

# A SUBFAMILIAL CLASSIFICATION OF SCINCID LIZARDS

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## ABSTRACT

The subfamilial classification of skinks which is proposed is based primarily on the osteology of the skull, particularly on the relationships of the bones of the secondary palate and the frontal bones, and on external morphology. These, plus other characters important in understanding the evolution and classification of the higher taxa of skinks, are discussed in some detail.

Four subfamilies are recognized. The Scincinae (approximately 28+ genera and 182 species) are considered to be the most primitive subfamily of skinks and are apparently independently ancestral to the other three subfamilies. The scincines occur in Asia and Africa, and in the New World north of Costa Rica (*Eumeces* and *Neoseps*), but are conspicuously absent from the Australian Region. The center of abundance and diversity of scincines today is in subsaharan Africa and the islands of the western Indian Ocean. The Feylininae (2 genera and 4 species) and Acontinae (3 genera and 15 species) are specialized burrowing taxa which almost surely evolved independently from the scincines of subsaharan Africa where both subfamilies are confined today. The fourth subfamily, the Lygosominae (approximately 40+ genera and 600+ species), is the most numerous and diverse subfamily of skinks. They appear to have arisen from a scincine ancestry and have radiated spectacularly in the Australian Region and southeast Asia. From this area, they have spread west into

Africa and across the Atlantic into the New World (*Mabuya*), and north and east across a Bering Straits land bridge into North and Central America (*Leiolopisma*). It is suggested that the radiation and expansion of the lygosomines is responsible in part for the apparent decline of the scincines in certain areas such as Asia.

## INTRODUCTION

The only attempt at a suprageneric classification of skinks was provided by Mittleman (1952) as a kind of preface to his synopsis of the genera that are related to or often grouped under (as subgenera) the catch-all genus *Lygosoma*. The four subfamilies recognized were diagnosed by means of a key, and the general distribution of each subfamily was given. Only the genera of the subfamily Lygosominae, however, received further attention.

Mittleman's (1952) diagnostic key to the four subfamilies of skinks is as follows:

- A. Palatine bones in contact on median line of palate.
  - 1. Pterygoid bones separated on the median line of palate; palatal notch extending anteriorly to level of centers of eyes ..... MABUYINAE.
  - 2. Pterygoid bones in contact anteriorly; palatal notch not extending anteriorly to level of centers of eyes ..... LYGOSOMINAE.
- B. Palatine bones separated on median line of palate.

1. Nostril pierced in nasal, or between two adjacent plates, but never touching rostral \_\_\_\_\_ SCINCINAE.
2. Nostril pierced between rostral and adjacent plate, thereby contacting rostral, or else within rostral itself \_\_\_\_\_ CHALCIDINAE.

In the course of my research on the supraspecific relationships of skinks, I have attempted to correlate skull osteology with external morphology in delimiting taxa. This study, which is based on data from the complete skulls of over 350 species of skinks, has suggested to me a subfamilial classification that has a sounder basis than that of Mittleman.

Mittleman's (1952) diagnoses of the three subfamilies Mabuyinae, Scincinae, and Chalcidinae are accurate descriptions of three possible assemblages of skinks, but none of these assemblages can be defended as a monophyletic unit. This should become evident in the discussion of the new classification. Mittleman's diagnosis of the Lygosominae, on the other hand, constitutes an inaccurate description of many of the genera which he included in the group, but his generic list for the subfamily includes most of the genera that I believe should constitute a subfamily Lygosominae. The Lygosominae of Mittleman is, in other words, an inaccurately diagnosed but well conceived taxonomic group.

In his characterization of the Lygosominae, Mittleman (1952) fell into the same trap as did Boulenger (1887) and M. A. Smith (1935) in their skink classifications. All three authors attempted to interpret the important relationships of the bones of the palate without removing the overlying buccal mucosa. In several lygosomine genera the pterygoids (i.e., their palatal

rami) are completely separated along the midline by the interpterygoid vacuity or by processes that project posteriorly from the palatines. Thus not only does the type species of the type genus of the subfamily Lygosominae, *Lygosoma quadrupes*, disagree with Mittleman's diagnosis of the subfamily, but the following genera do as well: *Ablepharus*, *Cryptoblepharus*, *Emoia*, *Eumecia*, *Eugongylus*, *Leiolopisma* (part), *Leptosiaphos*, *Riopa* (part), *Sia-phos* (part), and *Sphenomorphus* (part).

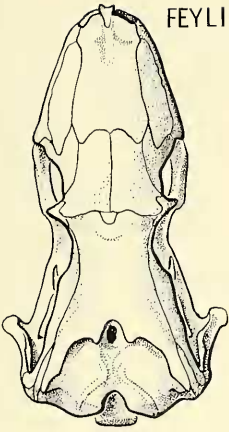
The four subfamilies in the classification proposed below are each based on the correlation of several skull and external characters, rather than on a single skull or external character, as were Mittleman's (1952) subfamilies, and the resulting distribution of the subfamilies is more meaningful zoogeographically than was Mittleman's arrangement.

#### CHARACTERS UTILIZED

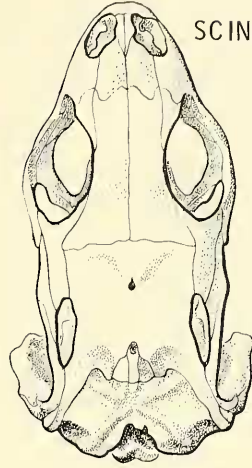
Before discussing the four subfamilies of skinks, it will be worthwhile to review briefly some of the characters that have been most useful in diagnosing the higher taxa of skinks. This discussion will be limited to the taxonomic use of these characters, as the phylogenetic significance of these and other characters will be considered in a later section of the paper.

*Secondary palate.* Apart from *Dibamus* and *Anelytropsis*, which appear to be related to one another but whose relationships with other lizards are obscure (Miller, 1966b), skinks are the only family of lizards with a bony secondary palate. The secondary palate may be complete or incomplete depending on the degree of apposition (meeting along the midline or not, respectively) of the horizontal lamellae of the palatine bones. As a further advance-

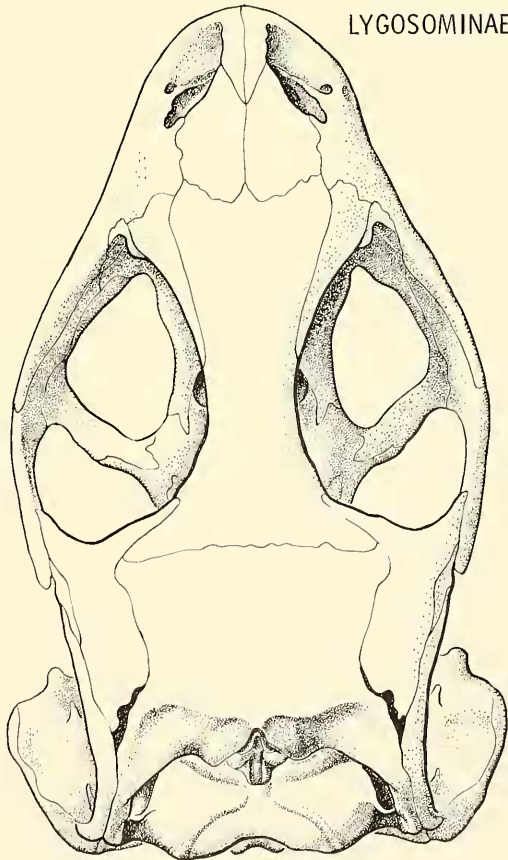
FEYLININAE



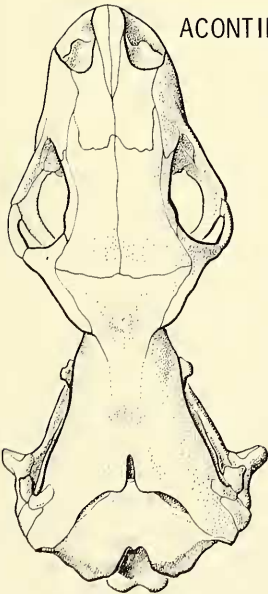
SCINCINAE



LYGOSOMINAE



ACONTINAE



ment on the complete secondary palate, the palatal rami of the pterygoids may also meet along the midline with the palatines to make an even more extensive secondary palate.

The secondary palate is a diagnostic feature of skinks as a family, and the complex relationships, as well as shapes, of the bones forming the palate (and those bordering it) are useful in recognizing subfamilies and taxa of lower rank (Greer, 1967a and b; Greer and Parker, 1968).

*Osteoderms.* The second partially diagnostic feature of skinks as a family is the characteristic arrangement of the tubules in the osteoderms, i.e., an approximately transverse canal with anteriorly and posteriorly projecting longitudinal canals (see Gosse, 1848; Duméril and Bocourt, 1881; Otto, 1908; Hewitt, 1929; Smith, 1935; Sibtain, 1938; Ali, 1947; Oliver, 1951; Fitch, 1954; Ganapati and Rajyalakshmi, 1958; Deraniyagala, 1960; Tilak and Rastogi, 1964, and Rathore, 1967 for figures of skink osteoderms).

A similar pattern of tubules is found in some gerrhosaurine osteoderms and serves to align this subfamily of cordylids with skinks.

Hewitt (1929) has sought to use the number of "cells" created by the radiating osteoderm tubules as a means of working out the relationships of major groups of skinks. No one has followed Hewitt's lead, but it might be profitable to do so in the future.

*Frontal bones.* The separation or fusion of the frontal bones correlates well with certain relationships of the bones in the secondary palate and is important in diagnosing the four subfamilies of skinks. The condition of the frontal is, of course, also an important character in diagnosing major taxa in other lizard families.

*Nasal bones.* These bones are fused in one subfamily (Feylininae) and distinct in the other three. Given the great number and diversity of species in these latter three

subfamilies, the fusion of the nasals in one group of skinks is important.

*Ectopterygoid.* This bone can show a good deal of variation in its relationships with the bones (palatine and pterygoid) of the secondary palate. These relationships are important at the subfamily level and below.

*Jugal.* This bone is lacking in one small subfamily (Feylininae), and, as it is lacking in only two other very closely related genera of skinks, its loss is an important feature.

*Teeth.* The presence or absence of pterygoid teeth and the number of premaxillary teeth seem to correlate well with other characters of taxa at the level of genus or species group. In general, these two characters, especially the number of premaxillary teeth, seem to be of greater taxonomic significance in skinks than in most other lizard families.

*Supratemporal arch.* Skinks are often diagnosed as displaying a complete supratemporal arch, that is, the postfrontal and squamosal bones articulate with one another either directly or through a postorbital bone. This is true in three of the subfamilies of skinks, the Feylininae, Scincinae and Lygosominae, but it is not true in the fourth subfamily, the Acontinae (with the exception of two species). In this last group the postfrontal and squamosal are generally small (a postorbital is lacking) and do not form a complete arch.

*Meckel's groove.* Meckel's groove may either be open anterior to the splenial or be closed by the overlapping and fusion of the dentary. There are only a few species with an intermediate condition (dentary overlapping but not fused along the resulting suture), and either one condition or the other seems to be characteristic of major groups of skinks.

*External naris.* In two of the four subfamilies (Feylininae and Acontinae) the external naris is situated in a large, posteriorly expanded rostral, and in the lygosomines the naris is in a discrete nasal

scale. The Scincinae, however, show a variety of relationships between the external naris and the surrounding scales; these relationships are of some value in recognizing the taxa within this group.

*Preal scales.* The single, transverse preanal scale in one subfamily (Acontinae) is unique among skinks, with the exception of a few species of *Tropidophorus*, and is unusual in lizards. The size of the preanal scales relative to one another and to the posterior ventral scales is a useful character for aligning major groups of lygosomine skinks.

*Appendages.* The relative frequency of the species that have completely lost the external appendages in the four subfamilies reflects, to some extent, the degree to which the subfamilies have "gone underground," that is, have become burrowers.

*Length of tail.* The relatively short tails (less than one-third of the total length) of two of the subfamilies (Feylinae and Acontinae) might be thought of simply as an adaptation to a burrowing way of life, but the burrowers of the other two subfamilies have the relatively longer tails characteristic of their groups.

*Mode of reproduction.* The two smallest subfamilies, the Feylinae and the Acontinae, seem to be live-bearing, whereas the two larger subfamilies, the Scincinae and Lygosominae, are both egg-laying and live-bearing. Since egg-laying habits are undoubtedly ancestral to live-bearing habits, this character helps to establish the possible phylogeny of the four subfamilies.

## THE SUBFAMILIES OF SKINKS

The four subfamilies discussed below are not arranged in any phylogenetic order, as is often the case in papers of this nature. Instead, the two small (in terms of number of species) and highly specialized subfamilies, the Feylinae and Acontinae, are discussed first; the Scincinae, which are considered to be independently ancestral to all three other subfamilies, come next

and are followed by the Lygosominae, the most numerous, diverse, and advanced group of skinks.

In the description of the skull features of the four subfamilies, only the taxonomically important characters will be considered. The bones of the secondary palate are described in detail first, as they offer the most diagnostic characters for recognizing the subfamilies. The remainder of the bones of the skull are then described in a generally anterior-posterior order. The teeth and mandible are described last.

### Feylinae

*Diagnosis.* Frontal bones separate (Fig. 1); premaxillae and nasal bones fused. Horizontal laminae from lateral sides of palatines approaching but not touching on ventral midline. An anteriorly projecting process from palatal ramus of pterygoid articulates with maxilla to exclude palatine from position on medial edge of infra-orbital vacuity (Fig. 2).

Post-temporal fenestra reduced in size; supratemporal arch complete, i.e., post-frontal articulates with squamosal, which is closely applied to parietal. Postorbital and jugal bones lacking. Lateral descending processes from frontals and parietal fingerlike, i.e., not expanded.

Bony shaft of stapes abutting directly against quadrate.

Seven teeth on premaxillae; 13-14 teeth on maxilla.

Meckel's groove open anterior to splenial.

Rostral and mental scales slightly enlarged. External naris connected with posterior edge of rostral by short suture. Limbs totally lacking. Preanal scales not enlarged, i.e., approximately same size as other ventral, posterior body scales.

*Description of skull.* Cope (1892) has figured and described certain features of the skull of *Feylinia currori*. The following account is based on the skulls of two species, *Feylinia polylepsis* and *F. currori*. The skulls of both species are very similar.

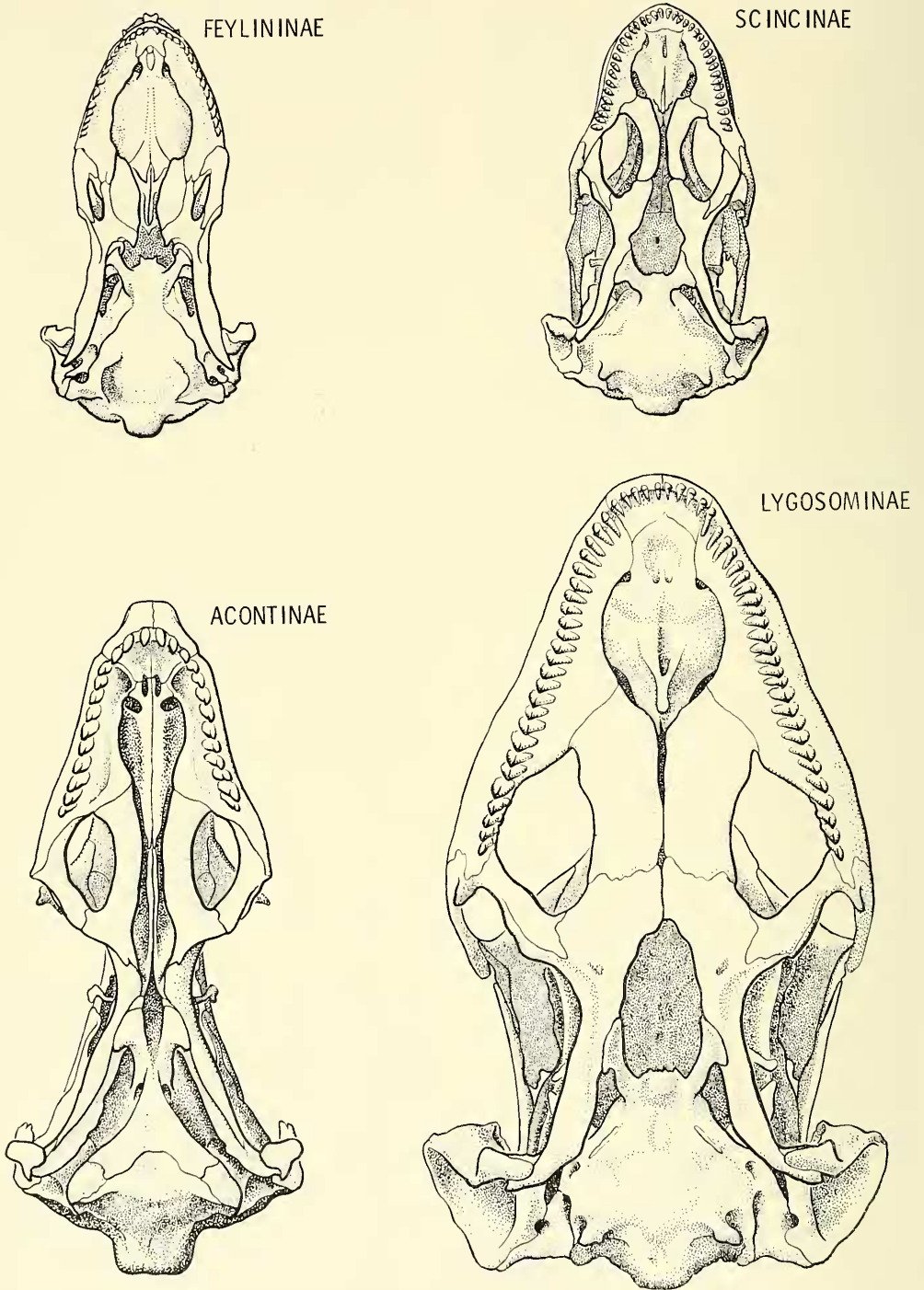


Figure 2. Ventral view of the skulls of representatives of the four subfamilies of skinks. Same species as represented in Figure 1 except for the Acontinae, which are represented by *Acontias meleagris* (MCZ 11934). Drawn to scale.

The skull as a whole is somewhat depressed for its length, and the postorbital region is not as elongate as might be expected in a lizard so obviously adapted to a burrowing existence.

The palatines are scroll-like, with the two free edges of each "scroll" just failing to meet medioventrally. Each palatine thus forms a separate air passage, with the ventral surfaces of the palatines acting as a rudimentary secondary palate to partially separate the food and air passages. The palatal rami of the pterygoids are separated medially and therefore do not participate in the formation of the secondary palate.

The palatal ramus of the pterygoid articulates with the ectopterygoid along the posterior edge of the infraorbital vacuity and sends an anterior process forward to the maxilla to exclude the palatine from a position on the medial edge of the infraorbital vacuity (Fig. 2).

The premaxillae, vomers, and nasals are each fused to form single elements, but the frontal is paired. The parietal is single and anteriorly bears a foramen, which, however, is overgrown by a bony boss on the dorsal surface.

The prefrontal is very large and occupies most of the anteromedial side of the orbital area. On the dorsal surface of the skull, the prefrontal articulates with the nasal. The suborbital bar is composed entirely of the ectopterygoid and an articulating process from the palatal ramus of the pterygoid. A jugal (postorbital bar) is lacking. The postfrontal bone is small and compact.

There is a single pair of thin, fingerlike, lateral processes descending from both the frontals and parietal. Those from the frontal are closely applied to the prefrontal and curve inward toward the midline but do not meet to encircle the forebrain. The processes from the parietal hang free and touch only the dorsally projecting epipterygoid. These parietal processes are similar to those of most non-burrowing lymnodynastine skinks and are not in the least

expanded into long processes such as those which enclose most of the hindbrain of such typical burrowers as the Acontinae.

There is a small post-temporal fenestra, but although the supratemporal arch is complete, the supratemporal fenestra is obliterated by the close apposition of the squamosal to the parietal. A postorbital bone is absent.

The quadrate is short and stout, with a vertical ridge on its anterior surface. A horizontal, posteriorly projecting process with a ventral, terminal inflection arises from the posterodorsal surface of the quadrate. The footplate of the stapes is large, and the bony shaft abuts against the inner side of the ventral inflection of the posterior process of the quadrate.

Posteriorly curved, almost fanglike teeth are present on the fused premaxillae, maxillae, and dentaries. There are no teeth on any of the other bones of the skull or jaw. Both species of *Feylinia* examined possess seven teeth on the fused premaxillae and 13-14 teeth on the maxilla.

The skull and mandible lack pigment.

In the lower jaw, the articular, prearticular, and surangular are fused. The angular is reduced in size. The splenial extends posteriorly to occupy much of the position held by the angular in other skinks. The coronoid process is low, and Meckel's groove is present.

*Description of external characters.* The single rostral and mental scales are slightly enlarged; the external naris lies within the rostral and is connected with the posterior edge of the rostral through a short horizontal or curved suture. The middorsal head scales consist of a pair of postrostral scales (in *Feylinia*) or a single postrostral scale (in *Chabanaudia*), and following this, three single, large, median scales.

An external ear opening is lacking. The body scales are smooth and disposed in 16-30 longitudinal rows at midbody. The preanal scales are subequal with the other ventral, posterior body scales.

Limbs are absent, although rudimentary

pectoral and pelvic girdles are present (Essex, 1928). The tail is relatively short, comprising approximately one-third of the total length.

*Mode of reproduction.* The only information available on this topic is a note by de Witte (1953) on two gravid *Feylinia currori*, which contained two and three "embryons." This meager evidence suggests that *F. currori* is probably live-bearing.

*Distribution.* Central and west Africa and Principe Island, primarily in lowland, evergreen forest (Fig. 3).

*Genera.* Two genera and four species are currently recognized in the subfamily Feylininae:

*Feylinia* Gray, 1845; 3 species; central and west Africa and Principe Island.

*Chabanaudia* de Witte and Laurent, 1943; 1 species; Gabon.

*Discussion.* *Chabanaudia* has been separated from the genus *Feylinia* by de Witte and Laurent (1943) on the basis of its single rather than double postrostral scale. As I have not examined a skull of the single species of *Chabanaudia* (*boulengeri*), I can add nothing to our knowledge of its generic characters or relationships.

*Feylinia* is, on the basis of osteoderms and the secondary palate, clearly a skink and, according to Miller (1966a), the cochlear duct of *Feylinia* is so "similar in all details to the scincid duct that it may be included in that general group."

Boulenger (1887) distinguished *Feylinia*, *Typhlosaurus*, and *Anelytropsis* as a separate family (Anelytropsidae) and regarded it as a "degraded type of the *Scincidae* (italics his), with which they are closely connected through the genus *Acontias*." As will be shown below, *Typhlosaurus* is indeed very closely related to *Acontias*, comprising, with this genus and the monotypic *Acontophiops*, a separate subfamily of skinks.

The affinities of the rare monotypic Mexican genus *Anelytropsis* are not so clear, however. Recent studies of the

cochlear duct (Miller, 1966b), skull (McDowell, personal communication), and vertebral morphology (Etheridge, 1967) indicate that this genus is perhaps related to the Southeast Asian-New Guinean *Dibamus*, but the broader relationships of these two genera are obscure.

*Specimens examined.*<sup>1</sup> I have examined the skulls of the following species of feylinines: *Feylinia currori elegans* (MCZ 42886), *F. currori* (MCZ 106990), and *F. polylepis* (MCZ 61215).

### Acontinae

*Diagnosis.* Frontal bone divided (Fig. 1); palatine bones just separated ventrally along midline of secondary palate; palatine in broad contact with ectopterygoid along posterior edge of infraorbital vacuity, thereby usurping extensive contact of pterygoid with ectopterygoid and excluding palatal ramus of pterygoid from a position on infraorbital vacuity (Fig. 2).

Supratemporal arch and post-temporal fenestra usually completely lacking (except in *Acontias plumbeus* and *Typhlosaurus lineatus*, see below). Prefrontal and squamosal bones reduced in size (except in *Acontias plumbeus* and *Typhlosaurus lineatus*), the squamosal especially so, being much smaller than the supratemporal bone directly posterior to it.

Maxilla borders orbit ventrally, the jugal being reduced to a small, vertical element suspended between postfrontal and maxilla.

Four to six teeth on premaxillae and three to ten teeth on maxilla.

Meckel's groove closed and fused.

Rostral and mental scales greatly enlarged, the external naris being situated well forward in rostral and connected to its posterior edge by a horizontal suture. No external trace of limbs. A single, transversely enlarged preanal scale. Tail less than 22 per cent of total length.

*Description of skull.* Detailed descrip-

<sup>1</sup> Abbreviations used in this section and similar sections to follow will be found on pp. 180 and 181.



tions of the skull of *Acontias meleagris* have been provided by de Villiers (1939), Brock (1941), and van de Merwe (1944), and figures of the skulls of *Acontias plumbeus* and *Typhlosaurus awantiacus* in Peters (1882). As practically all the important skull features of the subfamily can be seen in the well-described *A. meleagris*, no more than a brief description of the skull morphology characteristic for the group will be given here.

As is generally true in other burrowing lizards, the postorbital region of the skull has become elongated, a feature which, along with the blunt rounded snout, gives the whole skull a bullet-shaped appearance.

The palatines are two long, almost complete scroll-like tubes whose ventral sides approach closely, but do not meet, along the midline of the palate. The medial sides of the palatines do touch, however, and articulate with medial posterior projections of the vomers to separate partially two tubular air passages.

The palatine is in broad contact with the ectopterygoid along the posterior edge of the infraorbital vacuity. The palatal ramus of the pterygoid thus lacks the broad contact with the ectopterygoid seen in all other skinks and is completely excluded from the edge of the infraorbital vacuity. The pterygoids are also widely separated from one another along the midline of the palate (Fig. 2).

The premaxillae, vomers, nasals, and frontals are divided by a median suture. Closely apposed medial processes from the vomers project posteriorly for about half the length of the palatines and articulate with the closely apposed medial sides of the palatines to separate partially the two air passages formed by the scroll-like palatines.

The parietal bone is single; there is a parietal foramen in the anterior part of the parietal, although in some specimens it tends to be covered dorsally with a bony boss.

A long, thin, anteriorly projecting process from each frontal bone wedges part way between the nasal and maxilla to separate the reduced prefrontal from the nasal. The prefrontal is a very small bone on the dorsal edge of the orbit, which articulates with the postfrontal to exclude the frontal from the orbit.

Lateral descending processes from each frontal approach closely or meet below the forebrain. The lateral descending parietal processes are expanded longitudinally to varying degrees, thereby enclosing the hindbrain to varying degrees.

The supratemporal arch and the post-temporal fenestra are lacking, except in *Acontias plumbeus*, which has retained both the arch and the fenestra, and *Typhlosaurus lineatus*, which has retained the supratemporal arch but has lost the post-temporal fenestra. The postfrontal and squamosal are reduced in size, the squamosal especially so, being much smaller than the supratemporal bone directly posterior to it. In *A. plumbeus* and *T. lineatus* the squamosal and postfrontal are well developed and form a supratemporal arch. There is also a clear post-temporal fenestra in *A. plumbeus*, but not in *T. lineatus*. All species in the subfamily lack the post-orbital bone.

The jugal does not take part with the maxilla in forming the ventral border of the orbit as in most skinks, but is reduced to a small vertical element hanging between the postfrontal and maxilla. An epipterygoid is present.

The quadrate is short, stout, and slightly concave posteriorly. The end of the bony shaft of the stapes never articulates directly with the quadrate. In some species (e.g., *Typhlosaurus caecus* and *T. vermis*), however, the quadrate is very compressed, and the shaft of the stapes projects anteriorly, oblique to the lateral edge of the quadrate.

Teeth are present only on the premaxillae, maxillae, and dentaries. The number of teeth ranges from four to six on the premaxillae and from three to ten on

the maxilla. The maxillary teeth vary from the short, blunt crushing teeth of *Acontias plumbeus* to the pointed, slightly curved teeth of *Typhlosaurus vermis*.

The skull and mandible lack pigment.

In the lower jaw, the articular, pre-articular, and surangular are usually fused, although the labial suture between the surangular and articular may be evident. The splenial is usually reduced in size, but the angular is well developed. Meckel's groove is obliterated by the overlapping and fusion of the dentary.

*Description of external characters.* The rostral and mental scales are greatly enlarged. The external naris is situated well forward in the large rostral and is connected with its posterior suture through a horizontal suture. The middorsal head scales consist of one to three single, large, median scales between the posterior edge of the enlarged rostral and a pair of parietals.

The external ear opening is completely covered by scaly epidermis. The body scales are smooth and disposed in 12 to 20 longitudinal rows at midbody. There is a single, transversely enlarged preanal scale.

All external traces of limbs are lacking, although there are rudimentary pectoral and pelvic girdles (Essex, 1928). The tail is very short, comprising less than 22 per cent of the total length.

*Mode of reproduction.* The three species of acontines for which the mode of reproduction is known (*Acontias meleagris*, *Typhlosaurus bicolor*, and *T. lineatus*) are live-bearing and produce one to four young in a clutch.

*Distribution.* Southern Africa with an isolated population in extreme southeastern Kenya (Fig. 3).

*Genera.* Only three genera, encompassing 15 species, are included in the subfamily:

*Acontias* Cuvier, 1817; 6 species; southern Africa, with an isolated population in extreme southeastern Kenya.

*Acontophiops* Sternfeld, 1911; 1 species; northern Transvaal of South Africa.

*Typhlosaurus* Wiegmann, 1834; 8 species; southern Africa.

*Discussion.* An important problem is the status of the Malagasy *Acontias*. Boulenger (1887) included Cingalese and Malagasy species as well as South African species in his genus *Acontias*. Hewitt (1929) pointed out certain differences in the head scales and tubular system of the osteoderms among the *Acontias* of Ceylon, Madagascar, and Africa. He thereupon referred the Cingalese skinks to their (original) genus *Nessia* Gray, 1839 (type species: *burtoni*), and proposed the generic name *Pseudacontias* for the two Malagasy species (type species: *holomelas*), leaving the name *Acontias* Cuvier, 1817 (type species: *meleagris*), for the mainland African forms.

M. A. Smith (1935) noticed the great differences in the relationships of the bones of the palate between *Nessia* and *Acontias* (outlined here in the diagnoses of the respective subfamilies, the Scincinae and Acontinae) and supported Hewitt's taxonomic decisions for these two groups.

Angel (1942) noted that the generic name *Pseudacontias* Hewitt, 1929, was preoccupied by *Pseudacontias* Bocage, 1889, another genus of Malagasy skinks, and, minimizing the differences pointed out by Hewitt (1929), put the two disputed Malagasy skinks back in *Acontias*.

In addition to the differences in the tubular pattern of the osteoderms and the relationships of certain head scales, Hewitt (1929) had noted that the *Acontias* of Africa differed from those of Madagascar in having very much shorter tails and fewer scales around midbody. These two differences distinguish the subfamily Acontinae and the subfamily next discussed, the Scincinae, to which in fact the Malagasy (and the Cingalese *Nessia*) belong. The skull differences between South African *Acontias* and Malagasy *Acontias* are also those of the two subfamilies.

I have examined only the secondary

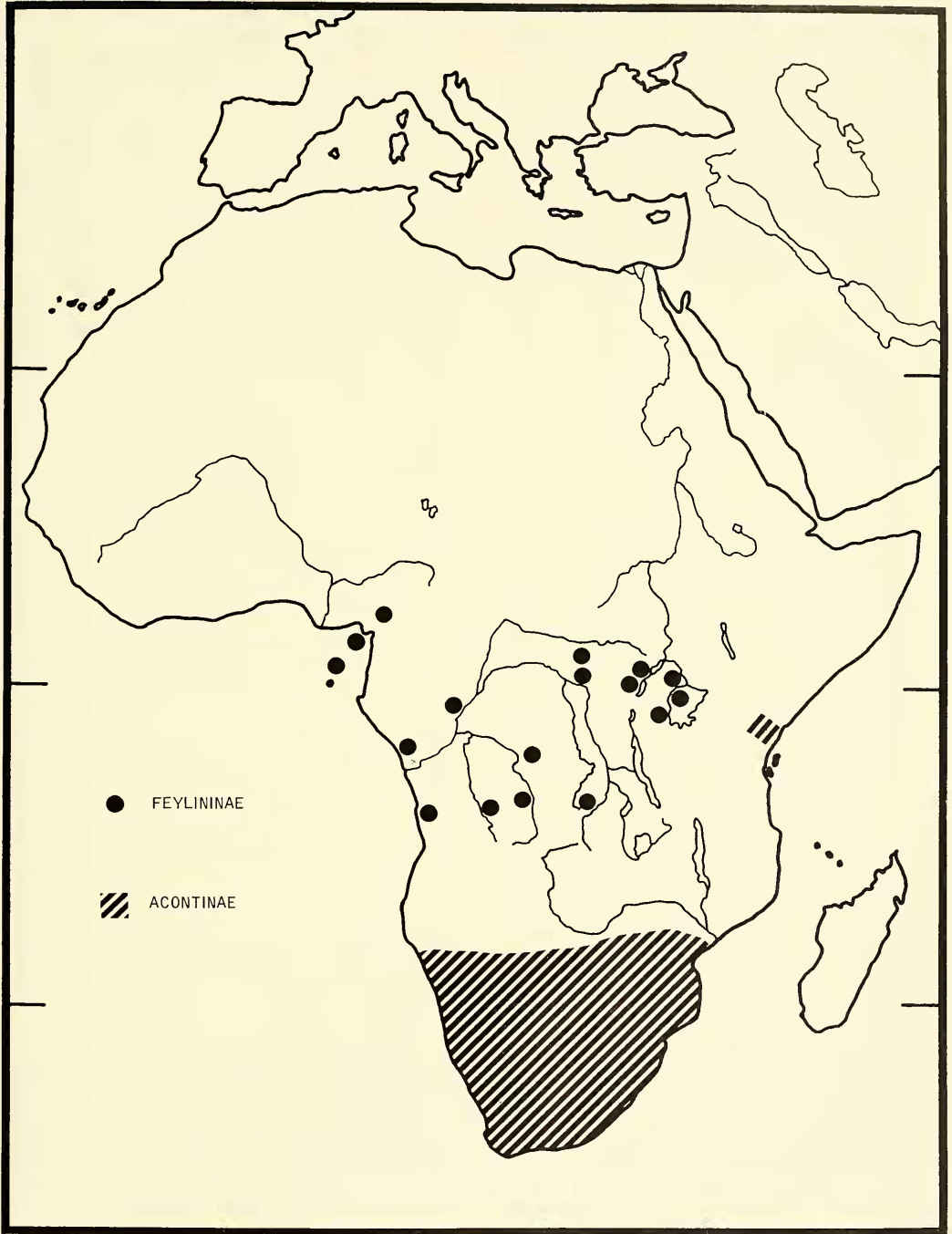


Figure 3. Distribution of the Feylininae and Acontinae, two subfamilies which have apparently evolved independently from the scincines in Africa.

palate in the skull of the Malagasy *Acontias*, and both species differ from *Nessia* (*layardi*) in having the postero-medial edges of the palatal rami of the pterygoids smoothly diverging, instead of deeply emarginated as in *Nessia*. Such palatal differences are indicative of generic separation. I therefore suggest that the two species of Malagasy "*Acontias*" (*holomelas* and *hildebrandti*) be placed in a distinct genus which may be known as

*Malacontias*<sup>1</sup> new genus

The type species, herewith designated, is *Acontias holomelas* Günther, 1877.

*Specimens examined.* The skulls of the following acontine species have been examined:

*ACONTIAS: breviceps* (MCZ 38559), *g. gracilicauda* (MCZ 100905), *g. occidentalis* (MCZ 67859, 67861), *g. tasmani* (MCZ 96905), *lineatus* (MCZ 21416, 21659), *meleagris* (MCZ 11934, FMNH 84189), *plumbeus* (MCZ 14233), *percivali* (MCZ 40180).

*TYPHLOSAURUS: caecus* (AMNH 50669), *cregoi* (MCZ 41935), *lineatus* (FMNH 142754), *vermis* (MCZ 41938).

Scincinae

*Diagnosis.* Frontal bone divided (Fig. 1). Palatines almost always separated medially except in some *Scelotes*, *Proscelotes* and *Gongylomorphus*<sup>2</sup> *bojeri*. Palatal rami of pterygoids almost always separated medially except in *Gongylomorphus bojeri* and the three endemic "*Scelotes*" of the Seychelles (*gardinieri*, *braueri* and *veseyfitzgeraldi*). Palatine

bones widely separated from ectopterygoid along posterior edge of infraorbital vacuity in most genera and species, i.e., palatal ramus of pterygoid borders infraorbital vacuity and articulates with ectopterygoid along posterior edge of this vacuity (Fig. 2). In a few species, ectopterygoid contacts palatine along posterior edge of infraorbital vacuity by anteriorly projecting process that excludes palatal ramus of pterygoid from infraorbital vacuity.

Supratemporal arch complete, i.e., squamosal and postfrontal bones always in contact directly or by way of postorbital bone. Lateral descending processes from parietal to epipterygoid sometimes expanded longitudinally, but more frequently simply fingerlike projections.

Nostril usually pierced in rostral, or between rostral and various other small head scales, or between two or more small head scales, rarely in large, discrete nasal scale. Limbs present in most species. At least one pair of enlarged preanal scales; tail more than 30 per cent of the total length.

*Description of skull.* The skulls of the following scincines have been figured and discussed in the literature: *Barkudia insularis* (Ganapati and Rajyalakshmi, 1958); *Chalcides guentheri* (Haas, 1936); *Chalcides ocellatus* (Kamel, 1965); *Chalcides* sp. (Romer, 1956); *Eumeces schneideri* (Duméril and Bocourt, 1881); *Eumeces quinquelineatus* (Rice, 1920); *Eumeces* spp. (Kingman, 1932); *Nessia smithi* (Deraniyagala, 1953); *Scincus scincus* (El-Toubi, 1938); *Voeltzkowia mira* (Rabanus, 1911).

The palatine bones are apposed to varying degrees, but do not actually meet along the ventral midline except in some *Scelotes*, *Proscelotes*, and *Gongylomorphus*, where the palatines meet along their medial edges to various degrees. Dorsally the palatines meet above the air passage.

The pterygoids (palatal rami) are always separated medially except in *Gongylomorphus bojeri* from Mauritius and the three endemic "*Scelotes*" on the Seychelles.

<sup>1</sup>The generic name *Malacontias* derives from the first syllable of the word "Malagasy"—an inhabitant of Madagascar—and the previous generic name (*Acontias*) for the species now placed in the new genus.

<sup>2</sup>Loveridge (1957) has shown that the generic name *Thyrus* Gray, 1845, for the endemic Mauritian scincine is antedated by the more unwieldy name *Gongylomorphus* Fitzinger, 1843.

In these species the palatines and pterygoids form as complete a secondary palate as that seen in any lygosomine.

The palatine is usually separated from the ectopterygoid by the palatal ramus of the pterygoid along the posterior edge of the infraorbital vacuity, but in the genus *Scincus* and in a few species or even individuals of one species of some genera (e.g., *Chalcides ocellatus* and "*Scelotes astrolabi*"), the ectopterygoid may make contact with the palatine by an anteriorly projecting process that excludes the palatal ramus of the pterygoid from the infraorbital vacuity.

At the anterior edge of the infraorbital vacuity, the ectopterygoid may extend along the bordering edge of the maxilla to varying degrees and in some species may actually articulate with the palatines to exclude completely the maxilla from the infraorbital vacuity.

The premaxillae and vomers may be paired, partially fused, or completely fused. The nasals and frontals are always divided. The parietal is single and bears a parietal foramen.

The frontal may form a surface suture with the maxilla to separate the nasal and prefrontal, or the nasal may articulate with the prefrontal to separate the frontal and maxilla, or all four bones may meet at a point.

Lateral descending processes from the frontal may be present or absent. When present, they may be long and deep, virtually meeting below the forebrain. Lateral parietal processes are always present and are usually fingerlike projections to the epipterygoid. In some species, however, the parietal processes become somewhat expanded longitudinally, enclosing part of the hindbrain. This is especially true of species adapted to a burrowing existence.

The post-temporal fenestra is often reduced or obliterated in burrowing species, but otherwise the arch is usually present. The postfrontal and squamosal bones are always present and in contact with one

another directly or through a separate post-orbital bone. An epipterygoid is always present, as is the jugal in all species examined except in the closely related *Typhlacontias gracilis*, *T. rohani*, and *Fitzsimonsia brevipes*.

The quadrate is usually concave posteriorly and convex anteriorly, although in some species this bone becomes very stout and rodlike. The bony shaft of the stapes articulates directly with the quadrate in some genera (*Fitzsimonsia*, *Melanoseps*, *Ophiomorus*, *Scolecoseps*, *Typhlacontias*, and *Brachymeles vermis*, although in no other species of *Brachymeles* examined). In these scincines, as in the feylinines, the distal end of the stapes abuts against a ventral inflection of a posteriorly projecting nub of the quadrate.

Teeth are always present on the premaxillae, maxillae, and dentaries. In some species teeth also occur on the palatal ramus of the pterygoid. There may be 5–11 teeth on the premaxillae, although many genera are characterized by having fewer than nine premaxillary teeth. The number of teeth on the maxilla varies from 10–25.

The skull may contain some pigment, although usually it does not.

The surangular, articular, and prearticular bones may be distinct or variously fused to one another. The splenial and angular are always distinct except in *Gongylomorphus bojeri*, where the angular is fused to the surangular, articular, and prearticular. Meckel's groove is open in all but a few species.

*Description of external characters.* The head scales in members of this subfamily are extremely variable. The external naris may be situated entirely in the rostral, between the rostral and one or more of the small head scales (diagnosis of Mittleman's subfamily Chalcidinae), between two or more smaller head scales exclusively, or, less frequently, entirely within a discrete nasal scale (diagnosis of Mittleman's subfamily Scincinae).

An external ear opening may or may not

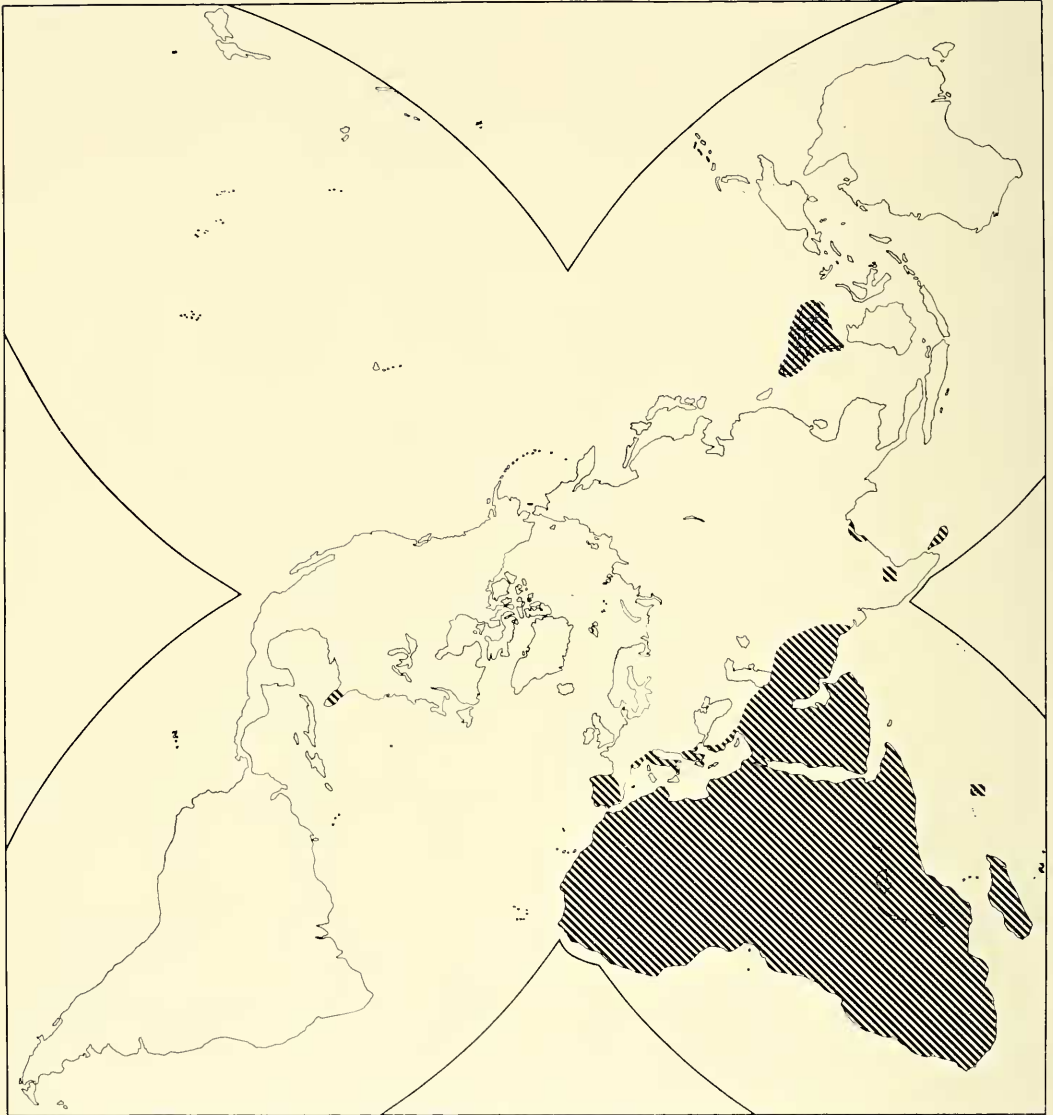


Figure 4. Distribution of the Scincinae (exclusive of the genus *Eumeces*), the most primitive subfamily of skinks.

be present. The body scales are cycloid, imbricate, and generally smooth. The scales are disposed in 14–42 longitudinal rows at midbody, and there are two or more pre-anal scales.

Limb reduction is a common trend in the subfamily, although only about 28 of the approximately 182 species totally lack any external trace of limbs.

*Mode of reproduction.* Of the 44 species of scincins for which the mode of reproduction is known, half lay eggs and half bear living young, and, as yet, only in the genus *Eumeces* is the mode of reproduction known to transcend taxonomic boundaries.

*Distribution.* With the exception of *Eumeces*, the genera of scincins show a disjunct distribution in east and south

central Asia. It is only in southwest Asia, north Africa and more especially in Africa south of the Sahara, Madagascar and the islands of the West Indian Ocean that scincines are widely distributed (Fig. 4) and constitute a significant part of the skink fauna.

*Eumeces* is the largest and most widespread scincine genus (Fig. 5). The group is distributed along the northern periphery of the world distribution of skinks. The "cold" tolerance implied by this distribution has undoubtedly helped *Eumeces* cross the Bering Land Bridge into the New World and probably accounts for the group's success in the high plateau country of Mexico.

There are no scincines in the Indo-Australian Archipelago or the Australian Region.

*Genera.* The following genera are included in the Scincinae. I have arranged them in geographic order proceeding west through North America into the Old World.

*Eumeces* Wiegmann, 1834; approximately 46 species; Bermuda, North and Central America; east and southeast Asia; southwest Asia; North Africa (see Fig. 5).

*Neoseps* Stejneger, 1910; 1 species; south and central Florida.

*Brachymeles* Duméril and Bibron, 1839; 13 species; Philippine Islands.

*Barkudia* Ammandale, 1917; 1 species; Calcutta and Chilka Lake Area.

*Sepsophis* Beddome, 1870; 1 species; central and southern India.

*Nessia* Gray, 1839; 8 species; Ceylon.

*Chalcidoseps* Boulenger, 1887; 1 species; Ceylon.

*Ophiomorus* Duméril and Bibron, 1839; 9 species; Greece through southwest Asia to northwest India.

*Chalcides* Laurenti, 1768; 14 species; southern Europe, southwest Asia, north Africa, Canary Islands.

*Scincus* Gronovius, 1763; 12 species; north Africa to southwest Asia.

*Scincopus* Peters, 1864; 1 species; north Africa from Khartoum, Sudan to Mauritania.

*Proscelotes* de Witte and Laurent, 1943; 3 species; southeast Africa.

*Sepsina* Bocage, 1866; 5 species; southern Africa.

*Scelotes* Fitzinger, 1826; 15 species; southern Africa.

*Scolecoseps* Loveridge, 1920; 2 species, east central Africa.

*Fitzsimonsia* de Witte and Laurent, 1943; 1 species; southern Africa.

*Typhlacontias* Bocage, 1873; 5 species; central and southern Africa.

*Melanoseps* Boulenger, 1887, 2 species; central east Africa and Cameroon.

*Pygomeles* Grandidier, 1867; 3 species; Madagascar.

*Pseudacantias* Bocage, 1889; 1 species; Madagascar.

*Paracontias* Mocquard, 1894; 2 species; Madagascar.

*Cryptoscincus* Mocquard, 1906; 1 species; Madagascar.

*Grandidierina* Mocquard, 1894; 4 species; Madagascar.

*Voeltzkowia* Boettger, 1893; 1 species; Madagascar.

*Malacontias*, new generic designation, see p. 162 above; 2 species; Madagascar.

*Gongylomorphus* Fitzinger, 1843; 1 species; Mauritius.

*Incertae sedis*, 25 species of Malagasy "*Scelotes*" and 3 endemic "*Scelotes*" of the Seychelles.

*Discussion.* The systematics of the Malagasy scincines is undoubtedly the biggest problem remaining in the taxonomy of this subfamily. Many species of Malagasy scincines are known from only a few specimens—too few to allow skulls to be prepared. Unfortunately this dearth of specimens is not likely to be remedied in the near future, as many of the species are apparently very secretive in their habits, and Madagascar is not, at present, a popular place for collecting reptiles.

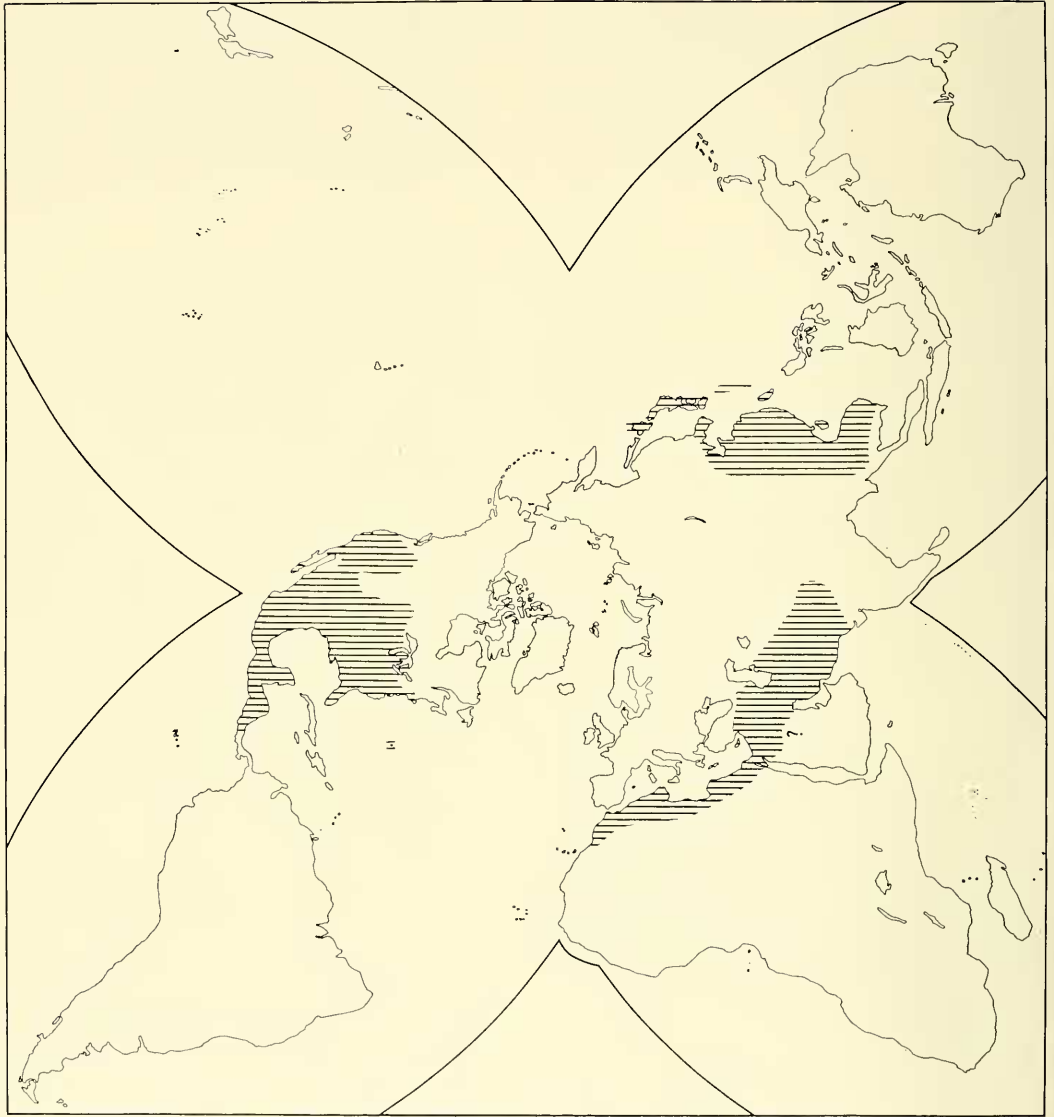


Figure 5. Distribution of the scincine genus *Eumeces*.

The disjunct distribution of the scincine genera in east and central Asia implies, of course, that the scincine ancestors (possibly, but not necessarily, *Eumeces*) were more widespread at one time in the past. Just how widespread these scincines may have been is a very interesting question that future paleontological discoveries may answer. It would be interesting to know,

for example, whether the scincines ever inhabited the Australian Region—a region where now only lygosomines are found.

*Specimens examined.* I have seen the following scincine skulls:

*BARKUDIA: insularis* (MCZ 54712).

*BRACHYMELES: bonita* (MCZ 20129),  
*gracilis boulengeri* (MCZ field tag 710,  
 MCZ 20131, 26540, 26545, 54253, 26552,



26553, + 1 untagged specimen), *gracilis taylora* (AMNH 86661), *vermis* (MCZ 26587).

**CHALCIDES:** *bedriagai* (MCZ 15692), *mionecton* (MCZ 7753, 25145), *ocellatus* (MCZ 9817, 9828, 9837, 9839, 9842, 9844, 9849, 9851, UMMZ 1930, CAS(SU) 18137), *sepsoides* (MCZ 27483, 18351, CAS(SU) 18143).

**EUMECES:** *algeriensis* (MCZ 4281), *anthracinus* (MCZ 29312), *brevilineatus* (MCZ 79776), *brevirostris* (FMNH 111614), *chinensis* (MCZ 29005), *copei* (UINHM 33238), *elegans* (MCZ 28983, 28992, 29000), *fasciatus* (MCZ 54126, UINHM 33239, 33240), *gilberti* (USNM 5310), *indubitus* (FMNH 114201), *inexpectatus* (MCZ 45498, 55506), *kishinouyei* (MCZ 55935), *laticeps* (MCZ 55505, + 1 untagged specimen), *laticutatus* (FMNH 55511), *longirostris* (MCZ 20503, 20508), *lynxe* (MCZ 19086, 19087, 24533, 24534), *marginatus* (MCZ 57111, 57112 part, 7409), *multivirgatus* (UINHM 33244), *obsoletus* (MCZ 35547, 61366, 61367), *ochoterena* (FMNH 114493), *schneideri* (MCZ 6986, UMMZ 2119, 2148), *schwartzzi* (USNM 113603), *skiltonianus* (MCZ 6617—2 specimens, 8887, + 1 untagged specimen, CAS 28138), *stimsoni* (CAS 21660), *taeniolatus* (FMNH 1868), *tunganus* (USNM 82751).

**FITZSIMONIA:** *brevipes* (MCZ 96702).

**GONGYLOMORPHUS:** *bojeri* (MCZ 46677).

**GRANDIDIERINA:** *lineata* (PM 3378).

**MALACONTIAS** (palatal characters only): *hildebrandti* (PM 99-376), *holome-las* (PM 95-215, 7792).

**MELANOSEPS:** *ater* (MCZ 50955, 52487), *occidentalis* (BM 1907.5.22.6A).

**NEOSEPS:** *reynoldsi* (MCZ untagged specimen).

**NESSIA:** *layardi* (MCZ 38174).

**OPHIOMORUS:** *brevipes* (FMNH 141550), *persicus* (FMNH 141557), *raith-mai* (AMNH 85846), *tridactylus* (AMNH 75610).

**PROSCLOTES:** *aenea* (MCZ 18709),

*arnoldi* (MCZ 55145), *eggeli* (MCZ 24217, 24218, 24220).

**PYGOMELES:** *braconnieri* (PM 1715).

**SCELOTES:** *anguina* (MCZ 96791), *arenicolor* (MCZ 14205), *bidigittata* (MCZ 96789), *bipes* (BM XVII.2.F), *brevipes* (MCZ 21237), *caffer* (MCZ 96792), *gronovi* (BM 97.5.15.8), *limpopoensis* (MCZ 96906), *mira* (MCZ 96790), *uluguruensis* (MCZ 24206).

**SCINCUS:** *scincus* (MCZ 27456—2 specimens, 27462, 27464).

**SCOLECOSEPS:** *boulengeri* (MCZ 18357).

**SEPSINA:** *angolensis* (AMNH 40734, FMNH 142793), *bayoni* (BM RR 1967.80), *tetradactylus* (MCZ 42885, 47770—3 specimens, 47775, 56963, 56965, 56967, 85536).

**TYPHLLACONTIAS:** *gracilis* (USNM 159338), *rohani* (FMNH 142787).

**VOELTZKOWIA:** *mira* (MCZ untagged specimen).

**Incertae sedis:** Malagasy "Scelotes": *astrolabi* (MCZ 20953, 20955), *melanura* (MCZ 11733); *splendidus* (FMNH 72086); Seychelles "Scelotes": *braueri* (BM 1910.3.18.33), *gardineri* (BM 1910.3.18.91).

### Lygosominae

**Diagnosis.** Frontal bone single (Fig. 1). Palatines usually in contact along ventral midline except in most *Egernia* and *Corucia zebra*. Palatine making contact with ectopterygoid if at all only through an anteriorly projecting ectopterygoid process; palatal ramus of pterygoid but not palatine itself in broad contact with ectopterygoid along posterior edge of infraorbital vacuity (Fig. 2). Supratemporal arch complete, i.e., postfrontal and squamosal always in contact directly or by way of postorbital bone; post-temporal fenestra obliterated in some species. Lateral descending processes from frontal not large when present; lateral descending processes from parietal only fingerlike projections to epipterygoid.

Single discrete nasal scale (except in *Sphenomorphus schultzei* and *Ateucho-*

*saurus*) bearing the external naris; almost always some external indication of limbs (limbs totally lacking in only four of 600+ species in the subfamily); at least one pair of preanal scales; tail more than 30 per cent (usually 50 per cent or more) of total length.

*Description of skull.* A number of descriptions of the skulls of single species in this subfamily have been published as follows: *Ablepharus pannonicus* (Haas, 1935); *Didosaurus mauritanus* (Hoffstetter, 1945 and 1949); *Lygosoma* sp. (Pearson, 1921); *Mabuya carinata* (Rao and Ramaswami, 1952); *Sphenomorphus quoyi* (King, 1964). In addition, there are figures of whole skulls of *Dasia smaragdina*, *Ctenotus leseuri*, *Mabuya multifasciata*, *Sphenomorphus australe*, and *S. quoyi* in Siebenrock (1892), and Brühl (1886) figures the skull of *Tiliqua rugosa*. Waite (1929) figures ventral palatal views of *Sphenomorphus quoyi*, *Egernia stokesi*, and *Tiliqua* sp. and Duméril and Bocourt (1881) figure a ventral view of the skull of *Mabuya mabouya*. Mitchell (1950) also has line drawings of the palates of several *Egernia* and *Tiliqua*, and Greer (1967a and b) and Greer and Parker (1968) figure the palates of "*Ablepharus*" *lineocellatus*, "*Ablepharus*" *smithi*, *Carlia bicarinata*, *Emoia samoense*, *Eumecia anchietae*, *Geomyersia glabra*, "*Leioliopisma*" *metallica*, *Leptosiphos blochmanni*, *Lerista elegans*, *L. bougainvilli*, *Mabuya polytropis*, *Riopa punctata*, and *Sphenomorphus pardalis*.

The general shape of the skull is highly variable. In burrowing forms the post-orbital region may be elongate and the whole skull bullet-shaped, or conversely, in surface forms, the skull may be short and rather deep. In other instances the skull may be depressed.

The palatines meet along the ventral midline to form a secondary palate, above which is the main air passage. Anteriorly the palatines arch over this passageway, but posteriorly most of the air passage is

enclosed dorsally by a membranous tissue. This is in contrast to the condition in the Acontinae, where the entire dorsal arch of the air canal is formed by the palatine bones.

In only a few species (most *Egernia* and *Corucia zebrata*) are the palatines separated ventrally along the midline. In these species the palatines are never separated by as great a distance as in most of the genera of the more primitive scincines (e.g., *Scincus*, *Eumeces*, and *Chalcides*).

The palatine may or may not be in contact with the ectopterygoid. When the palatine is in contact with the ectopterygoid, it is by means of an anteriorly projecting process from the ectopterygoid. The palatal ramus of the pterygoid is the only bone in broad contact with the ectopterygoid along the posterior edge of the infra-orbital vacuity (Fig. 2).

The pterygoids may be in contact along the medial edge of their palatal rami or separated either by the interpterygoid vacuity or by two medioposterior processes of the palatines.

The premaxillae and nasals are paired. The vomer may be single or divided. The frontal and parietal are single. There is a parietal foramen in the anterior part of the parietal except in *Ateuchosaurus*, where the parietal foramen is in the posterior part of the frontal or in a small, median azygous bone between the frontal and parietal.

The frontal may form a surface suture with the maxilla and thereby separate the prefrontal from the nasal, or all four bones may meet at a common point, or the nasal and prefrontal may meet to separate the frontal and maxilla.

There is a pair of descending lateral processes from the frontal in a few species, but these processes are never very deep. There is also a pair of usually well-developed, fingerlike lateral processes descending from the parietal to the ectopterygoid. In some species, however, these parietal processes are barely distinguish-

able from the shallow crest from which they arise.

The post-temporal fenestra is obliterated in burrowing species, but in other forms the fenestra is usually well developed. The primary elements of the supratemporal arch, i.e., the postfrontal and squamosal, are always present and in contact with each other directly or by the intermediary of a postorbital when this bone is present. A well-developed jugal and epipterygoid are always present.

The quadrate tends to become reduced to a short, rodlike element in forms lacking an external ear opening; this modification of the quadrate occurs in non-burrowing species as well as burrowing forms.

Teeth are always present on the premaxillae, maxillae, and dentaries, and are found on the palatal rami of the pterygoids in a few species of several genera. The number of teeth on the premaxillae ranges from 6–15 (usually 9–11) and from 8–40 on the maxilla.

The skull and mandible may or may not contain pigment.

In the mandible the dentary, coronoid, splenial, and angular are always distinct, but the articular, prearticular, and surangular may be fused to various degrees. Meckel's groove may be present or absent or in various states of closure.

*Description of external characters.* The external naris is in a discrete nasal, although in *Sphenomorphus schultzei* and *Ateuchosaurus* the nasal is fused to the first supralabial. The dorsal head scales most commonly consist of the following scales from anterior to posterior: a single rostral; a single frontonasal; paired supranasals (present or absent); paired prefrontals (fused, meeting along the midline, separated or absent); a single frontal in contact with one to seven of the one to nine supraoculars; paired (or fused) frontoparietals and a single (or fused to the frontoparietals) interparietal, and paired (rarely fused) parietals. The parietal foramen is in the interparietal scale.

An external ear opening may or may not be present. Some species have auricular lobes along the edge of the external ear opening. The body scales are cycloid and imbricate (except in *Tribolonotus*, which has granular and tubercle-like scales on the dorsum and sides) and are either smooth or keeled. At midbody the scales are disposed in 18–112 rows. There are two or more preanals, except in a few species of *Tropidophorus* which have but a single, large preanal scale.

Most of the species have both fore and hind limbs, although digit and limb reduction is a recurrent trend in the group. The fore limbs and digits are usually reduced and lost ahead of the hind limbs and digits. However, in only four of the 600+ species of the subfamily are limbs totally lacking.

*Mode of reproduction.* The mode of reproduction is known for 193 species of lygosomines; of these 193 species, 124 (64.3 per cent) lay eggs and the remaining 69 (35.7 per cent) are live-bearing.

*Distribution.* The lygosomines, being the most numerous, in terms of numbers of species, and most diverse subfamily of skinks, are, not surprisingly, the most widespread subfamily (Fig. 6). Lygosomines are best represented both in numbers of species and in diversity of adaptations in the Australian Region. It is also this group, exclusively, that has seeded the far-flung islands of the Pacific, where they extend as far north as the Bonin Islands and Laysan (*Ablepharus boutoni*) and as far south as Stewart Island (*Leiopisma lineoocellata* and *L. zelandica*).

The lygosomines seem to be absent from the more arid regions of central north Africa and the Arabian Peninsula.

*Genera.* The genera in this subfamily are as yet too poorly known taxonomically to list. While I do not agree with many of Mittleman's (1952) new generic groupings of lygosomines, his work does provide a convenient list of most of the species in the subfamily. In addition, he provides a

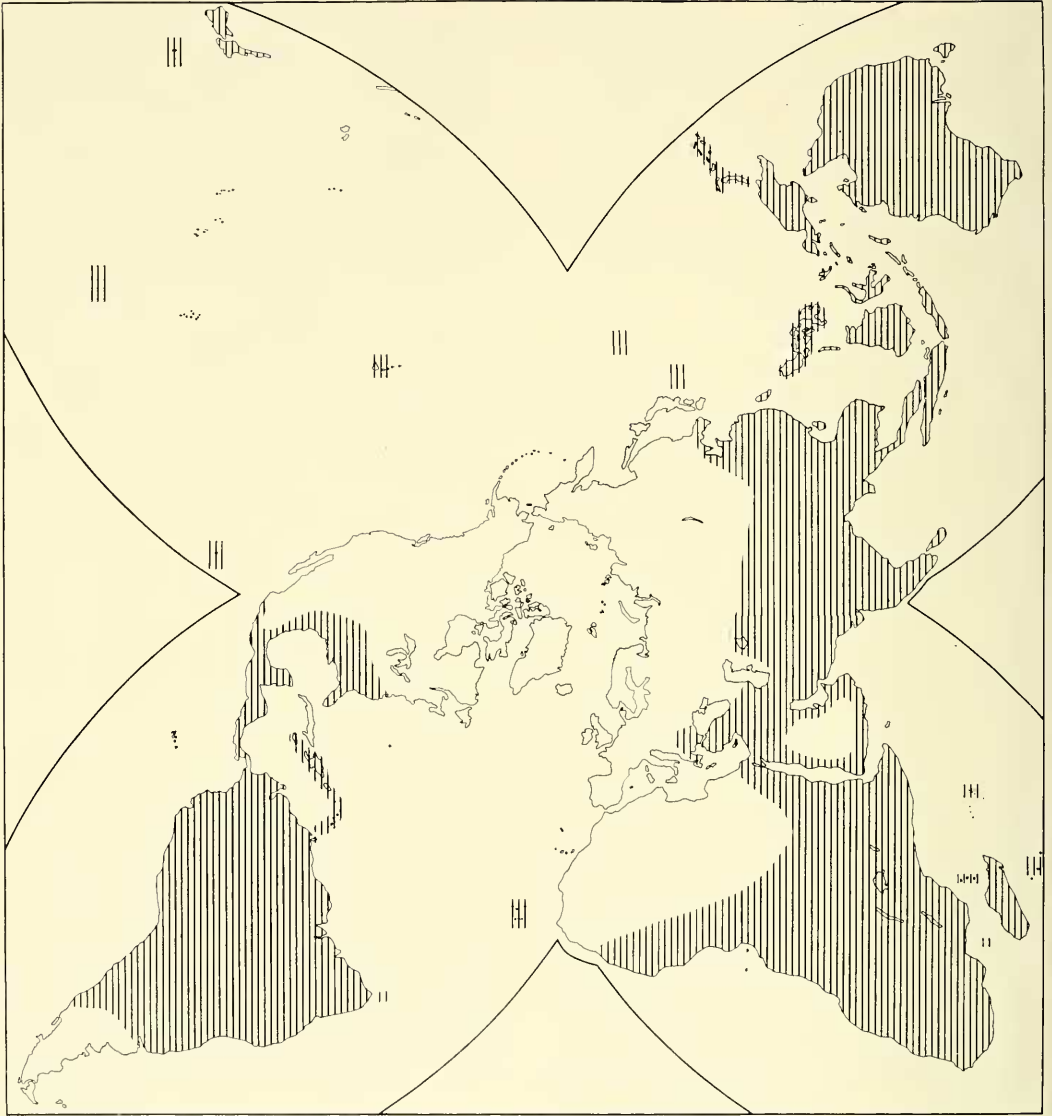


Figure 6. Distribution of the Lygosominae, the most advanced subfamily of skinks. In the oceans only the islands that bound the northern and southern limits of the range are marked with distribution lines.

nearly complete primary generic synonymy.

Mittleman (1952) did not regard the genera *Tiliqua*, *Egernia*, *Corucia*, and *Mabuya* as lygosomines. *Mabuya* and *Tiliqua* fit the diagnosis of the lygosomines as given here in every regard, but some *Egernia* and *Corucia zebra* differ from other lygosomines in having the palatine

bones slightly separated along the midline of the secondary palate. The two genera represented by these species are very closely related (Greer, unpublished work) and on all other characters, especially the fusion of the frontals, are lygosomines.

At this point, the separation of the palatines seems most readily interpreted as

either a secondary separation or, less probably in my mind, as a primitive character retained from a scincine ancestry.

*Discussion.* The greatest single taxonomic problem with the Lygosominae is the delimitation and relationships of genera. Recent work has shown that among the lygosomines, as well as in other major skink taxa, the correlation of skull and external morphology is a very effective method for recognizing taxa worthy of generic rank (Greer, 1967a and b, and Greer and Parker, 1968).

*Specimens examined.* Listed below are the skulls of the lygosomine skinks I have examined. In this list I have tried to indicate my present opinions of species' relationships by an informal nomenclature, e.g., alpha and beta *Leiopisma*, and geography. Some of these groups have been discussed in other papers (Greer and Parker, 1967 and 1968).

*ABLEPHARUS:* alpha Asian: *brandti* (MCZ 56533), *deserti* (MCZ 5364), *grayanus* (MCZ 84084, CAS 99883), *kitaibeli* (CAS 47453), *pannonicus* (MCZ 3961); alpha Australian: *boutoni* (MCZ 31040), *lineocellatus* (MCZ 33143, 33144, CAS 77404, BM XL.4.A), *spenceri* (AMNH 83929), *taeniolepterus* (MCZ 35321); beta African: *megalurus* (MCZ 31065), *smithi* (MCZ 42880), *wahlbergi* (MCZ 55827).

*ANOTIS:* *mariae* (MCZ 92393).

*ATEUCHOSAURUS:* *pellolepterus* (MCZ 55925, 55927), *sowerbyi* (AMNH 34153).

*CARLIA:* *bicarinata* (MCZ 64315), *fusca* (MCZ 49412, 49423, 73791, 73793, CAS 100777), *novaeguineae* (MCZ 83758), *vivax* (AMNH 82758).

*COPHOSCINCOPUS:* *durus* (MCZ untagged specimen).

*CORUCIA:* *zebrata* (MCZ 68815, 72918, 77375, AMNH 69434).

*CTENOTUS:* *australis* (MCZ 79537, CAS 76722), *fasciolatus intermedius* (MCZ 35442), *labillardieri* (MCZ 24730), *leonhardi* (MCZ untagged specimen), *leseuri* (MCZ 74891); *spaldingi* (MCZ 35374), *taeniolepterus* (MCZ 6302).

*DASIA:* *olivacea* (MCZ ex 7726), *semicincta* (MCZ 26414), *smaragdina* (MCZ 4094—2 specimens), *smaragdina moluccarum* (MCZ 7709), *s. perviridis* (MCZ 49315, 72275, 72508), *s. philippinicum* (MCZ 26429), *vittata* (MCZ 16352).

*EGERNIA:* *bungana* (FMNH 35146), *cunninghami* (FMNH 31041), *depressa* (MCZ 33062), *formosa* (MCZ 33067, 33070, 33071, 33078, 33076), *hosmeri* (AMNH 87779), *inornata* (MCZ 35289, 35291, 35294, 35297), *kingi* (MCZ 33087), *luctuosa* (MCZ 33104), *m. major* (AMNH 69434), *nitida* (CAS 76619), *stokesi* (MCZ 33105, 33106, 33108, FMNH 51707), *s. striolata* (MCZ 24552), *whiti napoleonis* (MCZ 24491).

*EMOIA:* *adpersa* (AMNH 29227), *atrocostata* (MCZ 15074, 15080, 26476, 26479), *boettgeri* (MCZ 22074), *callisticta weneri* (MCZ 67203, 67308, + 3 untagged specimens), *cyanogaster* (MCZ 15121, 15135, 72278, 72287), *cyanura* (MCZ 14582, 14584, 14586, 75954, 75956), *flavigularis* (MCZ 65869), *kordoana* (MCZ 48603), *kuken-thali* (FMNH 134594), *loveridgei* (MCZ 49321), *maculata* (MCZ untagged specimen), *mivarti fuscolineata* (MCZ 73807, 75984), *nigra* (MCZ 15153, 15157, 67770, 72510, 72514, 72515, 72517, 72523, 75522), *p. pallidiceps* (MCZ 79856), *p. physicae* (AMNH 95772), *ruficauda* (MCZ 26482—2 specimens, 26492), *samoensis* (MCZ 16931), *sanfordi* (AMNH 40169), *sorex* (MCZ 7705), *submetallica* (AMNH 59015).

*EUGONGYLUS:* *albofasciolatus* (MCZ 4097, 72703), *rufescens* (MCZ 49341).

*EUMECIA:* *anchietae* (MCZ 41557, 41562).

*GEOMYERSIA:* *glabra* (MCZ 87611).

*HEMIERGIS:* *decrensiensis* (MCZ 49173), *initiale* (MCZ 74976), *peroni* (MCZ 24648, 24652), *quadrilineatum* (MCZ 33210), *tridactylum* (MCZ 24595).

*LEIOLOPISMA:* *telfairi* (MCZ 3077); alpha Asian: *bilineata* (MCZ 3923), *himalayana* (MCZ untagged specimen), *modesta* (AMNH 23669), *reevesi* (MCZ 39234, 39237, 39236); alpha Southeast

Asian-New Guinea: *cheesmanae* (AMNH 62461), *longiceps* (MCZ 48585), *miotis* (MCZ untagged specimen), *noctua* (MCZ 76006, 76008), *pulchella* (MCZ 26440, + 1 untagged specimen), *quadrivittata infra-lineolata* (MCZ untagged specimen), *q. quadrivittata* (AMNH 86665), *rabori* (AMNH 93698), *semperi* (MCZ 20120); alpha Australian South Pacific: *austrocaledonica* (MCZ 15970), *elegantoides* (MCZ 80111), *entrecasteauxi* (MCZ 33223), *maccoyi* (MCZ 33199), *metallica* (MCZ 67129), *moco* (MCZ untagged specimen), *nigrofasciolata* (MCZ 27943), *pretiosa* (MCZ 10232), *stanleyana* (MCZ 47904, 47906), *suteri* (MCZ untagged specimen), *zelandica* (MCZ 92261); alpha North American: *laterale* (MCZ 2436, CAS 31123), *cherrei cherrei* (MCZ 29400), *c. lampropholis* (MCZ 15479); *flavipes* species group: *flavipes* (MCZ 22189, x-21440), *prehensicauda* (MCZ 85561 + 1 untagged specimen), *virens* (MCZ 76270, 76917, 76920); beta African: *reichenovaei* (AMNH 11195); beta Australian: *challengeri* (MCZ 35455, AMNH 82792), *guichenoti* (MCZ 61379), *mustelina* (MCZ 61386), *weeksae* (MCZ 49190).

**LEPTOSIAPHOS:** *blochmanni* (MCZ untaggd specimen), *graneri* (MCZ 47662), *kilimense* (MCZ 24189, 41577), *meleagris* (MCZ 47676).

**LERISTA:** *bipes* (AMNH 86089), *bougainvillei* (MCZ 61403), *elegans* (FMNH 11319), *fragilis* (MCZ 42988, CAS 77190), *gerrardi* (MCZ 33255), *lineata* (MCZ 33265), *lineopunctulata* (BM 1902.7.30.5), *miopa* (MCZ 33260), *muelleri* (MCZ 86699), *planiventrale* (BM 1954.1-2.21), *praepedita* (MCZ 33265), *punctatovittata* (MCZ 79494), *tetradactyla* (BM 1902.7.30.6), *timida* (MCZ 13246).

**LYGOSOMA:** *equale* (MCZ 35344), *quadrupes* (MCZ 20518), *verreauxi* (MCZ 10263).

**MABUYA:** *aurata septentaeniata* (MCZ 56550), *bayoni* (MCZ 39731), *bensoni* (MCZ 22583), *binotata* (MCZ 22421),

*blandingi* (MCZ 55171), *brachypoda* (MCZ 71410), *brevicollis* (MCZ 41306), *capensis* (MCZ 21433), *comorensis* (MCZ 24151—2 specimens, 24155), *dorsovittata* (MCZ untagged specimen), *elegans* (MCZ 67954), *englei* (MCZ untagged specimen), *fasciata* (MCZ 37835 + 2 untagged specimens), *f. frenata* (MCZ 49547), *gravenhorsti* (MCZ 11609), *hildebrandti* (MCZ 70248, 70254), *lacertiformis* (MCZ untagged specimen), *mabouya* (CAS 71456, UMMZ s-1047), *m. mabouya* (MCZ 32040, 38935, 54201, 81182, 81184), *m. sloani* (MCZ 36617), *macrorhyncha* (MCZ 49551, 49552), *macularia* (MCZ untagged specimen), *maculilabris* (MCZ 24820, 24821), *megalura* (MCZ 47611), *multicarinata* (CAS 60430), *multifasciata* (MCZ 25198, 25199, 37843, CAS 60692, 362 + 2 untagged specimens, UMMZ s-1831, s-1830), *occidentalis* (MCZ 43180), *perroteti* (MCZ 19711), *planifrons* (MCZ 54559, 85545), *polytropis* (MCZ 8103), *quinquetaeniata margaritifera* (MCZ 52424—2 specimens, 55179, 67838—67840), *sulcata* (MCZ 21645), *striata* (MCZ 74472—74474), *varia* (MCZ 18658—2 specimens, 18668, 50823, 50824, 85543).

**MENETIA:** *greyi* (MCZ 79498).

**OPHIOSCINCUS:** *anguinoides* (MCZ 74098), *roulei* (MCZ 74099).

**PANAPSIS:** *breviceps* (MCZ untagged specimen).

**RIOPA:** *afer* (MCZ 41517, 41519, 71881), *albopunctata* (MCZ 8360, UMMZ 122269), *bowringi* (MCZ untagged specimen, CAS 60737), *fernandi* (MCZ 49696), *laeviceps* (MCZ 71889), *lineata* (AMNH 46379), *mabuiiformis* (MCZ 40267), *pembana* (MCZ 46106), *popae* (MCZ 44706), *punctata* (MCZ 3238), *sundevalli* (MCZ 41537, 41543), *taeae* (MCZ untagged specimen), *vinciguerrae* (MCZ 17892).

**RISTELLA:** *beddomi* (BM 82.5.22.152), *guentheri* (BM 82.5.22.137), *rukki* (BM 74.4.29.1329), *travancorica* (BM 74.4.29.437).

**SPHENOMORPHUS:** *fasciatus* species group: *antimorus* (MCZ 25374), *australe*

(MCZ 24568), *cranei* (MCZ 76048), *crassicaudus* (MCZ untagged specimen, AMNH 82606), *elegantulus* (BM 83.4.14.20), *emigrans* (MCZ 27043), *fasciatus* (MCZ 26357), *maindroni* (MCZ 64273, 72737), *muelleri* (MCZ untagged specimen), *nigricaudus* (MCZ 35407), *p. pardalis* (MCZ 35413), *pratti* (MCZ 48596), *pumilus* (MCZ 48824), *punctulatus* (MCZ 5250), *quoyi* (MCZ 3301, 3307, 79549, 79552), *rufus* (MCZ 47064), *solomonis* (MCZ 72618, 72626, 72664, 72665, 77373, 77374), *tanneri* (MCZ 76507, 76509, 89126, 92227), *tenuis* (MCZ 35398), *tryoni* (MCZ 35387, 35388); *variegatus* species group: *acutus* (MCZ 20114), *aignanus* (BM 1946.8.15.48), *anomalopus* (MCZ 37849), *boulengeri* (AMNH 33180), *concinatus* (MCZ 72732, 72733, 91426), *cumingi* (MCZ 20113), *darlingtoni* (MCZ 83965), *dussumieri* (BM 1946.8.15.42), *florensis nitidus* (MCZ 27018, 27019, 27022, 27024), *formosensis* (AMNH 34909), *fragosus* (MCZ 92267), *granulatus* (AMNH 95782), *i. indicus* (MCZ 44724), *j. jobiensis* (MCZ 44190, 99336, BM 1935.5.10.108), *maculatus* (MCZ 3336), *melanopogon* (MCZ 68919, x-10113), *nigrolabris* (FMNH 14255, BM 96.4.29.19-21), *sanctus* (MCZ 7663), *striolatus* (MCZ 27034), *taylori* (MCZ 78090), *tersus* (MCZ 39284), *variegatus* (MCZ 25398); alpha SPHENOMORPHUS: *bignelli* (MCZ 19602), *minutus* (MCZ 54259), *ornatus* (MCZ 6154); *incertae sedis*: *fallax* (MCZ 19602), *louisiana-dense* (BM 1946.8.19.25), *monotropis* (BM 1908.5.28.54-55), *striatopunctatus* (BM 1948.1.7.60).

**TILIQUA:** *branchiale* (MCZ 78652), *nigrolutea* (MCZ 1077-2 specimens, FMNH 22498), *occipitalis multifasciata* (MCZ 35310), *rugosus* (MCZ 24456, UMMZ s-2346), *scincoides* (MCZ 65221), UMMZ s-1864, s-1863, FMNH 51702, 51710).

**TROPIDOPHORUS:** *beccari* (MCZ 43524), *laotus* (MCZ 100512), *misaminus* (MCZ 44163-3 specimens), *robinsoni* (MCZ 39374).

**TRIBOLONOTUS:** *blanchardi* (MCZ 72763), *gracilis* (AMNH 82364), *novae-guineae* (MCZ 21063), *pseudoponceleti* (MCZ 72766, 76424, 76425, 76456), *schmidti* (AMNH 66219).

## A KEY TO THE SUBFAMILIES OF SKINKS

The following key is as much a review of the diagnostic characters of the subfamilies of skinks as it is a device for their identification. In each section the character states are listed in the order of their taxonomic importance.

1. Frontal bones separate (Fig. 1); palatine bones separated ventrally along midline of secondary palate (Fig. 2), except in some *Scelotes*, *Proscelotes*, and *Gongylomorphus bojeri*; supratemporal arch complete or incomplete; external naris often not in a discrete nasal scale; many species without any trace of limbs ..... 2

Frontal bones fused (Fig. 1); palatine bones meeting ventrally along midline of secondary palate (Fig. 2), except in some *Egernia* and *Corucia zebrata*; supratemporal arch always complete; external naris almost always in a discrete nasal scale; rarely without any external trace of limbs ..... LYGOSOMINAE

2. Palatine excluded from position on infraorbital vacuity by anteriorly projecting process from palatal ramus of pterygoid to maxilla (Fig. 2); nasal bones fused; jugal absent; supratemporal arch complete ..... FEYLININAE

Palatine borders edge of infraorbital vacuity (Fig. 2); nasal bones separate; jugal present except in *Typhlacontias gracilis*, *T. rohani*, and *Fitzsimonsia brevipes*; supratemporal arch complete or incomplete ..... 3

3. Palatines in broad contact with ectopterygoid along posterior edge of infraorbital vacuity to partial exclusion of palatal ramus of pterygoid (Fig. 1); supratemporal arch incomplete except in *Acontias plumbeus* and *Typhlosaurus lineatus*; 4-6 teeth on premaxillae, 3-10 teeth on maxilla; limbless; a single transversely en-

larged preanal scale; tail 22 per cent or less of total length ----- ACONTINAE

Palatines separated from ectopterygoid by palatal ramus of pterygoid along posterior edge of infraorbital vacuity (Fig. 2) or palatines in contact with ectopterygoid by way of anteriorly projecting process from ectopterygoid that excludes palatal ramus of pterygoid from a position on infraorbital vacuity, but palatine never excludes the palatal ramus of pterygoid from a major contact with ectopterygoid as in Acontinae; supratemporal arch complete; 5-11 teeth on premaxillae, 10-25 teeth on maxilla; only a few species lack any trace of limbs; at least two preanal scales; tail 30 per cent or more of total length -----

SCINCINAE

#### FOSSIL RECORD OF SKINKS

In spite of the great diversity and abundance of skinks today, the family has a very poor fossil record (Hoffstetter, 1944 and 1961). Only two genera of pre-Pleistocene fossil skinks have been accurately reported.

*Sauriscus cooki* (Estes, 1964a) is known from the late Cretaceous Lance Formation of eastern Wyoming. The diagnostic characters of the available fragments, i.e., weakly bifid teeth and striations on the lingual surface of the tooth crown, do not serve to align the species with any living skink. If the fossil is in fact a skink, rather than a representative of another scinciform family, its primary importance is that it indicates that skinks were extant by at least the late Cretaceous.

All other skink fossils are referable to the scincine genus *Eumeces* and come from deposits within the present geographic range of the genus. The oldest of these fossils is Oligocene in age (Estes, 1964b) and is as easily recognizable as a *Eumeces* as is any recent skull. The later, pre-Pleistocene fossils of *Eumeces* are distributed as follows: early Miocene of Florida (Estes, 1963), Miocene of Morocco

(Hoffstetter, 1961), Mio-Pliocene of Nebraska (Estes and Tihen, 1964), and the late Pliocene of Kansas (Taylor, 1941, and Twente, 1952).

#### PHYLOGENY OF THE FOUR SUBFAMILIES OF SKINKS

Although the fossil record is thus of little value in elucidating the phylogeny of skinks, much can be inferred from the morphology and distribution of living species. The strength of this approach to the phylogeny of skinks, or any other group without a fossil record, for that matter, is, of course, only as sound as the reasons given for believing that one particular character state is historically antecedent to other alternative and contemporaneous character states. For the present, I will limit the discussion to the four subfamilies of skinks. The phylogenetic relationships of lower level taxa will be considered separately in papers on those taxa.

The fusion and loss of bones in the skull, the reduction and loss of appendages, and the acquisition of live-bearing habits are general trends in vertebrate evolution and are accepted here as advanced character states for skinks. Thus the fusion of the nasals and frontals,<sup>1</sup> the loss of the jugal and postorbital bones, and an incomplete supratemporal arch are advanced characters, as are complete limblessness and a live-bearing mode of reproduction.

Other clear evolutionary trends among

<sup>1</sup> That paired frontals are antecedent to the single frontal in skinks is supported by evidence from the ontogenetic development of this bone in lygosomine skinks. In the embryos of the live-bearing lygosomines I have examined (*Eumecia auchietae*, *Hemiergis tridactylus*, *Leiopisma elegantoides lobula*, *Mabuya lacertiformis*, *Sphenomorphus australe*, *S. concinnatus*, and *S. quoyi*; also *Lygosoma* sp. according to Pearson, 1921), there are two centers of ossification in the development of the single frontal of the adult. The frontals remain separated in these embryos until quite late in development (squamation and color pattern fully developed) but have fused by the time of hatching.



squamates, such as the loss of pterygoid teeth and the loss of an external ear opening, also help in reconstructing the phylogeny of skinks (Fig. 7).

The formation of the bony secondary palate in the four subfamilies of skinks offers further clues to phylogeny. First, it should be pointed out that with the exception of *Anelytropsis* and *Dibamus*, the bony secondary palate of skinks is unique among squamates and has surely been derived from the primary palate of other lizards.

The secondary palates of the Feylininae and Acontinae are quite different from one another, and both palatal types are also quite complex, suggesting that they have been derived independently from some less complex palate.

Of the two remaining subfamilies of skinks, the scincine secondary palate appears to be more primitive than and ancestral to the lygosomine palate. The basic differences between the palates of the two taxa are that, in general (the exceptions will be discussed below), the scincines have the palatine bones apposed but not meeting on the midline, and the palatal rami of the pterygoids are widely separated, whereas the lygosomines have at least the palatines meeting medially, and in some groups the palatal rami of the pterygoids meet as well. Three lines of evidence indicate that the sequence of palatines and pterygoids not meeting medially (general scincine condition), palatines but not pterygoids meeting medially, and palatines and pterygoids both meeting medially (the two general lygosomine conditions) is in fact probably the actual developmental sequence in the evolution of a complete secondary palate in skinks.

(1) To derive the complete secondary palate of scincids from the non-scincid squamate primary palate, one would expect *a priori* that a proto condition to the medial contact of the palatines and pterygoids of the complete secondary palate would be the progressively closer medial

apposition of these bones, instead of the construction of a complete secondary palate in one macromutation. It would also be functionally more efficient first to appose the more anterior bones of the primary palate (the palatines) before the more posterior bones (the pterygoids) were incorporated; that is, it is difficult to imagine the efficiency of a secondary palate consisting of the pterygoids in contact medially but the palatines widely separated.

(2) The development of a secondary palate in different groups in the fossil record, e.g., turtles and crocodylians, involves the progressive incorporation of successively posterior bones of the primary palate.

(3) The ontogenetic development of a complete secondary palate in lygosomines involves first the medial closure of the palatines, followed by the closure of the palatal rami of the pterygoids.

The close correlation between the closure of the palatines on the midline of the secondary palate and the fusion of the frontals is the primary justification for recognizing the lygosomines as a distinct taxon of skinks. And in that the divided frontals and the separated palatine bones in the secondary palate of the scincines are primitive characters, the lygosomines must be considered an advanced group derivable from the scincines. Those few lygosomines which have the palatines not quite meeting along the midline of the palate and those few scincines which do have the palatines and sometimes the pterygoids meeting along the midline of the palate do no damage to the foregoing outline of the phylogeny of the scincines and lygosomines.

Thus the lygosomines in which the palatines do not quite meet medially (most *Egernia* and *Corucia zebrata*) may be either very primitive lygosomines, in which the palatines have never met medially, or they may be advanced lygosomines, in which the palatines are secondarily separated. Although the two genera to which

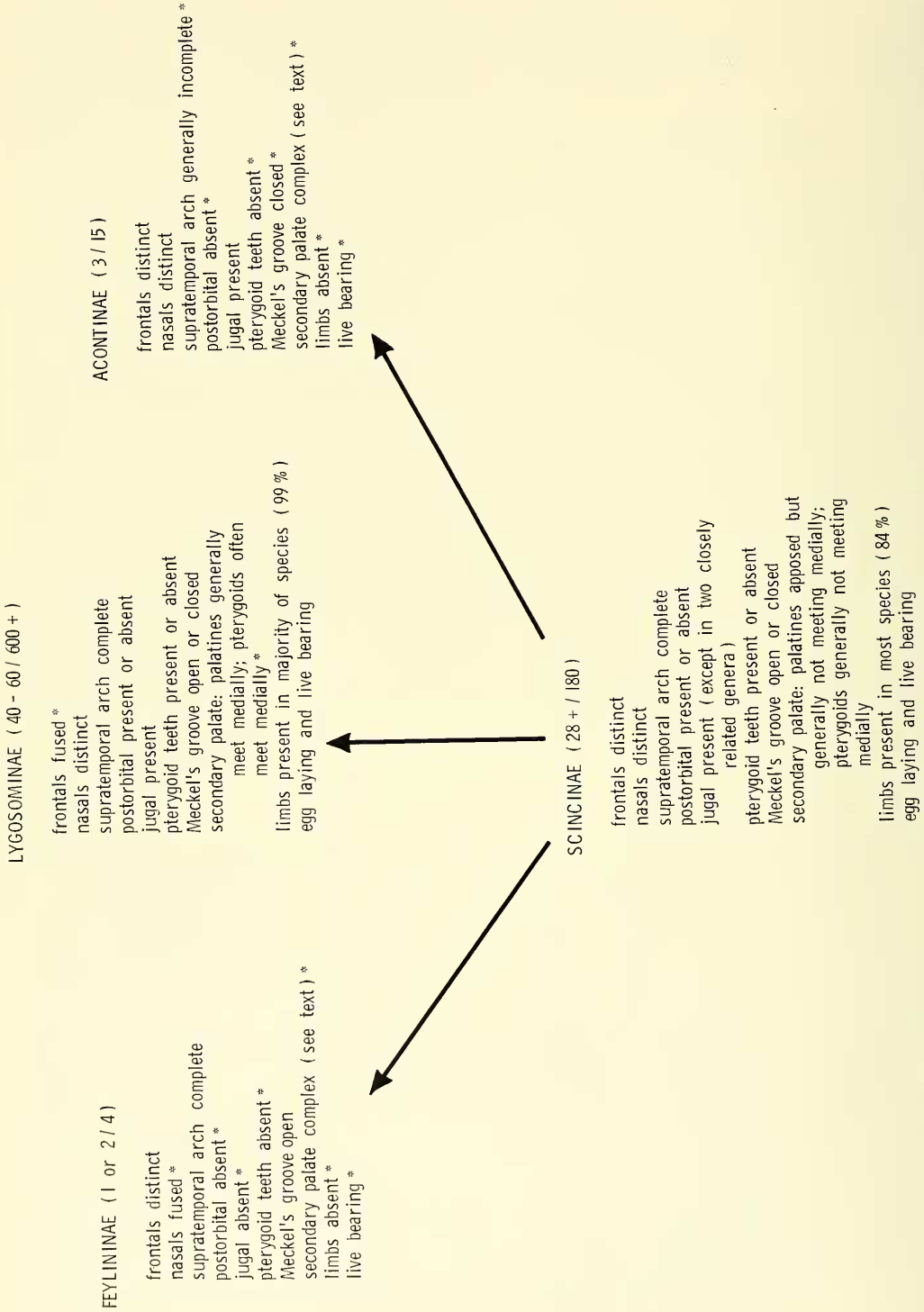


Figure 7. Hypothetical phylogeny of the four subfamilies of skinks. Derived character states are indicated by an asterisk (\*). The number of genera and species for each taxon are given in parentheses on the left and right sides of the slash mark.

these aberrant species belong are quite closely related, the diversity in morphology and behavior displayed by these species (within the group formed by the two genera) leads me to view them more as distantly related end products, in which the palatines have secondarily separated, than as a closely knit, basal lygosomine stock retaining the primitive scincine palate.

Similarly, the few scincines with only the palatines meeting medially (*Proscelotes* and *Scelotes*) appear to be a monophyletic group and could be viewed, on the basis of this character, as being either immediately ancestral to the lygosomines or independently specialized scincines. Although it is difficult to make a decision between these two hypotheses, my feeling is that the latter hypothesis is correct.

It seems fairly clear, however, that the three endemic scincine Seychelles "*Scelotes*" and the Mauritian scincine *Gongylomorphus bojeri* have, as a group,<sup>1</sup> independently evolved a very advanced, complete secondary palate involving both the palatine and pterygoid bones. If this were not the case, and these four species were to be considered as ancestral to the lygosomines, then we would have to look upon those lygosomines with the palatines and pterygoids meeting medially as being primitive, and the lygosomines with only the palatines either meeting medially or separated as advanced. Such a hypothetical developmental sequence, however, has no evidence whatsoever to support it and is, in fact, refuted by the ontogenetic and fossil evidence discussed above. To believe this hypothesis would require us to throw out the only evidence we have on the evolution of the secondary palate in

skinks and to accept the hypothetical alternative purely on faith.<sup>2</sup>

It would seem, then, that a complete secondary palate has evolved from an incomplete secondary palate at least twice and perhaps three times in skinks: once in the lygosomines (concomitant with the fusion of the frontals) and once or twice in the scincines (depending on the as yet unanswered question of whether the complete secondary palate in the *Proscelotes-Scelotes* group and the Seychelles "*Scelotes*"-*Gongylomorphus bojeri* group is due to relationship or convergence).

It thus seems fairly clear that scincines are ancestral to lygosomines, but we have yet to place the feylinines and acontines in the phylogeny of the subfamilies. These two groups are highly specialized burrowers and are unlikely to have been ancestral to any major group of skinks living today. Their divided frontals and incomplete secondary palates align them much more closely with the scincines than with the lygosomines. This notion is further supported by the fact that both acontines and feylinines are limbless, and it has been the scincines more than the lygosomines that have tended to lose the limbs entirely.

The secondary palates of the acontines and feylinines are extremely complex and extremely unlike each other, which makes it seem very probable that the two taxa arose independently from a scincine ancestry. It is difficult to distinguish the scincine relatives of the acontines, but the scincine *Typhlacontias* and *Fitzsimonsia*,

<sup>2</sup>I intend to refute this hypothesis only as a broad explanation of the evolution of the secondary palate in skinks. Minor "reversals" in the general trend from an incomplete secondary palate to a complete and ever more extensive secondary palate might be expected and would not be strong enough evidence, in my mind, to offset the ontogenetic and fossil evidence in favor of this general trend. Indeed, as suggested above, it seems possible that such a minor "reversal" in the general trend is what we see in the incomplete secondary palates of a few lygosomines (most *Egemia* and *Corucia zebata*).

<sup>1</sup>On the basis of other characters, as well as the relationships of the bones of the palate, the endemic Seychelles "*Scelotes*" and the Mauritian *Gongylomorphus bojeri* appear to be each other's closest relatives and form a monophyletic group. This relationship and its interesting zoogeographic implications will be discussed elsewhere.

with their peculiar stapes-quadrate articulation (see page 163), and the absence of the jugal bone, are similar to the feylinines. However, this similarity may well be the result of convergence (both taxa are burrowers) rather than relationship.

The data discussed in this section are summarized in the phylogenetic tree of Figure 7.

#### ZOOGEOGRAPHY OF THE MAJOR TAXA OF SKINKS

The zoogeography of the major taxa of skinks can be readily understood on the basis of the morphological and distributional data for the many living and very few fossil species summarized in the preceding sections of the paper.

Basic to the following discussion is the idea developed above that the scincines have given rise independently to the other three major groups of skinks, the Feylininae, Acontinae, and the most speciose and morphologically "advanced" group of skinks, the Lygosominae. The present distribution of the four subfamilies of skinks seems to support this broad phylogenetic hypothesis.

With the exception of *Eumeces* (the largest genus in the subfamily, 46 species) and the monotypic *Neoseps* of Florida, the Scincinae are entirely Old World in distribution and, again with the exception of the widespread *Eumeces*, show a relict distribution in south central and eastern Asia (Fig. 4). For example, the only scincine, with the exception of *Eumeces*, in eastern Asia is *Brachymeles* (13 species) in the Philippines. As one moves west through Asia, no other scincines are encountered until, on reaching India, the monotypic *Barkudia* is known from the regions around Chilka Lake and Calcutta. Further south in India there is a single species of *Sepsophis* in the central and southern part of the subcontinent and two endemic genera, *Nessia* (8 species) and *Chalcidoseps* (1 species), on Ceylon.

It is not until one reaches southwest Asia

and the Mediterranean area that one encounters widely distributed genera with many species, e.g., *Ophiomorus* (9 species), *Scincus* (12 species), and *Chalcides* (14 species). It is south of the Sahara Desert in Africa, Madagascar, and the islands of the western Indian Ocean that the scincines become an important part of the skink fauna (76 of the 136 species of non-*Eumeces* scincines occur in this area).

Two of the other three subfamilies are also found in subsaharan Africa. The Acontinae, with approximately 15 species, and the Feylininae, with 4 species, are undoubtedly derived from scincines in Africa; this, along with the present large number of species and their extensive distribution in subsaharan Africa, Madagascar, and the islands of the western Indian Ocean, appears to indicate that the scincines have been in subsaharan Africa for much, if not most, of their evolutionary history.

Whether the scincines were ever in the Australian Region is an interesting question. The furthest east scincines range in the Old World today is the Philippines (*Brachymeles*, 13 species). It is, of course, possible that the scincines have been completely replaced in the Australian Region by the lygosomines, although the total absence of any scincine relicts in Australia or the numerous island groups of the Region makes me believe that the scincines never reached this part of the world.

The reasons for the relict distribution of the scincines in south and east Asia and their abundance in southwest Asia, Africa, and Madagascar are undoubtedly complex but may be due in part to the evolution and radiation of the Lygosominae in southeast Asia and the Australian Region. The lygosomines are clearly derived from scincines and are morphologically the most advanced skinks. This group is most numerous and diverse in southeast Asia and the Australian Region, and its expansion from this area of origin may account in part for the relict distribution of the scincines in south and east Asia. In southwest Asia,

Africa, and Madagascar, the area of the Old World furthest from their area of origin, the lygosomines are fairly well represented by species, but they are not morphologically diverse (i.e., there are not many genera). Presumably the lygosomines are only recent arrivals in this area and have not yet swamped their ancestral scincine relatives. Perhaps if we could return in several million years, the scincines would show a relict distribution in Africa, Madagascar, and the islands of the west Indian Ocean as they do in southern and eastern Asia today.

The overall geographic picture of skink evolution in the Old World is distinctly bipolar. The scincines appear to have had a long evolutionary history in Africa, giving rise to numerous genera and species as well as to two other subfamilies of skinks, whereas the spectacular radiation of the more advanced lygosomines appear to be predominately a phenomenon of the Australian Region—an area that was probably never reached by the scincines.

The origin of the New World skink fauna is of special interest. In view of the great diversity and abundance of skinks in the Old World, the most remarkable aspect of the New World skink fauna is its paucity. This, plus the fact that three of the four genera in the New World are also widespread in the Old World, indicates that the Old and not the New World is surely the ancestral home of the family.

*Eumeces* is represented by 31 species in the New World and 15 in the Old World. The genus has been in North America at least since the late Oligocene (see Fossil Record of Skinks, above) and in that time has successfully rafted to Bermuda (*E. longirostris*), but, peculiarly, the group has not spread further south than Costa Rica.

*Eumeces* undoubtedly arrived in the New World via a Bering Land Bridge. The group is very primitive even for scincines<sup>1</sup>

(Greer, in preparation), and its distribution along the northern periphery of the range of skinks in the Old World (Fig. 5) implies a greater cold tolerance than in most other skinks. In both time and place, therefore, *Eumeces* would have been in a good position to take advantage of a Bering Land Bridge.

The relationships of the New World *Leiopisma* with each other and with their supposed Old World congeners is a major unsolved problem in skink systematics. For the moment I am treating the *Leiopisma* of the New World as congeneric with a group of southeast and east Asian *Leiopisma*. In east Asia, this group ranges as far north as about 41°N lat., which is only slightly further south than the northern limit of the range of *Eumeces* in Asia (about 45°N lat.). Thus, like *Eumeces*, these *Leiopisma* would be "cold tolerant" enough to have taken advantage of the Bering Land Bridge during slightly warmer times.

There is no fossil record for *Leiopisma* in the New World, so the time of arrival of the group is unknown, but the few species in the New World and their absence from islands like Bermuda may indicate that the group arrived in North America after *Eumeces*. Like *Eumeces*, however, *Leiopisma* has not entered South America, although it is known as far south as Panama.

The fact that both *Eumeces* and *Leiopisma* come so close, but fail to enter South America, seems a bit peculiar to me and merits further discussion. The water gap that persisted through most of the Tertiary across Panama and northern

be quite similar to the ancestor of all skinks. In view of this primitiveness, it might seem peculiar that the group should be so successful—if number of species is acceptable as a criterion for success (*Eumeces*, with about 46 species, is the most speciose genus of scincines). But the primitiveness discussed here is morphological, and on other characters, such as the maternal care of the eggs, *Eumeces* shows the greatest advancement of any lizard for which such data are available.

<sup>1</sup> Morphologically *Eumeces* is very possibly the most primitive living skink taxon and may, in fact,

Colombia probably aided in excluding both genera from South America, but this cannot be the whole answer, as skinks have few peers among squamates in crossing water barriers and, regardless of the Tertiary water gap, both genera have had ample time since the closure of the isthmus to enter South America (as has apparently been the case with the genus *Rana* and the two genera of Bolitoglossine salamanders).

Competitive exclusion by resident South American lizards filling niches similar to those filled by *Leiolopisma* and *Eumeces* may be of as great importance in explaining the absence of these two genera from South America as is the Panamanian-Colombian water gap. For example, the micro-teiids, which probably arose in South America and have only recently invaded Central America, are very skink-like in their external morphology and habits and may be South America's candidate for the skink niche (along with the endemic *Mabuya*).

The genus *Mabuya* is currently thought to comprise approximately nine species in the New World (Dunn, 1936), although this estimate may be low. These species are distributed throughout South America, the West Indies, Central America, and Mexico as far north as Veracruz and Colima. The lack of diversity of the New World species may indicate that the group has not been in the New World very long. There are many *Mabuya* both in Asia and Africa, so it is difficult to decide whether the group arrived from Asia via the Bering Land Bridge or from Africa by over-water rafting. Three bits of evidence make me favor the latter possibility. First, the genus is very good at crossing water gaps, as evidenced by the endemic *Mabuya* of the Cape Verde Islands, Madagascar, the Seychelles, and Fernando de Noronha and the *Mabuya* of the West Indies. Second, there are no *Mabuya* in the southeastern United States, unlike the case with many Asian immigrants (*Magnolia*, pattlefishes, *Ophisaurus*, *Leiolopisma* and *Eumeces*). And third, there are endemic South Ameri-

can and West Indian species of other African lizard genera (*Lygodactylus*, *Tarentola*) whose ancestors almost surely arrived in the New World across the Atlantic. Also, Dunn (1936) thinks that "the nearest relationship of the mainland and Caribbean forms [of *Mabuya*] seems to be with the mainland African species of the *raddoni-affinis* group."

The fourth group of New World skinks is the monotypic scincine genus *Neoseps* of peninsular Florida. *Neoseps* is an attenuate burrower in sandy loamy soil and presents no great zoogeographic problem, as it has probably simply evolved from a *Eumeces* ancestor *in situ* (Telford, 1959). Not only is there a close morphological similarity between the two genera (Greer, personal observation), but they are also the only skinks yet known in which the female guards the eggs.

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