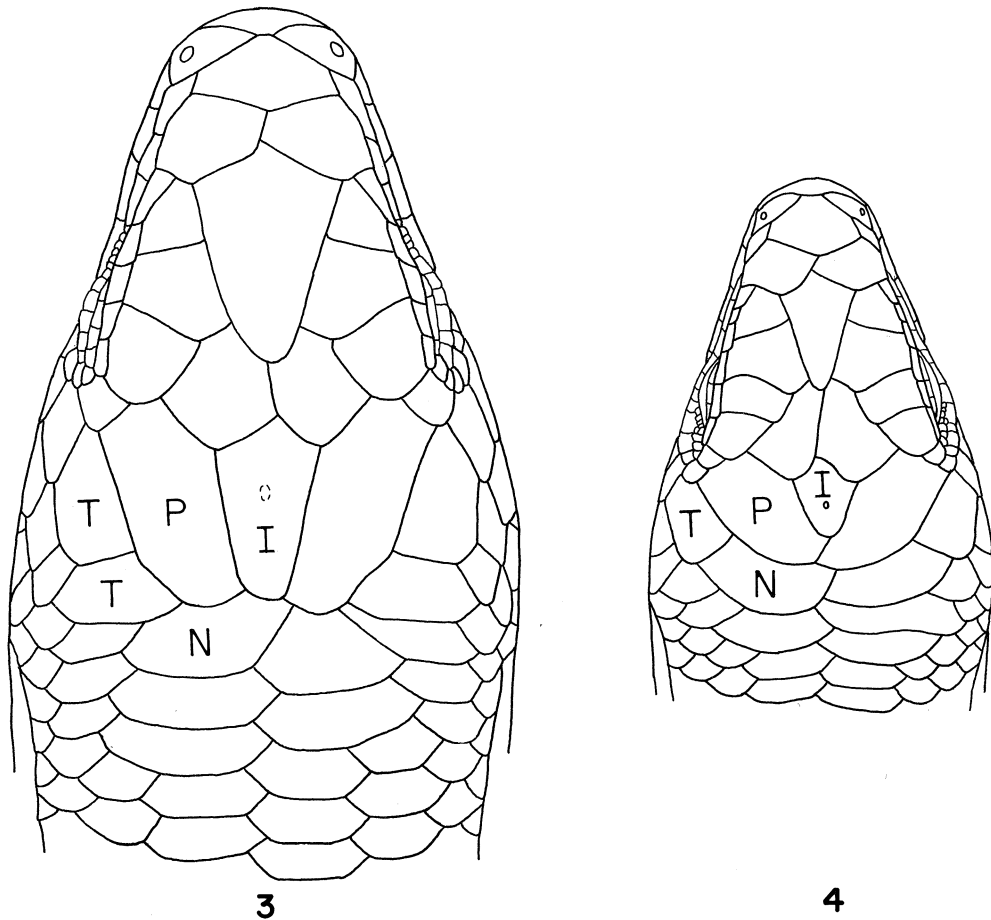
Most members of the *Sphenomorphus* group have two or more temporals and a nuchal bordering each parietal, but several species of *Lerista* and *Ctenotus* have only one temporal and a nuchal.

Some species show both states, sometimes even in the same individual. In these cases a survey of the population may be required to characterize the species accurately. I have found, however, that those species which show appreciable variation in this character are often most closely related to species characterized by state D.

The phylogenetic polarity of the two states of this character is difficult to infer. The situation in gerrhosaurines is not particularly telling in that there are numerous small temporals and nuchals bordering each parietal, but perhaps this condition is closest to

state D. *Eumeces* has only a single temporal and a nuchal (d) whereas *Mabuya* has two temporals and a nuchal (D). The evidence is thus not conclusive but in general I believe it indicates that the character state suggested by gerrhosaurines and shown by *Mabuya*, i.e., two or more temporals and a nuchal, is probably primitive (D) and the state shown by *Eumeces*, i.e., a single temporal and a nuchal, is derived (d).

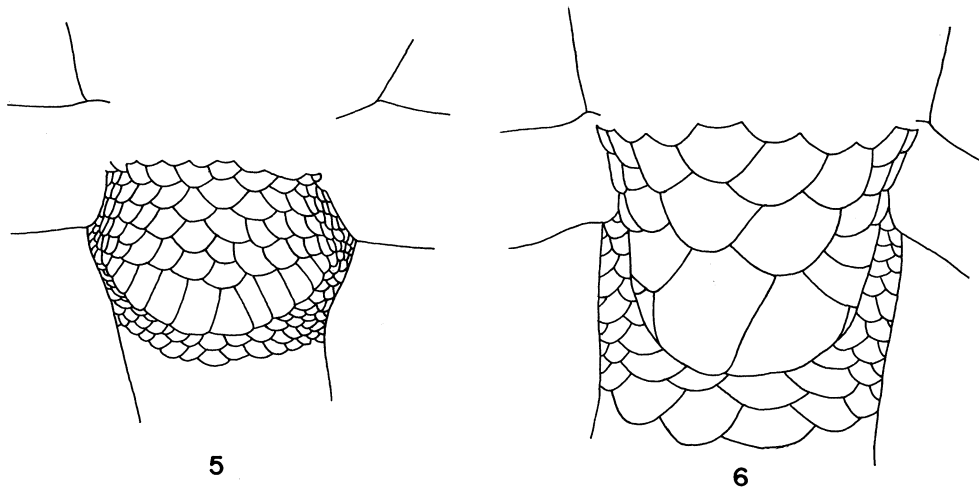
When I evaluated this character in an earlier paper (Greer 1974), I emphasized the orientation of the nuchal instead of the number of temporals, and because *Mabuya* had flush nuchals I took character state d as primitive. I now believe, however, that the number of temporals is the least equivocal and hence most important aspect of this character, and because *Mabuya* has two temporals bordering each parietal, I can now accept state D as primitive.



Figs. 3 and 4. Dorsal view of the head of two Australian skinks showing the relationship between the parietal (P) and interparietal (I) scales and the arrangement of the nuchal (N) and temporal (T) scales along the posterolateral edge of the parietal scale: 3, *Tiliqua casuarinae*; 4, *Leiopisma entrecasteauxii*.

(E.) *Medial pair of preanal scales.* The medial pair of preanal scales may be either (E) more or less equal in size to the lateral preanals (Fig. 5 this paper and Fig. 29 in Greer 1974) or (e) moderately to greatly enlarged (Fig. 6 this paper and Fig. 28 in Greer 1974).

Gerrhosaurines appear to have a few large but equal sized preanals which are perhaps most similar to state E. *Eumeces* has a very large medial pair of preanals (e) whereas *Mabuya* has a series of moderate but more or less equal sized preanals (E). As in the case of the nuchal and temporal scales (character D), I find it a bit difficult to make a decision as to the probably phylogenetic polarity of these two character states, but I am again inclined to take the condition suggested by gerrhosaurines and shown by *Mabuya*, i.e., equal sized preanals, as primitive (E) and the condition shown by *Eumeces*, i.e., a large medial pair of preanals, as derived (e).



Figs. 5 and 6. The two conditions in the size of the preanal scales in Australian skinks: 5, the subequal preanals of the *Egernia* and *Eugongylus* groups (*Leiolopisma ocellatum*) and 6, the enlarged medial pair of preanals of the *Sphenomorphus* group (*Sphenomorphus gracilipes*).

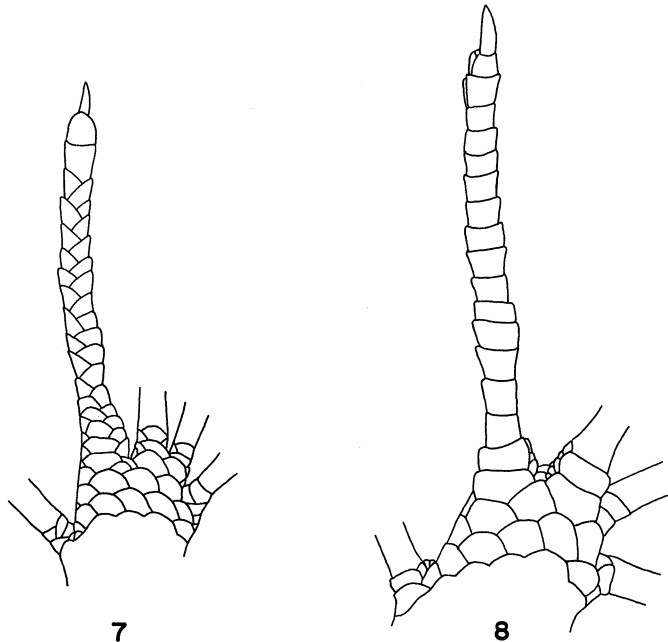
(F.) *Supradigital scales*. The scales on the dorsal surface of the fourth toe appear to be separable into two modal conditions: F.) two or more longitudinal rows of scales extending over at least the basal part of the digit but often extending much further (Fig. 7 this paper, Fig. 1b-h in Brongersma 1942 and Fig. 30 in Greer 1974) and f.) a single row of scales throughout the entire length of the digit (Fig. 8 this paper, Fig. 1 a in Brongersma 1942 and Fig. 31 in Greer 1974).

There is some variation in character state F that serves to separate the two major groups with this character. In the *Sphenomorphus* group there are generally two or more longitudinal scale rows extending over at least the basal half of the digit while in the *Egernia* group there is generally only a short second row comprising two to four scales confined to the base of the digit. Most *Tiliqua*, which are in the *Egernia* group, have but a single row of scales throughout the length of the digit.

The *Eugongylus* group generally has a single row of scales throughout the length of the digit, but in a few of the larger species, e.g., *Eugongylus* and some *Emoia*, there is a short second row of scales at the extreme base of the digit.

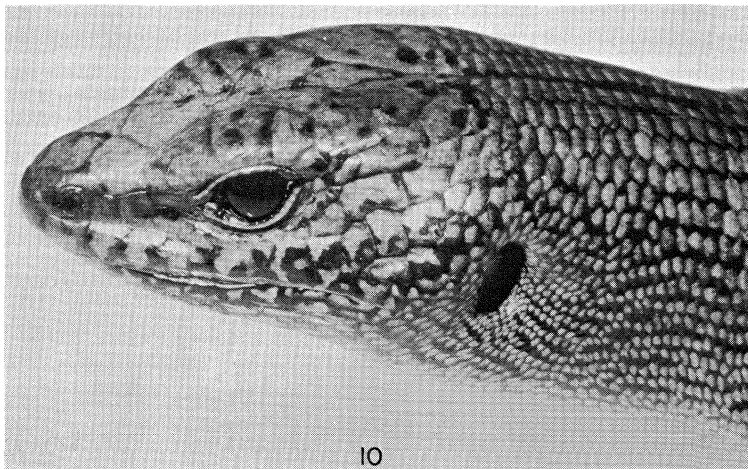
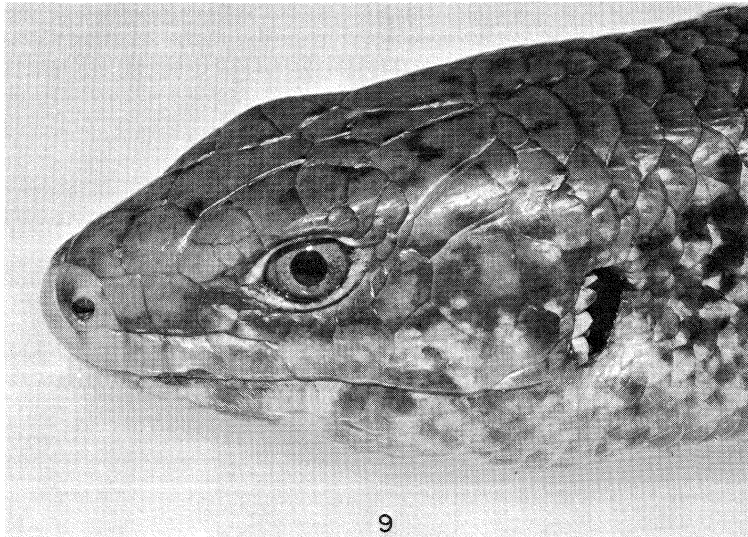
The genera *Lerista* and *Notoscincus* which are in the *Sphenomorphus* group are exceptional in having but a single row of scales covering the fourth toe.

Gerrhosaurines, *Eumeces* and *Mabuya* all have a multiple row of supradigital scales extending over at least the basal part of the digit; this character state is therefore taken as primitive (F) and a single row is taken as derived (f).



Figs. 7 and 8. The two conditions of the scales covering the dorsal surface of the fourth toe in Australian skinks: 7, the multiple rows of scales of the *Egernia* and *Sphenomorphus* groups (*Sphenomorphus gracilipes*) and 8, the single row of scales of the *Eugonylus* group (*Leiopolisma entrecasteauxii*).

(G.) *Iris colour*. The iris may be either (G) distinctly paler than the black pupil in showing cream, pale green, yellow, orange or gold colour often with metallic tints and textures (Fig. 9) or (g) virtually as dark as the pupil in being very dark liver or blackish brown in colour (Fig. 10). In the first condition the iris is generally easily distinguishable from the pupil with the naked eye in good light but in the second both a hand lens and good light may be required. In either case the determination is best made on live material.



Figs. 9 and 10. The two types of iris colour in Australian skinks: 9, the iris appreciably lighter than the pupil as in the *Egernia* and *Eugongylus* groups (*Egernia frerei*) and 10, the iris virtually as dark as the pupil as in the *Sphenomorphus* group (*Sphenomorphus* new species).

In my experience iris colour can be determined in most skinks without difficulty. Some *Egernia cunninghami* and *Tiliqua rugosa* in the *Egernia* group have a dark grey iris while their relatives have a distinctly lighter iris. Some *Cryptoblepharus* in the *Eugongylus* group also have a large amount of black pigment in the iris, especially around the pupil, but close inspection will reveal light pigment in more peripheral areas. Many species in the *Eugongylus* group also may have a small diffuse-edged section of dark pigment directly behind the iris and often a smaller section in front, but the basic light colour of the iris is generally obvious in these forms. It should perhaps be noted that none of these exceptions, which are somewhat "dark eyed" forms in basically "light eyed" groups, have the iris as dark as in the basically "dark eyed" *Sphenomorphus* group.

Gerrhosaurines, *Mabuya* and most other lizards generally appear to have a light iris, whereas *Eumeces* generally appears to have a very dark iris. A light iris is therefore taken as primitive (G) and a dark iris is taken as advanced (g).

(H.) *Hemipenis*. The morphology of the fully everted hemipenis can be resolved into one of two types: H.) one with a relatively short, columnar base and a slightly bulbous or bilobed cap (Figs. 11-13), and h.) the other with a long narrow base and two equally long bifurcations (Figs. 14-15).

Although these two hemipenial types are quite distinct, it is clear that there is a good deal of important variation within each type, especially the first. This variation should be of great value in work on the relationships of both species and genera.

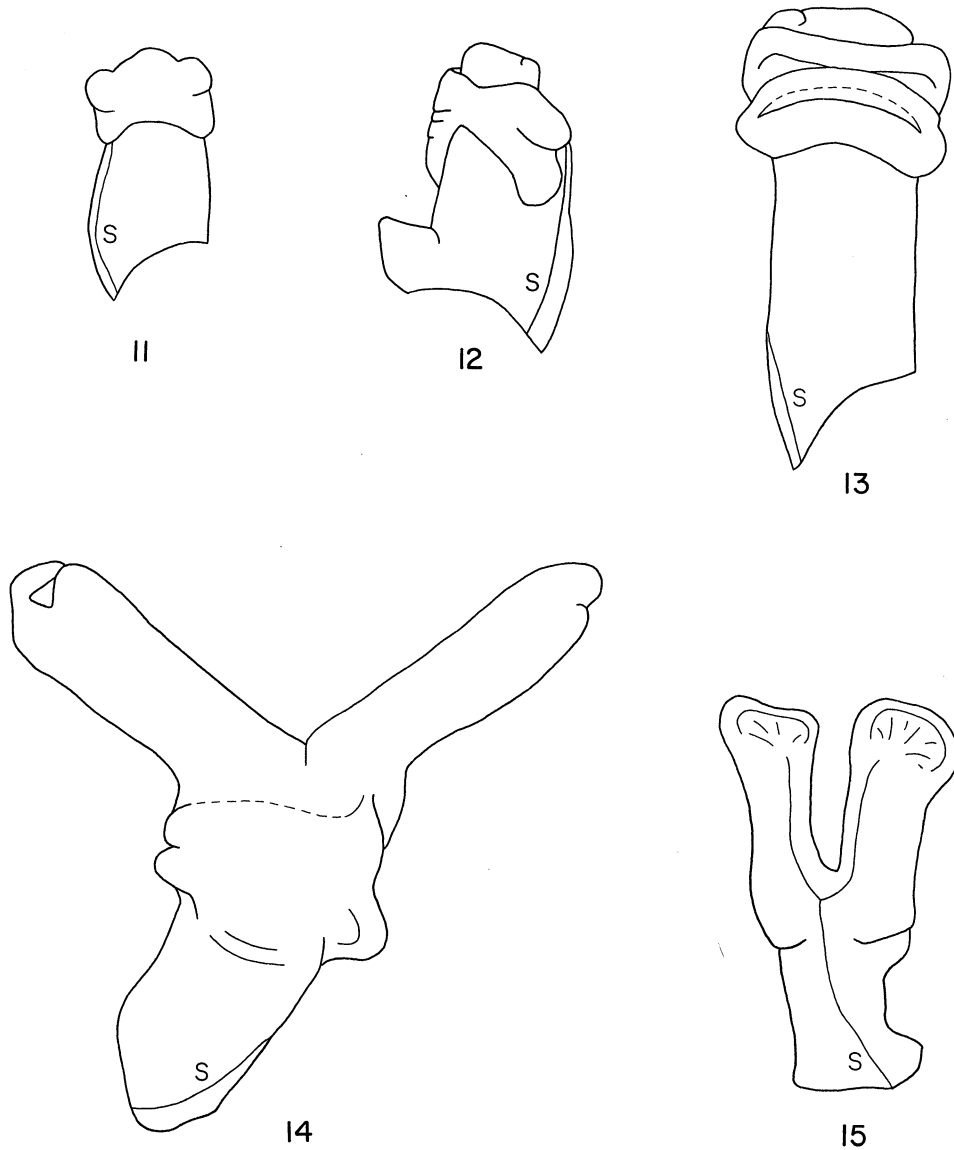
I have not examined the hemipenis of any gerrhosaurine but in that both *Eumeces* and *Mabuya* have a basically columnar structure, I take this as the primitive condition (H) and the deeply bifurcated structure as derived (h).

THE THREE GROUPS OF SKINKS REPRESENTED IN AUSTRALIA

Egernia Group

DIAGNOSIS: Premaxillary teeth 8 or fewer¹; Meckel's groove completely obliterated by the overlapping and fusion of dentary; parietals completely separated by interparietal; parietal bordered along its posterolateral edge by two or more temporals and a nuchal; medial pair of preanals more or less equal in size to more lateral preanals; scales on dorsal surface of fourth toe in two rows at least basally (the second row is generally made up of only two to four small scales); iris lighter than pupil; hemipenis consisting of short columnar base and bulbous cap.

1. The closely related *Egernia coventryi* and *E. luctuosa* from extreme southeastern and southwestern Australia, respectively, are exceptional in having nine premaxillary teeth (Table 1). In that *Egernia* probably evolved from a rather primitive species of lygosomine (perhaps similar to a living species of southeast Asian *Mabuya*, *vide* Horton 1972) which probably had nine premaxillary teeth, this tooth number may mark *Egernia coventryi* and *E. luctuosa* as primitive within *Egernia*. This supposition is supported by the species' distribution in areas that are well known for harbouring primitive relicts in other groups, e.g. plants (Burbridge 1960) and insects (Mackerras 1970).



Figs. 11-15. The two types of hemipenis in Australian skinks. 11-13, the basically columnar hemipenis of the *Egernia* and *Eugongylus* groups: 11 — *Leiolopisma coventryi*; 12 — *Lampropholis challengerii*; 13 — *Morethia obscura*. 14-15, the deeply bifurcated hemipenis of the *Sphenomorphus* group: 14 — *Sphenomorphus gracilipes*; 15 — *Lerista terdigitata*. Right hemipenis (ventral aspect) illustrated for all species except *Lampropholis challengerii*. The sulcus spermaticus is indicated by the letter "s".

Australian Genera.

Egernia. The recent work of Cogger (1975) and Storr (1978a) brings the total number of currently recognised species to 27; one of these, *cunninghami*, however, is widely recognised to be composite.

The genus is widespread throughout Australia (including Tasmania) and one Australian species extends north into southern New Guinea.

Tiliqua (including *Omolepida* and *Trachydosaurus*). A total of 11 species are now recognised as the result of work by Cogger (1975) and Storr (1976c).

The genus is widespread throughout Australia with one species or subspecies (*gigas*) extending north through New Guinea and west through the Sunda Islands to Sumatra.

Non-Australian Genera.

The Giant Green Tree Skink of the Solomon Islands, *Corucia zebrata*, is definitely a member of this group. The bizarre, spiny skinks of the genus *Tribolonotus* from New Guinea, the Bismarck Archipelago and the Solomon Islands (Zweifel 1966, Greer and Parker 1968a and Cogger 1972) also appear to belong here.

Eugongylus Group

DIAGNOSIS: Premaxillary teeth 11 or more; Meckel's groove completely obliterated by the overlapping and fusion of dentary; parietals meet behind interparietal; parietal bordered along its posterior edge by upper secondary temporal and transversely enlarged nuchal; medial pair of preanal scales more or less equal in size to more lateral preanals; scales on dorsal surface of fourth toe in single row throughout length of digit; iris lighter than pupil; hemipenis consisting of short columnar base and bulbous cap.

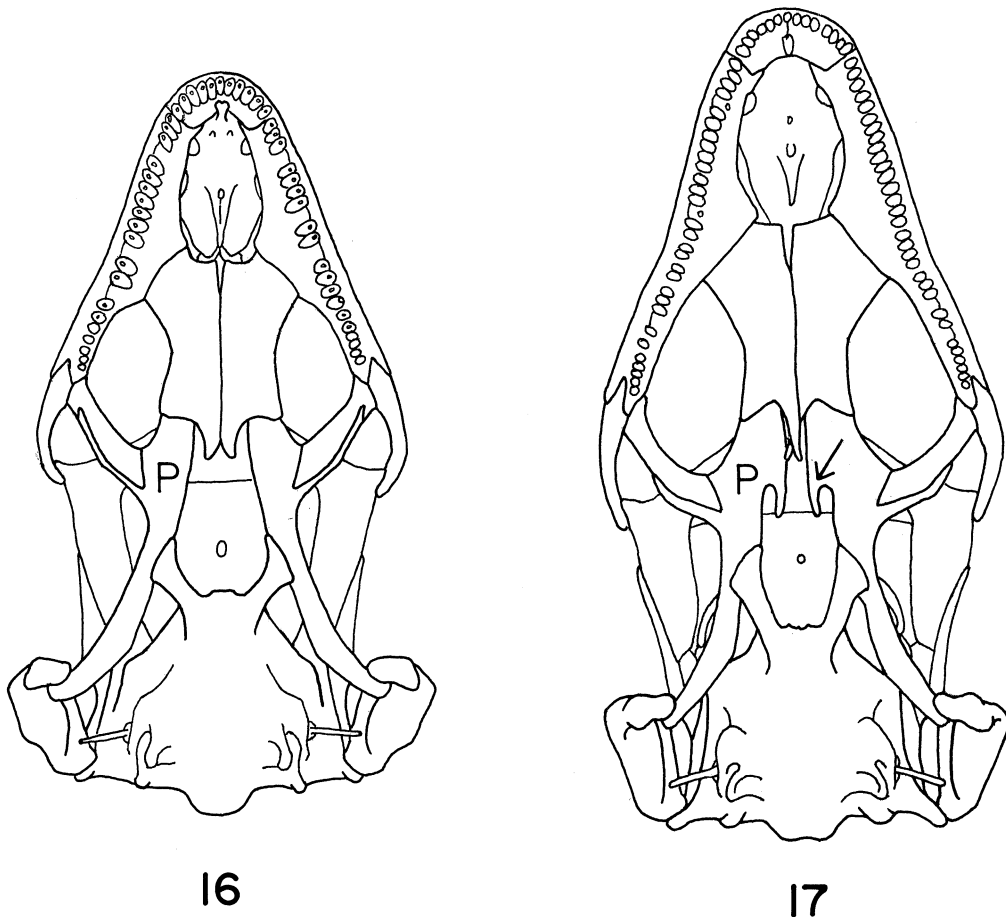
Subgroups of the *Eugongylus* group

There are two major subdivisions of the *Eugongylus* group based on the shape of the palatal rami of the pterygoids (Greer 1974). In the more primitive alpha condition, the palatal rami diverge smoothly along their medial edges (Fig. 16 this paper and Figs. 1-11 in Greer 1974), whereas in the advanced beta condition, the palatal rami each have a deep posterior emargination that gives them a distinctly hooked appearance (Fig. 17 this paper and Figs. 12-17 in Greer 1974).

Eugongylus Subgroup (Alpha Palate)*Australian Genera*

Anotis. Five species are currently recognised, two in south-eastern Australia (but not Tasmania) and three on New Caledonia (Greer 1974).

Cryptoblepharus. Thirty-six forms of this widespread genus are currently recognised (Mertens 1928, 1931, 1933, 1934, 1958 and 1964, Storr 1976a and Ingram and Covacevich, 1978). In the past, all forms were generally treated as subspecies of one species (*boutoni*)



Figs. 16-17. The two types of secondary palate in the *Eugongylus* group: 16, the alpha palate of the *Eugongylus* subgroup (*Leiolopisma pretiosum*); 17, the beta palate of the *Lampropholis* subgroup (*Carlia longipes*).

but the increasing number of cases of sympatry now make it more reasonable to regard most of these forms as species.

In addition to being widespread throughout Australia (but not in Tasmania), the genus occurs widely in the tropical western and central Pacific area and on islands in the far western Indian Ocean and the adjacent African mainland.

*Emoia*¹ Dr Walter Brown is revising this large and difficult group, and he currently recognises 37 species (letter of 22 September 1976).

1. A few species of *Emoia* have apparently evolved a beta palate independently of the *Lampropholis* subgroup discussed below (see Greer 1974, p. 13).

The genus is widespread in the tropical Pacific area from southeast Asia east to Arundel Island but enters Australia only in extreme northeastern Cape York Peninsula (Ingram, MS).

Eugongylus. Three species are currently recognised, but a review of the species taxonomy is badly needed.

The genus is widespread throughout the southwest Pacific but, like *Emoia*, enters Australia only in extreme northeastern Cape York Peninsula.

Leiolopisma (including *Pseudemoia*). A total of 41 species is currently recognised. The genus is centred over three disjunct areas: Australia and Tasmania (12 species); New Zealand and the Chatham Islands (21 species), and New Caledonia and the Loyalty Islands (6 species). Mr Peter Rawlinson (1974b and 1975) is currently revising the Australian species, and Mr Graham Hardy (1977) and Dr Joan Robb (1970, 1974 and in preparation) have revised the New Zealand species; our knowledge of the important New Caledonia and Loyalty Island fauna, however, is based solely on the egregiously outdated review of Roux (1913). In addition to these areas, the genus is also represented by single species in the Mauritius area (Vinson and Vinson 1969) and Lord Howe Island (Cogger 1971).

Morethia. This widespread Australian (but not Tasmanian) genus has been the subject of three recent reviews (Smyth 1972, Storr 1972, and Rawlinson 1976). Seven named species are known and an eighth from the Northern Territory will soon be described (Greer, MS).

Proablepharus. A recent review of Western Australian material by Storr (1975c) recognised two species and to these, I believe, should be added the little known *kinghorni* from the drier parts of eastern Australia (Greer 1974).

The genus is widespread throughout most of mainland Australia except for the more mesic southeast and southwest areas.

Non-Australian Genera

The very rare genera *Phoboscincus* of New Caledonia and the Loyalty Islands and *Tachygyia* from the Tonga Islands are members of the *Eugongylus* subgroup (Greer 1974). Four species currently placed on the genus *Sphenomorphus* also probably belong here. These are *aignanus*, *bignelli*, *louisiadensis* and *minutus* from the New Guinea — Solomon Islands area (per. obs).

Lampropholis Subgroup (Beta Palate)

Australian Genera

Carlia. The genus is centred over northern Australia and New Guinea. The species of this genus that occur in Australia are currently being revised by Ingram and Covacevich (MS), and they recognise 21 species. A similar revision of the remaining species, which may nearly equal the Australian species in number, is badly needed.

Lampropholis. Mr Peter Rawlinson is currently revising the species in the genus. I personally know of at least 11 or 12 species, although common practice recognises only four (Cogger 1975). The genus is confined to the mesic east coast of Australia (including Tasmania) and has been introduced to both New Zealand and the Hawaiian Islands. In Hawaii the introduced species (cf. *delicata*) is commonly misidentified as *Leiolopisma metallicum* (Rawlinson, pers. comm. and pers. obs.).

Menetia. The recent reviews of Storr (1976b and 1978b) and Ingram (1977) recognise a total of six species, and one more remains to be described (Rankin, MS).

The genus is widespread throughout most of mainland Australia except for the more mesic southeast and southwest areas and Cape York Peninsula.

Non-Australian Genera

The only non-Australian member of the *Lampropholis* subgroup in the southwest Pacific area appears to be *Geomyersia*, a rare monotypic endemic of the Solomon Islands (Greer and Parker 1968 b). In subsaharan Africa, however, there are a large number of skinks that are certainly members of the *Eugongylus* group and, unless the shape of the palatal rami of the pterygoids is convergent, they are also members of the *Lampropholis* subgroup. These skinks are currently in the genera *Cophoscincopus* (Greer 1974) and *Panaspis*, the latter with the four subgenera *Afroablepharus*, *Lacertaspis*, *Leptosiaphos* and *Panaspis* (Perret 1975).

The four poorly known south Indian skinks of the genus *Ristella* (Smith 1935) may also be members of the *Lampropholis* subgroup.

Sphenomorphus Group

DIAGNOSIS: Premaxillary teeth 9 in most surface dwelling forms but fewer in some burrowing forms and in *Ctenotus*; Meckel's groove open; parietals meet behind interparietal; parietal bordered along its posterolateral edge by two or more temporals; and a nuchal; medial pair of preanals moderately to much larger than more lateral preanals; scales on dorsal surface of fourth toe in two or more rows extending over at least basal half of digit; iris virtually as dark as pupil; hemipenis consisting of relatively long thin base and two long thin bifurcations.

Australian Genera

Anomalopus. Work in preparation by Greer and Cogger indicates that a total of 11 species is recognisable, but only seven of these are named. The group is almost certainly polyphyletic and will probably be split into three genera. The assemblage as it is now conceived occurs only in eastern Queensland and New South Wales.

Ctenotus. Thanks largely to Storr's (1968, 1969, 1971a, 1973, 1975a and 1978 c-d) revisionary efforts with the genus, 53 species are currently recognized. There are, however, several species yet to be described (Mr P. R. Rankin and Dr G. M. Storr) and the total number of species in the genus probably exceeds 60.

The genus is widespread throughout Australia (but not Tasmania), and two Australian species extend north into southern New Guinea.

Eremiascincus. Two species are currently recognised (Storr 1967 and 1974a and Greer 1979) but there is still a good deal of unexplained variation within the complex which indicates that more remains to be done with the alpha taxonomy of the group.

The genus is widespread in the arid and semi-arid interior of mainland Australia.

Hemiergis. Four species are currently recognised (Copland 1945, Smyth 1968, Storr 1975b and Coventry 1976). The genus is restricted to the southern periphery of temperate Australia but does not occur in Tasmania.

Lerista. A total of 34 species is now recognised (Storr 1971b and 1976d and Cogger 1975), and there are at least three additional species that have yet to be described. The genus occurs throughout most of Australia and extends through the islands of eastern Bass Strait to the extreme northeastern corner of Tasmania.

*Notoscincus*¹ This genus is currently thought to comprise either a single species with two subspecies (Storr 1974b) or two species (Smith 1976). The known localities are widely scattered throughout the arid, semi-arid and seasonally dry areas of northern Australia.

Saiphos. This monotypic genus is known only from the mesic east coast of New South Wales and southeastern Queensland (Cogger 1975).

Sphenomorphus. This is a very large and diverse, but probably largely monophyletic, group ranging from southwestern India and southern and eastern Asia east through the Philippines and Indo-Australian Archipelago to Australia and the Solomon Islands (Greer 1973, Greer and Parker 1967 and 1974 and Storr 1967). The group may also be represented in Middle America (Greer 1974). There are over 125 described species and many undescribed species are known. The group merits subdivision at the generic level.

"*Tropidophorus*" *queenslandiae*. This peculiar species is restricted to the rainforests of northeastern Queensland (Cogger 1975). In my opinion it is unlikely to be closely related to the "true" *Tropidophorus* of southeast Asia, Borneo and the Philippines; instead it is probably a bizarre offshoot of the *Sphenomorphus* radiation in Australia.

Non-Australian Genera

Three southwest Pacific genera are probably members of this group. These are *Lipinia*, *Lobulia* and *Prasinohaema* (Greer 1974). Also, if *Tribolonotus* is not a member of the *Egernia* group, it probably belongs here.

Several primarily Asian genera are also probably members of this group. They are *Ablepharus*, *Ateuchosaurus*, *Isopachys*, *Scincella* and *Tropidophorus*.

THE PHYLOGENETIC RELATIONSHIPS OF THE THREE GROUPS OF SKINKS REPRESENTED IN AUSTRALIA

In addition to the eight characters analyzed in an earlier section of this paper there are two other characters that are useful in inferring the relationships of the three groups of skinks represented in Australia. These are the presence (I) or absence (i) of pterygoid teeth and the presence (J) or absence (j) of a distinct postorbital bone. In both cases the presence of the structure is primitive and its absence derived (Camp 1923). Pterygoid teeth and a postorbital bone occur in a few members of the *Sphenomorphus* group and hence must have characterized its earliest representatives², but neither structure occurs in any member of the *Eugongylus* or *Egernia* group.

1. In an earlier paper (Greer 1974) I suggested that the genus *Notoscincus* was a member of what is here considered to be the *Eugongylus* group. At that time the basis for my concept of the genus was a single, poorly preserved specimen and a drawing of the ventral view of the skull (Fuhn 1969). Since then, however, I have examined all the preserved material in the Australian state museums and, through the courtesy of Dr. Glen Storr of the Western Australian Museum, I have been able to prepare and examine the skull of a single specimen (W.A.M. 45642). I have also examined six living specimens. As a result of these studies, I now think that *Notoscincus* is more likely a member of the *Sphenomorphus* group than the *Eugongylus* group. The reasons for this are that in only two of the seven characters in which the two groups differ, i.e., Meckel's groove (closed) and the supradigital scales on the fourth toe (in a single row), *Notoscincus* is most similar to the *Eugongylus* group, but in the remaining five characters, i.e., premaxillary teeth (7-9), scales along the posterolateral edge of the parietal (a transversely enlarged nuchal and two temporals), preanals (enlarged), iris colour (dark) and hemipenial morphology (deeply bifurcated), the genus is most similar to the *Sphenomorphus* group.

2. These two characters were omitted from the earlier analysis because they were not completely diagnostic for all groups.

Assuming that the phyletic analysis for all ten characters is correct and that no retrogressive changes of character state have occurred, then the three most parsimonious phylogenies relating the three groups of skinks represented in Australia are depicted in Fig. 18. The first phylogeny (a) hypothesizes 15 changes of character state and four cases of convergence ($B \rightarrow b$, $C \rightarrow c$, $l \rightarrow i$, and $J \rightarrow j$); the second (b) hypothesizes 14 changes of character state and three cases of convergence ($C \rightarrow c$, $l \rightarrow i$ and $J \rightarrow j$), and the third (c) hypothesizes 12 character state changes and one case of convergence ($C \rightarrow c$). On the basis of this analysis, therefore, the third phylogeny is the most parsimonious and hence the most reasonable as a working model.

Two observations can be made about the relationships hypothesized by this phylogeny. First, somewhere in the line between the common ancestor of the *Eugongylus* and *Egernia* groups and the common ancestor of all three groups there may have been a form similar to *Mabuya* (AbCDEFGHIJ). Furthermore, in that this form probably had a scaly lower eyelid, divided frontoparietals and an oviparous mode of reproduction (as evidenced by the retention of these primitive characters in living members of the *Eugongylus* and *Egernia* groups), it was probably most similar to the most primitive species of *Mabuya* living today. The second observation is that while the common ancestor of all three groups was itself probably rather similar to the most primitive living species of *Mabuya*, it was even slightly more primitive in having had an open Meckel's groove. It is interesting to note that no known living lygosomine is as generally primitive as this hypothetical form.

THE ZOOGEOGRAPHIC ORIGIN OF AUSTRALIAN SKINKS

Two independent lines of evidence indicate that, in the broadest terms, the area of origin of the Australian skink fauna lies to the north and northwest of present day Australia. First, the nearest living relatives of the ancestors of the three groups of skinks represented in Australia appear to be the most primitive living species of *Mabuya* (see above), and the fact that these forms are centred over southcentral and southeast Asia and the western end of the Indo-Australian Archipelago suggests that this area may have been coincident with or close to the area of origin of the three groups (also see below). And second, there is nothing in the distribution of skinks as a whole that suggests that any skink ever used a Gondwanaland dispersal route. None of the three groups represented in Australia, for example, occur in South America and the only group of skinks in South America (the most advanced species of *Mabuya*) is not represented in Australia¹

It is not yet possible to say how many times skinks may have colonized Australia, because knowledge of relationships within the three groups is incomplete. An educated guess as to the number of significant colonizations, i.e., those that led to speciation, however, would be somewhere in the range of two to eight. The minimum estimate is based on two lines of reasoning. First, the most primitive members of the *Sphenomorphus* group are centred over southeast Asia and the western end of the Indo-Australian Archipelago (Greer 1974 and 1978) and hence the group as a whole may have evolved here and then spread east to enter Australia at least once. And second, if the *Egernia* and *Eugongylus* groups did share a common ancestor, as the evidence discussed above seems to indicate, then the fact that both groups are centred over the Australian Region raises the possibility that this ancestor inhabited Australia and that one of its ancestors was itself a colonist of Australia. The maximum estimate is based on my own ideas about relationships

1. The presence of certain derived character states in the South American *Mabuya*, e.g., a clear window in the lower eyelid and viviparity, makes it unlikely that these species, more than the Asian species, are the closest living relatives of the three groups of skinks discussed here.

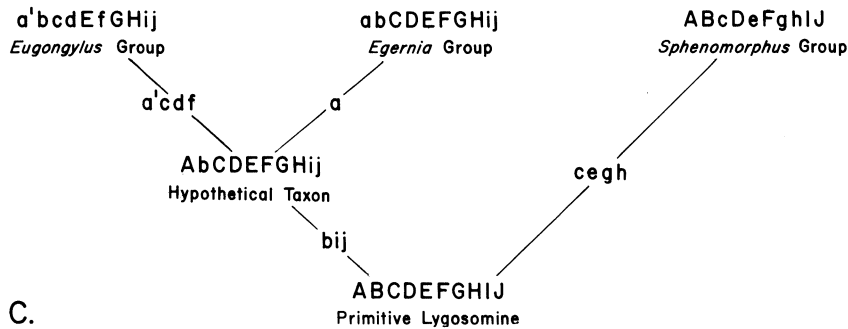
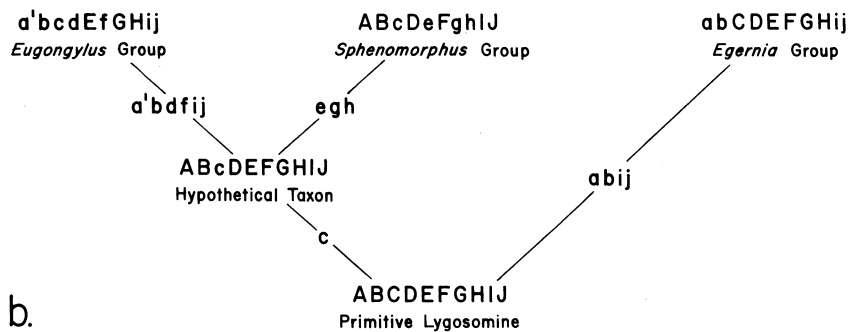
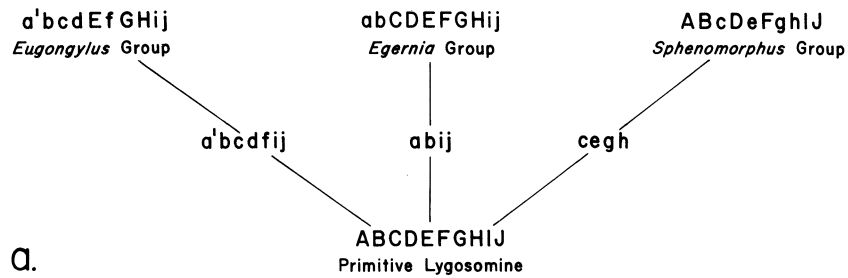


Fig. 18. The three most parsimonious phylogenies for the three groups of skinks represented in the Australian fauna. Each letter denotes a character, and the letter case denotes the inferred primitive (upper case) or derived (lower case) state of the character. Changes in character state between taxa are indicated by the letters beside the lines linking the taxa. Note that the number of character state changes and cases of convergence hypothesized by the first (a), second (b) and third (c) phylogenies are, respectively, 15 and four, 14 and three and 12 and one. See the text for the assumptions and rationale behind the phylogenies.

within the *Eugongylus* and *Sphenomorphus* groups, but since there is still much to be learned about relationships in both groups, but especially the *Sphenomorphus* group, the overall maximum estimate is highly speculative.

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APPENDIX

The Primitive Features of *Eumeces* and *Mabuya*

Eumeces and *Mabuya* appear to be the most generally primitive genera in their respective subfamilies, i.e., the Scincinae and Lygosominae. They are also very similar to each other, differing primarily in the two characters that distinguish their respective subfamilies, i.e., the distinct frontal bones and generally incomplete secondary palate of the scincines versus the fused frontals and generally complete secondary palate of the lygosomines (Greer 1970 a).

The character states which mark these two genera as the most generally primitive taxa within their subfamilies and which would be nearly universally accepted as primitive within skinks as a whole are outlined briefly below.

EXTERNAL MORPHOLOGY. Supranasal scales present; prefrontals present; single anterior and posterior loreal scales; frontoparietal and interparietal scales distinct; lower eyelid moveable and scaly; external ear opening present; fore and hind limbs well developed, pentadactyl; claws non-retractile.

OSTEOLOGY. Premaxillary bones distinct; nasals distinct; lacrimal present; squamosal present; postorbital distinct; supratemporal arch complete; post-temporal arch open; jugal present and extending dorsally to postfrontal; parietal eye foramen present; pterygoid teeth present; palatal rami of pterygoids separated in the secondary palate (applicable only to lygosomines); fenestra rotunda present; angular distinct; second epi and ceratobranchials present, caudal vertebrae with fracture planes.

INTERNAL ANATOMY. Oviducts paired.

BEHAVIOUR. Gait normal, i.e., not slow and deliberate.

ECOLOGY. Diurnal; surface dwelling (terrestrial to semi-arboreal).

REPRODUCTION. Oviparous; clutch size variable.

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Taxon	Number of premaxillary teeth													
	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>slateri</i>					6									
<i>stokesi</i>			1	6										
<i>striata</i>					2									
<i>striolata</i>				7	28									
<i>whitii</i>					22									
<i>Tiliqua</i>														
<i>adelaidensis</i>				1										
<i>branchialis</i>				5										
<i>casuarinae</i>				2	8									
<i>gigas</i>				1										
<i>multifasciata</i>				2										
<i>nigrolutea</i>				5	1									
<i>occipitalis</i>				2										
<i>rugosa</i>				6										
<i>scincoides</i>				3										
EUGONGYLUS GROUP														
<i>Eugongylus</i> Subgroup														
<i>Anotis</i>														
<i>graciloides</i>								5						
<i>maccoyi</i>								7						

Taxon	Number of premaxillary teeth													
	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Cryptoblepharus</i>														
<i>litoralis</i>								10	1					
<i>virgatus</i>								12						
species 1								8	1					
<i>Emoia</i>														
<i>atrocostata</i>								11						
<i>cyanogaster</i>							1	20	1					
<i>Eugongylus</i>														
<i>albofasciolatus</i>							2	1	5					
<i>rufescens</i>							1	7						
<i>Leiolopisma</i>														
<i>coventryi</i>							1	10	3					
<i>entrecasteauxii</i>							1	17	1					
<i>lichenigerum</i>							3	6						
<i>metallicum</i>								5						
<i>platynotum</i>						1		22	2					
<i>pretiosum</i>								9						
<i>trilineatum</i> (east coast)							1	5						
<i>trilineatum</i> (west coast)								32						
<i>spenceri</i>							1	11						

Taxon	Number of premaxillary teeth													
	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Morethia</i>														
<i>adelaidensis</i>								5						
<i>boulengeri</i>							1	33	1					
<i>butleri</i>								14						
<i>lineoocellata</i>								5						
<i>obscura</i>								16		1				
<i>ruficauda</i>								3						
<i>taeniopleura</i>								10						
species 1								1						
<i>Proablepharus</i>														
<i>kinghorni</i>								3						
<i>reginae</i>								1						
<i>tenius</i>								3						
<i>Lampropholis</i> Subgroup														
<i>Carlia</i>														
<i>amax</i>										5				
<i>bicarinata</i>										6	1	1		
<i>burnettii</i>										3		4		
<i>coensis</i>												1		
<i>dogare</i>										2				

Taxon	Number of premaxillary teeth													
	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>gracilis</i>										2				
<i>jarnoldae</i>										8	1	3		
<i>johnstonei</i>										4				
<i>melanopogon</i>									1	38	1	2		
<i>mundivensis</i>									1	3				
<i>novaeguineae</i>												11		
<i>pectoralis</i>										9				
<i>rhomboidalis</i>										2	1	1		
<i>rimula</i>												3		
<i>schmeltzii</i>										2				
<i>tetradactyla</i>								1		12				
<i>vivax</i>										5	2			
<i>species 1</i>										1	3	13		1
<i>Lampropholis</i>														
<i>challengeri</i>								5						
<i>delicata</i>						1	1	46	4	1				
<i>guichenoti</i>							1	18	2					
<i>mustelina</i>								30	1					
<i>species 1</i>								13	1					
<i>species 2</i>								8						

Taxon	Number of premaxillary teeth													
	4	5	6	7	8	9	10	11	12	13	14	15	16	17
species 3							1	3						
species 4										9	3			
species 5								1		13	1			
<i>Menetia</i>														
<i>greyi</i>							1	11						
<i>maini</i>								4						
<i>surda</i>								1						
<i>SPHENOMORPHUS</i> GROUP														
<i>Anomalopus</i>														
<i>frontalis</i>					2									
<i>lentiginosus</i>					13									
<i>ophioscincus</i>						2	6							
<i>reticulatus</i>						2								
<i>truncatus</i>					2		4							
<i>verreauxii</i>				1	11									
species 1	1	5												
species 2					1									
species 3				1	4									
species 4					8									

Taxon	Number of premaxillary teeth													
	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>saxatilis</i>				7										
<i>schevilli</i>				2										
<i>schomburgkii</i>			1	8	2									
<i>serventyi</i>				2										
<i>spaldingi</i>			1	11	1									
<i>strauchii</i>				2										
<i>taeniolatus</i>			1	7										
<i>uber</i>				4										
<i>Eremiascincus</i>														
<i>fasciolatus</i>					1	7								
<i>richardsonii</i>					2	4								
<i>Hemiergus</i>														
<i>decrensiensis</i>					8									
<i>initialis</i>				1	2									
<i>millewae</i>					1									
<i>peronii</i>				3	33	1								
<i>quadrilineatus</i>					1									
<i>Lerista</i>														
<i>bougainvillii</i>				30	1									
<i>elegans</i>				1										

Taxon	Number of premaxillary teeth													
	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>gerrardii</i>				1										
<i>microtis</i>				3										
<i>muelleri</i>		1		5										
<i>orientalis</i>		4	22	1										
<i>picturatum</i>				1										
<i>punctatovittatum</i>				6										
<i>stylis</i>				1										
<i>terdigitata</i>			5											
species 1		2												
species 2				1										
<i>Notoscincus</i>														
<i>ornatus</i>				2	4	1								
<i>Saiphos</i>														
<i>equale</i>				1	2	38								
<i>Sphenomorphus</i>														
<i>arnhemicus</i>								1						
<i>brachysoma</i>					1	13	1							
<i>darwiniensis</i>								1						
<i>douglasi</i>								14						
<i>gracilipes</i>				2	14	1								

Taxon	Number of premaxillary teeth												
	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>isolepis</i>				1	5								
<i>kosciuskoi</i>			1	5									
<i>mjobergi</i>					1								
<i>murrayi</i>			2	8									
<i>nigricaudis</i>				1									
<i>pardalis</i>				1	3								
<i>punctulatus</i>				8	8								
<i>quoyii</i>					9								
<i>scutirostrus</i>				3	26								
<i>tenuis</i>			1	2	5								
<i>tigrinum</i>					4								
species 1					10	1							
species 2				1									
" <i>Tropidophorus</i> "													
<i>queenslandiae</i>					6								