

THE GENERA *TILIQUA* AND *CYCLODOMORPHUS* (LACERTILIA: SCINCIDAE): GENERIC DIAGNOSES AND SYSTEMATIC RELATIONSHIPS

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A suite of morphological synapomorphies diagnoses a *Tiliqua* lineage in the subfamily Lygosominae. Two sister genera, *Tiliqua* and *Cyclodomorphus*, are diagnosed in this lineage. On the basis of the available evidence, *Trachydosaurus* is highly derived within *Tiliqua*, and is synonymised with it, while *Hemisphaeriodon* is synonymised with *Cyclodomorphus*. □ Scincidae, *Tiliqua*, *Cyclodomorphus*, taxonomy, osteology, morphology.

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The Scincidae has traditionally been considered to be systematically amongst the most complex and refractory of the lizard families. There are a very large number of species, a great morphological diversity with subtle differences between many of the species and frequent convergent evolution. Within this family, the large bluetongue skinks of Australia and New Guinea are amongst the most familiar and recognisable. Yet, even they have been the subject of debate regarding generic boundaries for over a century and a half. Six species, *Lacerta scincoides* Shaw, 1790, *Scincus gigas* Boddaert, 1783, *Scincus nigroluteus* Quoy and Gaimard, 1824, *Cyclodus adalaidensis* Peters, 1864, *Cyclodus occipitalis* Peters, 1864 and *Tiliqua occipitalis multifasciata* Sternfeld, 1919, have consistently been grouped together, either as *Tiliqua* Gray, 1825, or *Cyclodus* Wagler, 1828, a junior synonym. Associated with this core at various times have been four other groups of species.

The first of these associated groups, consisting only of *Trachydosaurus rugosus* Gray, 1825, was considered distinct from *Tiliqua*, though frequently closely allied to it, by all authors up until 1950, when Mitchell (1950) synonymised it with *Tiliqua*. Since that time, the generic status of *Trachydosaurus* has varied, being regarded as distinct by Copland (1953), Mertens (1958), Glauert (1960), Worrell (1963), Cogger (1975, 1983) and Wells and Wellington (1984, 1985) or synonymous with *Tiliqua* by Storr (1965), Rawlinson (1966), Greer (1979a) and Hutchinson (1981). In the first half of this paper, I refer to this group as *Trachydosaurus*.

The second group, also monotypic, consists of *Hemisphaeriodon gerrardii* (Gray, 1845). First described as a *Hinulia*, which was a predecessor of Boulenger's (1887) enormous polyphyletic assemblage *Lygosoma*, *gerrardii* was placed in a new genus, *Hemisphaeriodon*, by Peters (1867). Boulenger (1887) and Cope (1892a) accepted the generic status of *Hemisphaeriodon*, placing it alongside *Tiliqua* in their classifications. Mitchell (1950) synonymised it with *Tiliqua*, where it has largely remained to the present time, although Wells and Wellington (1984, 1985) resurrected the genus without discussion, and Czechura (1986) placed *gerrardii* with the next group. In the first half of this paper, I refer to this group as *Hemisphaeriodon*.

The third group, currently consisting of *Cyclodus casuarinae* Duméril and Bibron, 1839, *Hinulia branchialis* Günther, 1867 (unpublished work by the author and B. Miller indicates that five taxa are recognisable in this 'species') and *Omolepida maxima* Storr, 1976, has had a more varied history. Although originally described as a *Cyclodus*, *casuarinae* was subsequently removed to the monotypic genera, *Cyclodomorphus* Fitzinger, 1843 and *Omolepida* Gray, 1845. Duméril and Duméril (1851) returned *Omolepida* to the synonymy of *Cyclodus*, while Strauch (1866) recognised it as a subgenus of *Cyclodus*. Boulenger (1887) placed *casuarinae* and *branchialis* together in *Homolepida* (an emendation of *Omolepida*) as a subgenus of *Lygosoma*, an arrangement foreshadowed by Günther's (1867) description of *branchialis* in *Hinulia*. Frost and Lucas (1994) recognised a

relationship between this group and *Hemiphaeriodon* when they described *Hemiphaeriodon tasmanicum*, a synonym of *casuarinae*. Cope (1892a) elevated *Homolepida* to generic level, while Smith (1937) returned *Omolepida* to the synonymy of *Tiliqua*. Mitchell (1950) accepted Smith's synonymy, while Storr (1964, 1976) resurrected *Omolepida* as a genus. More recently, Greer (1979a), Hutchinson (1981) and Cogger (1983) have returned *Omolepida* to the synonymy of *Tiliqua*, while Wells and Wellington (1984, 1985) resurrect *Cyclodomorphus* as a genus. In the first half of this paper, I refer to this group as *Cyclodomorphus*.

The final group, the *Egernia luctuosa* species group, comprising *E. luctuosa* (Peters, 1866) and *E. coventryi* Storr, 1978, has generally been placed in *Egernia*. However, Peters (1866) and Mitchell (1950) placed *E. luctuosa* in *Tiliqua*. Peters assigned it to the then subgenus *Omolepida*, although he subsequently (Peters, 1872) placed it in a monotypic genus, *Lissolepis*. Mitchell's placement was accepted by Glauret (1960) and Worrell (1963).

It is clear that consensus has not yet been reached regarding the generic boundaries of *Tiliqua*. This paper begins the taxonomic revision of *Tiliqua* (sensu lato) by redefining what I believe to be the genera within this group, and critically reviewing the evidence for alternative classifications. I base my diagnoses on a range of characters, including scalation, cranial and post-cranial osteology, and coloration. I have not considered soft-tissue characters at this time, as there is insufficient comparative data for other skinks. Character polarity is determined by outgroup comparison (Arnold, 1981) and only derived states used in the diagnoses.

OUTGROUP SELECTION

For the purpose of determining character polarity, I have used three successively more distant outgroups:

1. the genus *Egernia*
2. other non-attenuate skinks of the subfamily Lygosominae, especially *Mabuya*
3. non-attenuate scincine skinks, with emphasis on *Eumeces*

My rationale for the selection of these outgroups is explained below.

Egernia has consistently been considered the genus closest to *Tiliqua* (s.l.) by most authors from Gray (1845) on. Although Boulenger

(1887) and Cope (1892a) separated *Tiliqua* and *Egernia* on the basis of separation or contact of palatine bones, Waite (1929) noted that this character was invalid in the form expressed by Boulenger. In both genera, the palatine bones are usually separated on the midline. Mitchell (1950) believed that the two genera 'separated relatively recently from a common stock and have developed along two monophyletic lines', although no characters of any utility were advanced to define this relationship. The two genera were separated on the basis of the presence or absence of contact of a medial palatine process of the ectopterygoid with the palatines, and tooth shape, but difficulty was experienced in assigning the *Egernia whitii* group, which has narrow contact between palatine and ectopterygoid process.

A close relationship between *Egernia* and *Tiliqua* was also implicit in the classifications proposed and argued by other workers in subsequent years (for review, see Hutchinson, 1981). Greer (1979a) considered the two genera, along with the monotypic *Corucia*, a lineage (the *Egernia* group) within the subfamily Lygosominae, diagnosed on the basis of a single character: a reduced modal number of premaxillary teeth (7-8 vs the primitive 9). Three other synapomorphies were employed in inferring a sister-group relationship between the *Egernia* and *Eugongylus* groups: closure of Meckel's groove in the dentary, loss of pterygoid teeth and loss of a distinct postorbital, although the latter two characters were not employed in diagnosing lineages as they 'were not completely diagnostic for all groups'. However, if the loss of pterygoid teeth and loss of a distinct postorbital be considered less than diagnostic, so too must the sole synapomorphy for the *Egernia* group, as three species of *Egernia*, *E. coventryi*, *E. luctuosa* and *E. major*, have a mode of 9 premaxillary teeth (Greer, 1979a; pers. obs.). Further, loss of pterygoid teeth is not a synapomorphy for the combined *Egernia*/*Eugongylus* group lineage, as they are present in both *Leiopisma telfairii* and *L. mauritanus* of the *Eugongylus* group (Arnold, 1980) and in *Corucia zebrata* in the *Egernia* group (pers. obs.).

Despite this, there remain three fairly clear lines of evidence for the monophyly of Greer's *Egernia* group. *Tiliqua*, *Egernia* and *Corucia* share a distinctive karyotype, with diploid number $2n=32$, nine pairs of macrochromosomes, six pairs of microchromosomes, and pair six smaller than pair five (King, 1973a,b; Donnellan, 1985).

This karyotype is not known from any other lygosomine, scincid or scincomorph group. While it is not possible to determine the direction of karyotypic evolution within the Scincidae, as no group has a demonstrably primitive karyotype as determined by outgroup comparison, each karyomorph may be uniquely derived (Donnellan, 1985). Secondly, immunoelectrophoretic studies (Hutchinson, 1981) have indicated that *Egernia* and *Tiliqua* are each other's closest relatives, with *Corucia* slightly more distant. Finally, intergeneric hybridisation has been reported between captive *E. cunningghami* and *T. gigas* (Rose, 1985), further suggesting that the genetic distance between the two genera is not great.

Although *Corucia* is a member of this lineage, I have not included it with *Egernia* in the first outgroup. *Corucia* displays a combination of recognisably very primitive characters (e.g., pterygoid teeth, double row of supradigital scales) with a number of bizarre autapomorphies (e.g., loss of central supraciliaries, extremely elongate last supralabial, separation of first pair of chin shields, grossly enlarged frontonasal scale, cuspidate teeth, distal end of tail forming a slight hook), at least some recognisably the result of a unique ecology (arboreal herbivory) amongst skinks. Immunological evidence has suggested that it is more distantly related to *Tiliqua* than is *Egernia* (Hutchinson, 1981), and I have consequently relegated it to the second outgroup, where its influence on determination of polarities is diluted.

The *Egernia* lineage has been placed in the subfamily Lygosominae (Greer, 1970a). This assignment has withstood critical evaluation, and the monophyly of the subfamily successfully defended (Donnellan, 1985; Greer, 1986a) against criticism (King, 1973b; Rawlinson, 1974; Hutchinson, 1981). Within the Lygosominae, many lineages have undergone convergent evolution towards a fossorial lifestyle (Greer and Cogger, 1985; Heyer, 1972), with a number of derived characters, especially those associated with burrowing, having evolved a number of times. Complete loss of limbs has evolved at least five times within the subfamily (Greer and Cogger, 1985) with some loss of phalanges and an increase in the number of presacral vertebrae occurring in many other genera. The resulting 'noise' hampers use of a uniform outgroup composed of all non-*Tiliqua* lygosomines. Greer (1977, 1979a, 1983) has attempted to block this 'noise' by placing em-

phasis on character states in *Mabuya*, as 'the genus that seems to comprise the most generally structurally primitive species among the lygosomines...' (Greer, 1979a: 340). However, of the many plesiomorphies advanced in support of this view (Greer, 1979a), most are also present in *Tiliqua*, *Egernia* and most other non-attenuate lygosomines. Only in the presence of supranasal scales, postorbital bones, and pterygoid teeth is *Mabuya* as a whole notably more primitive than *Egernia* and many other lygosomines. Consequently, I have not placed as much emphasis on character states in *Mabuya* as Greer, but instead have filtered out the influence of convergence in fossorial and cryptozoic species by only considering those lygosomine genera which possess the primitive number of presacral vertebrae ($n = 26$; Hoffstetter and Gasc, 1969), or only a slight elevation above this ($n \leq 30$). Fifty-eight genera or species groups are in this category (*Eugongylus* group: *Caledoniscincus*, *Carlia*, *Cophoscincopus*, *Cryptoblepharus*, *Cyclodina*, *Emoia*, *Erotoscincus*, *Eugongylus*, *Geomyersia*, *Geoscincus*, *Lampropholis*, '*Leiopisma*' *entrecasteauxii* species group, '*Leiopisma*' *nigrofasciolum* species group, Tasmanian '*Leiopisma*', New Zealand '*Leiopisma*', Mascarene Island *Leiopisma*, other Australian '*Leiopisma*' (*coventryi*, *jigurru*, *ziu*), other Pacific '*Leiopisma*' (*alazon*, *steindachneri*), *Lygisaurus*, *Marmorosphax*, *Menetia*, *Morethia*, *Nannoscincus* (part: *greeri*, *maccoyi*, *mariei*, *rankini*), *Panaspis*, *Phoboscincus*, *Proablepharus*, *Ristella*, *Saproscincus*, *Sigaloseps*, *Tachygyna*, *Tropidoscincus*, *Tribolonotus*; *Sphenomorphus* group: *Ablepharus*, *Asymb-lepharus*, *Ateuchosaurus*, *Calypotis*, *Ctenotus*, *Eremiascincus*, *Eulamprus*, *Fojia*, *Glaphyromorphus* (non *crassicaudis* group), *Gnypetoscincus*, *Lipinia*, *Lobulia*, *Notoscincus*, *Papuascincus*, *Prasinohaema*, *Scincella*, *Sphenomorphus fasciatus* species group, *Sphenomorphus variegatus* species group, *Tropidophorus*; '*Mabuya* group': *Apterygodon*, *Dasia*, *Lamprolepis*, *Mabuya*, *Macrosaurus*; *Egernia* group: *Corucia*; data from Greer, 1982, 1983, 1985, 1986b, pers. comm., Greer and Cogger, 1985, Sadler, 1987 and pers. obs.; species groups in '*Leiopisma*' follow Sadler (1987) and M. Hutchinson, pers. comm.) and these are used as the second outgroup.

Three other subfamilies of the Scincidae have been proposed by Greer (1970a). Two of these, the Acontinae and the Feyliniinae are composed of attenuate burrowing species with markedly

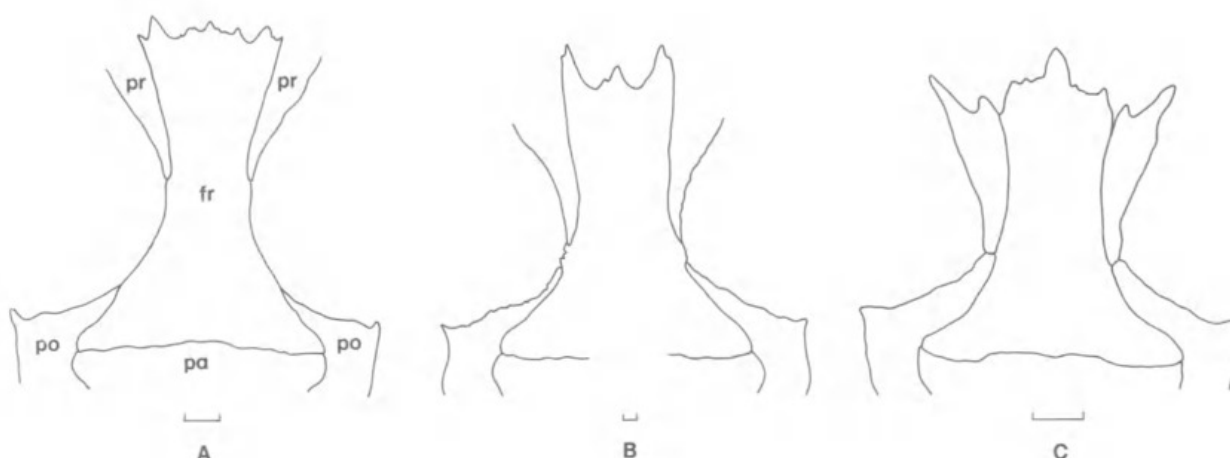


FIG. 1. Dorsal view of interorbital area of skull of A. *Egernia modesta* (Australian Museum (AM) R106893), B. *Tiliqua gigas* (AM R93222) and C. *Cyclodomorphus casuarinae* (AM R127932). Fr = frontal; po = postfrontal; pr = prefrontal. Scale bar = 1mm.

elevated numbers of presacral vertebrae. The remaining subfamily, the Scincinae, is plesiomorphic vis-à-vis the Lygosominae (Greer, 1970a, 1986a; Hutchinson, 1981; Estes, 1983). Within the Scincinae, most genera show marked limb reduction and body elongation, and I have excluded these from the third outgroup, for the same reason as given above. Six scincine genera or subgenera (*Amphiglossus* (*Madascincus*), *Eumeces*, *Janetaescincus*, *Pamelaescincus*, *Scincus* and *Scincopus*), however, have a primitive or near-primitive number of presacral vertebrae (El-Toubi, 1938; Brygoo, 1981; A.E. Greer, pers. comm.), and this group is used as the third outgroup. Brygoo (1981) also lists *Gongylomorphus* as having 26 presacral vertebrae, but two Australian Museum specimens of *G. b. bojeri* (R73340-41) have 32, and I have therefore not included *Gongylomorphus* in this outgroup. Within the Scincinae, *Eumeces* is recognisably the most primitive genus (Greer, 1970a, 1974, 1979a), as well as the largest. Fortunately, it is also the genus for which the greatest body of literature on scalation and osteology exists (Taylor, 1935; Kingman, 1932; Nash and Tanner, 1970; Hikida, 1978), and I have consequently placed most emphasis on this genus within the third outgroup.

DETERMINATION OF CHARACTER POLARITIES

1. Presacral vertebrae. The primitive number of presacral vertebrae in skinks is 26 (Hoffstetter and Gasc, 1969). All *Egernia* and *Corucia* have

a mode of 26 presacral vertebrae, while the range for *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* is 32-44 (Siebenrock, 1895; pers. obs.).

2. Phalangeal formula of manus. A phalangeal formula of 2.3.4.5.3 is considered primitive for lepidosaurs (Romer, 1956; Greer, 1983, 1987). All *Egernia* species and 44 of 53 genera and species groups in the next two outgroups have this configuration, while only 9 genera have a different formula, involving loss of phalanges in all but *Scincus* (El-Toubi, 1938). *Cyclodomorphus*, *Hemisphaeriodon* and *Tiliqua* have a manus formula of 2.3.4.4.3 (i.e., loss of one phalanx in the fourth finger), while *Trachydosaurus* has 2.3.3.3.2 (loss of a further three phalanges). These are assumed to be successive derivations from the primitive condition.

3. Phalangeal formula of pes. A phalangeal formula of 2.3.4.5.4 is considered primitive for lepidosaurs. All *Egernia* species and 50 of 53 genera and species groups in the next two outgroups have this configuration. *Cyclodomorphus*, *Hemisphaeriodon* and *Tiliqua* have a pes formula of 2.3.4.4.3 (i.e., loss of one phalanx in each of the fourth and fifth toes) while *Trachydosaurus* has 2.2.3.3.2 (loss of a further four phalanges). These are assumed to be successive derivations from the primitive condition.

4. Medial margin of orbit. In most skinks the prefrontal and postfrontal bones are widely separated along the lateral margin of the frontal, the separation generally equal to or greater than the smallest width of the frontal. Within *Egernia*, a slightly narrower separation occurs in *E.*

major, while in the members of the second and third outgroups examined, only in *Corucia*, *Macroscincus*, the Mauritian *Leiolopisma* and the *Sphenomorphus fasciatus* species group is the separation narrower. Broad separation of pre- and postfrontal bones is considered primitive, and the narrow separation to broad contact seen in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* (Fig. 1) derived. In *T. adalaidensis*, the separation is greater than in other species, but this is most likely to be a reversal.

5. Upper temporal arch. In most skinks the jugal and squamosal are narrowly to moderately separated along the lateral edge of the postorbital or postfrontal, while in only a few is there direct contact between jugal and squamosal. Within *Egernia*, distinct contact occurs only in most members of the *E. whitii* species group. In other non-attenuate lygosomines examined, the two bones are separated. In scincines, separation occurs in *Scincus* (El-Toubi, 1938) and moderate separation to variable point contact in 11 of the 13 *Eumeces* species for which data is available, while narrow to moderate contact has been reported for two *Eumeces* species (Kingman, 1932). Separation of the jugal and squamosal is assumed primitive for skinks, and the consistent narrow to broad contact seen in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* (Fig. 2) derived.

6. Coronoid process of dentary. In the majority of skinks examined, the coronoid process of the dentary articulates with only the rostral margin of the dorsal process of the coronoid, although in most *Egernia* species the articulation also extends slightly over the rostrolateral face of the coronoid. In *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus*, the coronoid process of the dentary largely covers or completely overlaps the dorsal process of the coronoid laterally (Hoffstetter, 1949). Articulation of the coronoid process of the dentary with only the rostral or rostrolateral margin of the coronoid is considered primitive, and extended lateral overlap of the coronoid (Fig. 3) derived.

7. Lacrimal bone. A distinct lacrimal forming the lateral margin of the lacrimal foramen is present in most skinks, though often very reduced in size and thickness in very small species. Despite a claim of absence in *E. whitii* (Siebenrock, 1892), a well-developed lacrimal was seen in all *Egernia* species examined ($n = 20$), including *E. whitii* and covering all species groups within the genus. Within the other out-

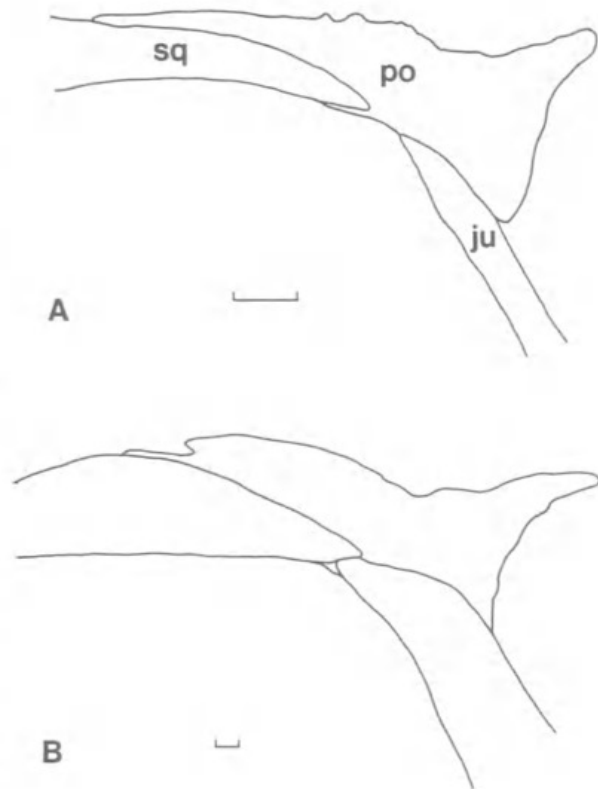


FIG. 2. Right oblique view of upper temporal arch in A. *Egernia saxatilis* (AM R122135) and B. *Tiliqua gigas* (AM R93222). Ju = jugal; po = postfrontal; sq = squamosal. Scale bar = 1mm.

groups, a distinct lacrimal was not found only in *Geomyersia* (Greer, 1982), *Ristella* (A. Greer, pers. comm.), *Menetia* and one species of *Lobulia* (pers. obs.). The presence of a lacrimal is considered primitive, and the loss of the lacrimal seen in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* (Fig. 4) derived.

8. Palatine process of ectopterygoid. A medial palatine process of the ectopterygoid, bordering the medial margin of the infraorbital fenestra, has been considered a derived character amongst skinks (Fuhn, 1969; Greer, 1970a,b, 1976; Greer and Cogger, 1985). Within *Egernia*, a long palatine process of the ectopterygoid reaching the palatine was seen in nine of the 20 species examined. However, these nine species comprised only three of nine recognisable species groups within the genus (Shea, in prep.). In the second outgroup, the process is lacking in 23 genera and species groups, present but not contacting the palatine in three, present and contacting the palatine in nine, and variably present (i.e.,

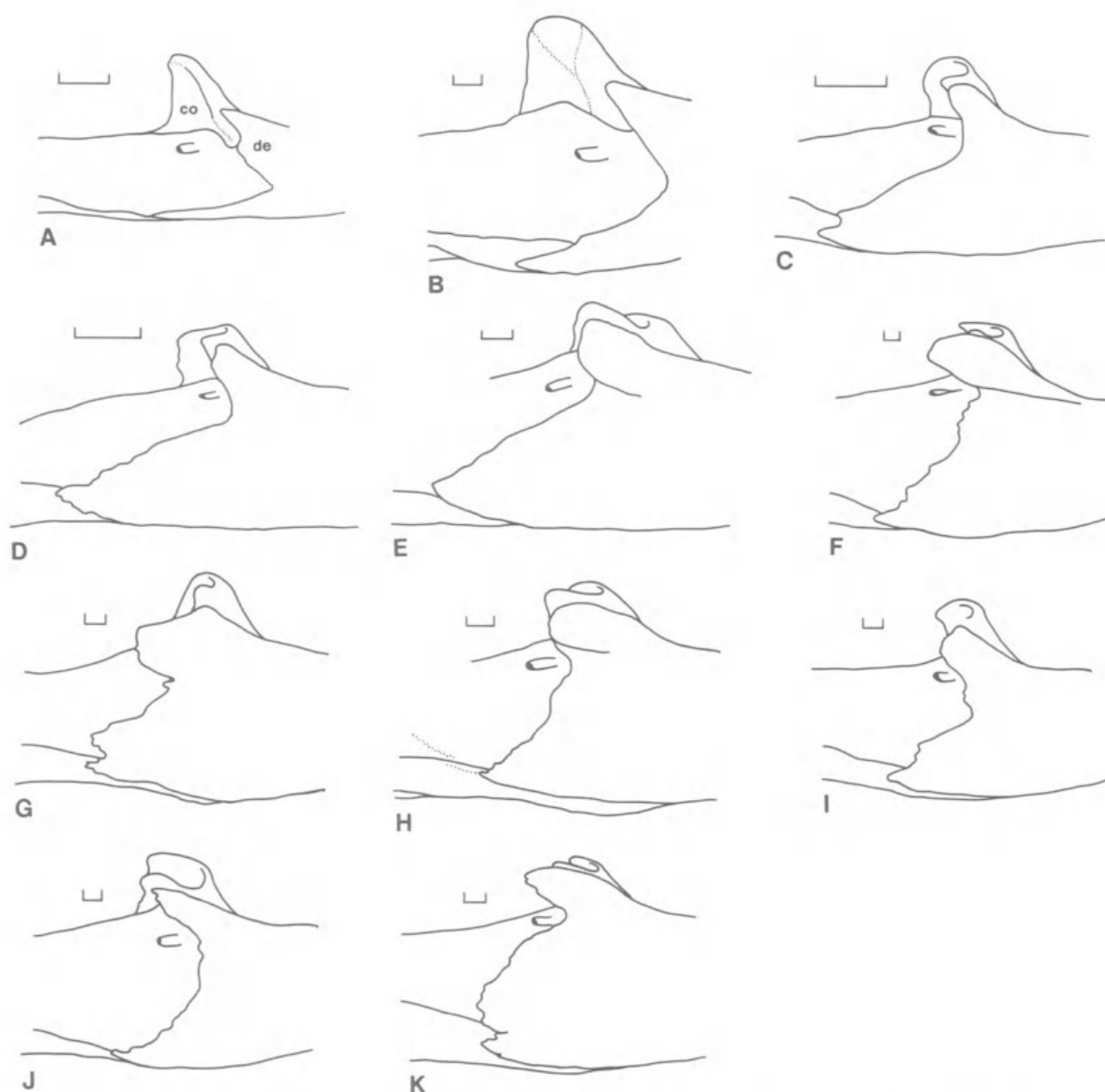


FIG. 3. Right lateral view of coronoid region of mandible of A. *Mabuya multifasciata* (AM R92623), B. *Egernia cunninghami* (AM R66018), C. *Cyclodomorphus branchialis* (AM R127930), D. *C. casuarinae* (AM R37706), E. *C. gerrardii* (AM R127926), F. *Tiliqua gigas* (AM R93222), G. *T. multifasciata* (AM R127920), H. *T. nigrolutea* (AM R106842), I. *T. occipitalis* (AM R127925), J. *T. rugosa* (AM R95260), K. *T. scincoides* (AM R127901). Co = coronoid; de = dentary. Scale bar = 1mm.

present in only some species) in three. Within *Mabuya*, the process has only been seen in five species (Greer, 1976; pers. obs.). In the third outgroup, the process is lacking in all genera. Absence of a medial palatine process of ectopterygoid is considered primitive, and its presence in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* (Fig. 5) derived.

9. Heterodonty. Most skinks have a homodont dentition, with marked heterodonty only

reported in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua*, *Trachydosaurus* and one species each of *Eumeces* and *Lerista* (Estes and Williams, 1984). *Egernia*, *Mabuya*, other *Eumeces* species, and all other species examined within the outgroups have homodont dentition. Although there is variation in the degree of heterodonty in adults, juveniles of all *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* species have a single markedly enlarged tooth in

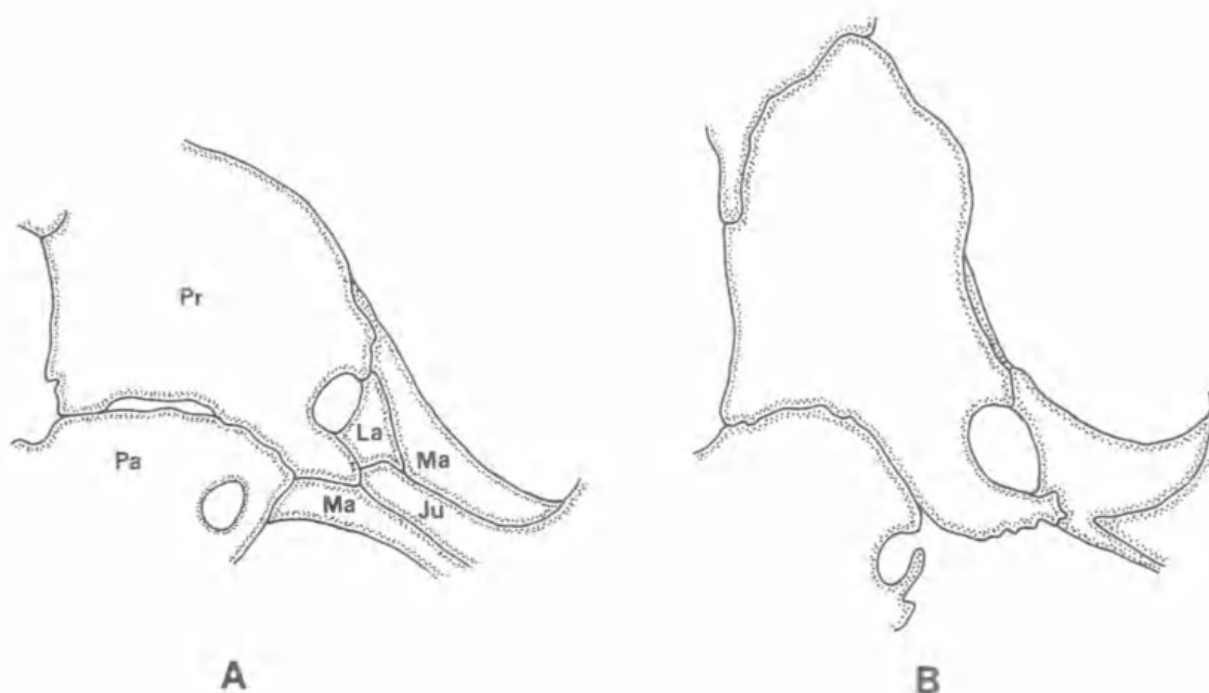


FIG. 4. Right caudal view of rostral margin of orbit of A. *Egernia carinata* (Western Australian Museum (WAM) R37926) and B. *Tiliqua nigrolutea* (AM R106842). Ju = jugal; La = lacrimal; Ma = maxilla; Pa = palatine; Pr = prefrontal. Scale bar = 1mm.

the maxillary (position number 7 or 8) and dentary (position number 10) arcades (Shea, pers. obs.). Homodonty is considered primitive and juvenile heterodonty derived (Estes and Williams, 1984).

10. Scales over temporal region. The majority of skinks have two supralabials caudal to the subocular supralabial, a single primary temporal dorsally between these, a single lower secondary temporal caudodorsal to the last supralabial, and a single upper secondary temporal dorsally, bordering parietal, primary temporal and lower secondary temporal, overlapping the latter scale. Generally, the last two supralabials are subequal in height, and both higher than the preceding supralabials (Fig. 6). This is assumed to be the primitive temporal configuration. All *Egernia* species, over two-thirds of the genera and species groups in the second outgroup, and *Eumeces*, *Scincus* and *Scincopus* in the third outgroup show this arrangement, although some genera in the *Sphenomorphus* group and a few *Eumeces* species have reversed the overlap of upper and lower secondary temporals. Other genera in the second and third outgroups show a variety of modifications to this pattern, mostly apparently involving subdivision of scales, par-

ticularly the lower secondary temporal and last supralabial scales. In *Cyclodomorphus*, *Hemisphaeriodon* and *Tiliqua*, the last supralabial is divided into an upper and a lower scale by a suture, leaving a single low 'last supralabial' bordering the lip. Most *Tiliqua* species additionally show further divisions of the primary and lower secondary temporal scales. In *Trachydosaurus*, the number and pattern of division of the supralabial and temporal scales is variable. However, the consistently low last two supralabials, frequent irregularity of the caudal margin of the 'lower secondary temporal' and the number and pattern of overlap of surrounding scales suggests that the two parts of the lower secondary temporal, and sometimes the upper part of the last supralabial, have fused again, as part of a general reduction of number of scales in this species (see below).

11. Supraciliary scales. Most species in the first two outgroups modally have eight or more supraciliaries, although most *Mabuya* have 5-6 supraciliaries. In the third outgroup, *Amphiglossus* (*Madascincus*), *Janetaescincus*, *Pamelaescincus* and over 70% of *Eumeces* species have modes of 7 or more supraciliaries. Seven to nine supraciliaries is considered primitive for skinks,

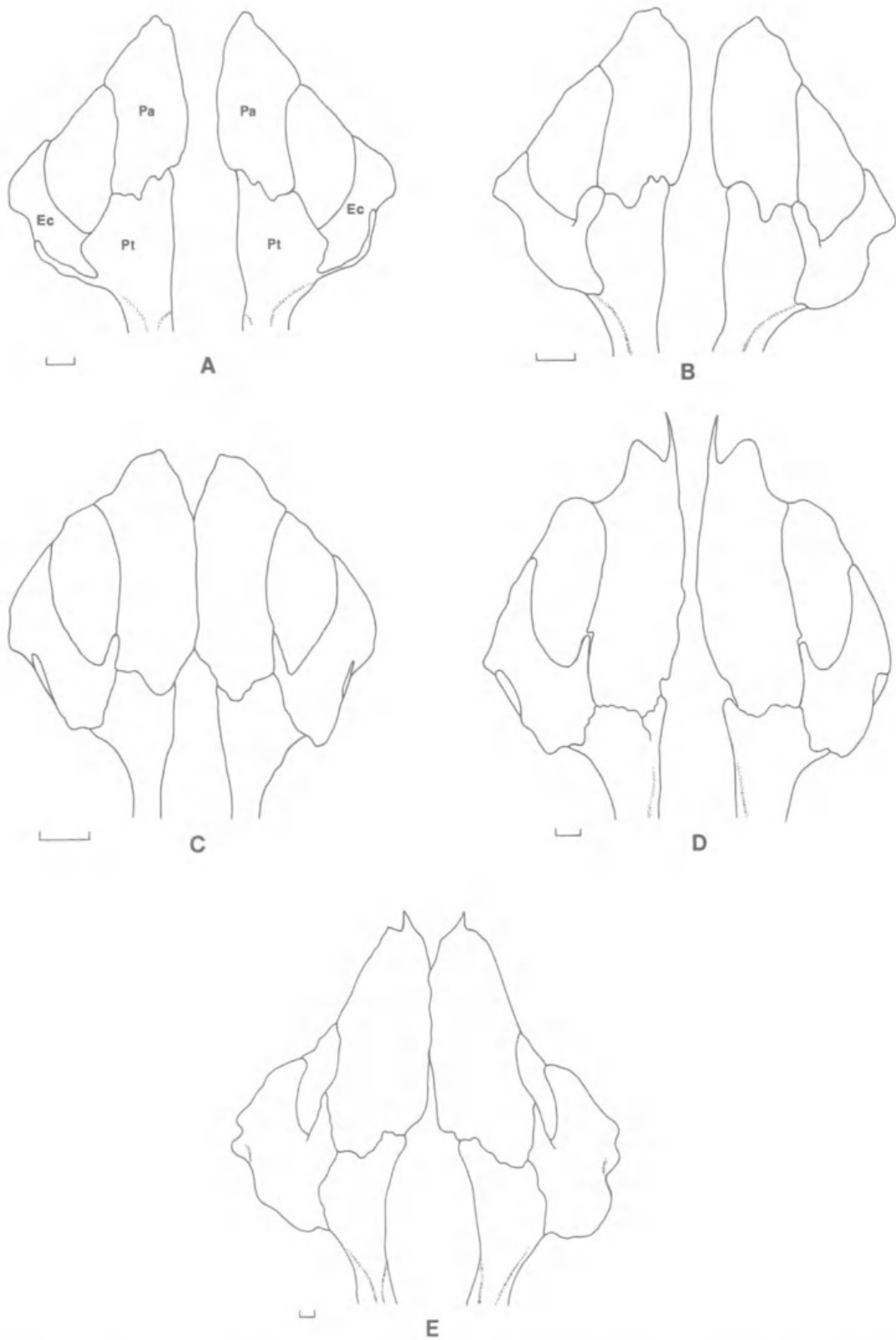


FIG. 5. Ventral view of palate of A. *Egernia mcphreei* (AM R127936), B. *E. pulchra* (WAM R47386), C. *Cyclodomorphus casuarinae* (AM R37706), D. *C. gerrardii* (AM R13084) and E. *Tiliqua scincoides* (AM R96439). Ec = ectopterygoid; Pa = palatine; Pt = pterygoid. Scale bar = 1mm.

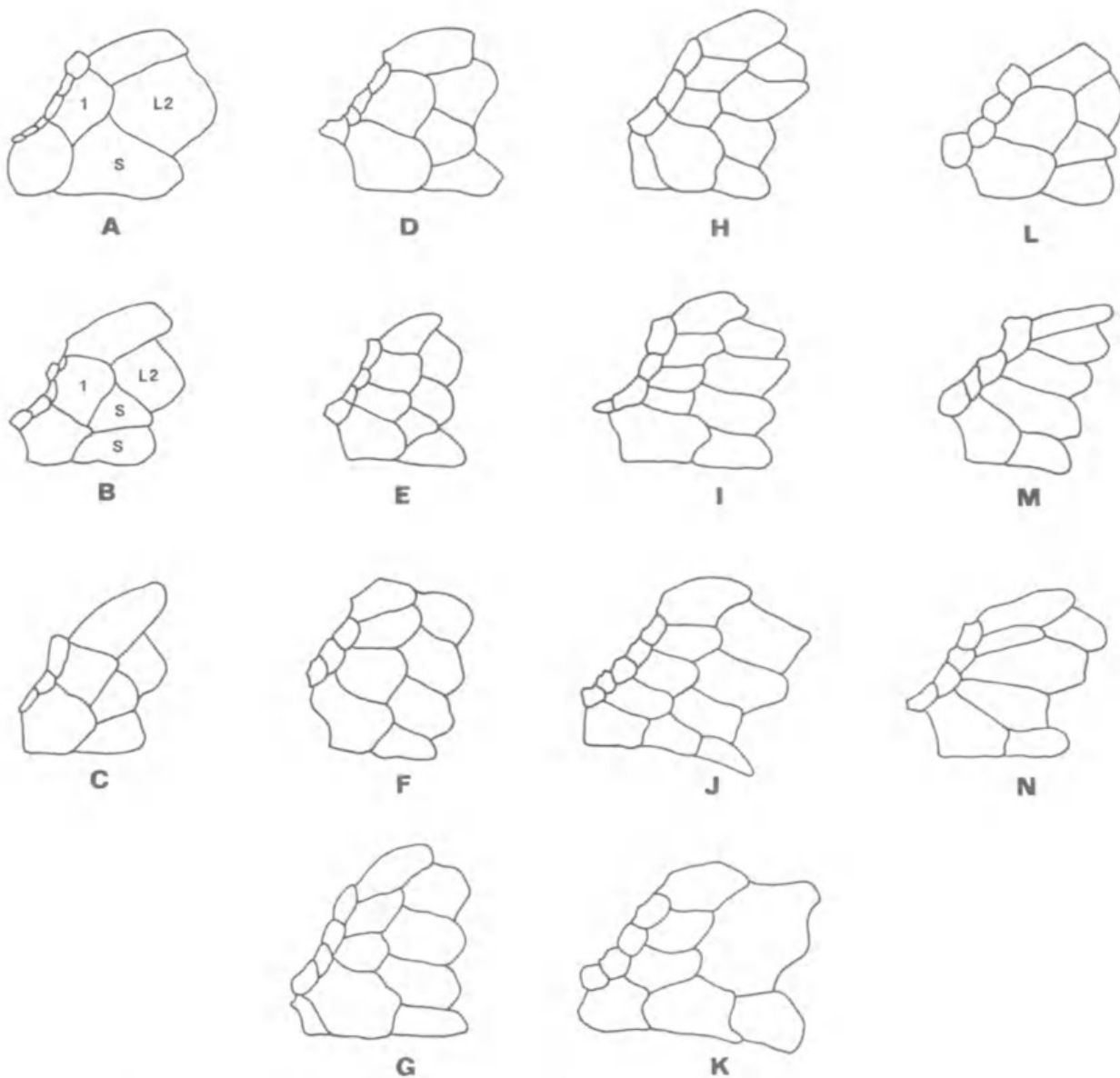


FIG. 6. Scales of temporal region of A. *Egernia saxatilis* (AM R15273), B. *Cyclodomorphus casuarinae* (AM R107594), C. *C. branchialis* (AM R102728), D. *C. gerrardii* (AM R47341), E. *C. gerrardii* (AM R47876), F. *Tiliqua multifasciata* (AM R10080), G. *T. occipitalis* (AM R123943), H. *T. nigrolutea* (AM R28494), I. *T. nigrolutea* (AM R106903), J. *T. rugosa* (AM R105622), K. *T. rugosa* (AM R102594), L. *T. adalaidensis* (Naturhistorisches Museum Vienna 20472.2), M. *T. scincoides* (AM R123927), N. *T. gigas* (Naturhistorisches Museum Basel 6218). 1 = primary temporal; L2 = lower secondary temporal; S = last supralabial.

and modes of six or fewer derived. *Cyclodomorphus*, *Hemisphaeriodon*, *T. gigas* and *T. scincoides* usually have six supraciliaries while other *Tiliqua* and *Trachydosaurus* usually have five or fewer supraciliaries (Fig. 7).

12. Tongue colour. Although this character has been relatively little studied in skinks, most Australian lygosomines I have examined in life (including 14 species of *Egernia*) have pink to

light grey tongues. *Corucia* also has a pink tongue. Consequently, I believe that a pink or only lightly melanised tongue is primitive and the dark blue-black to bright blue tongues of *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* are derived. Although *Hemisphaeriodon* variably has a pink or blue tongue as an adult, the tongue is dark blue-black in juveniles. Tongue colour in life is not known

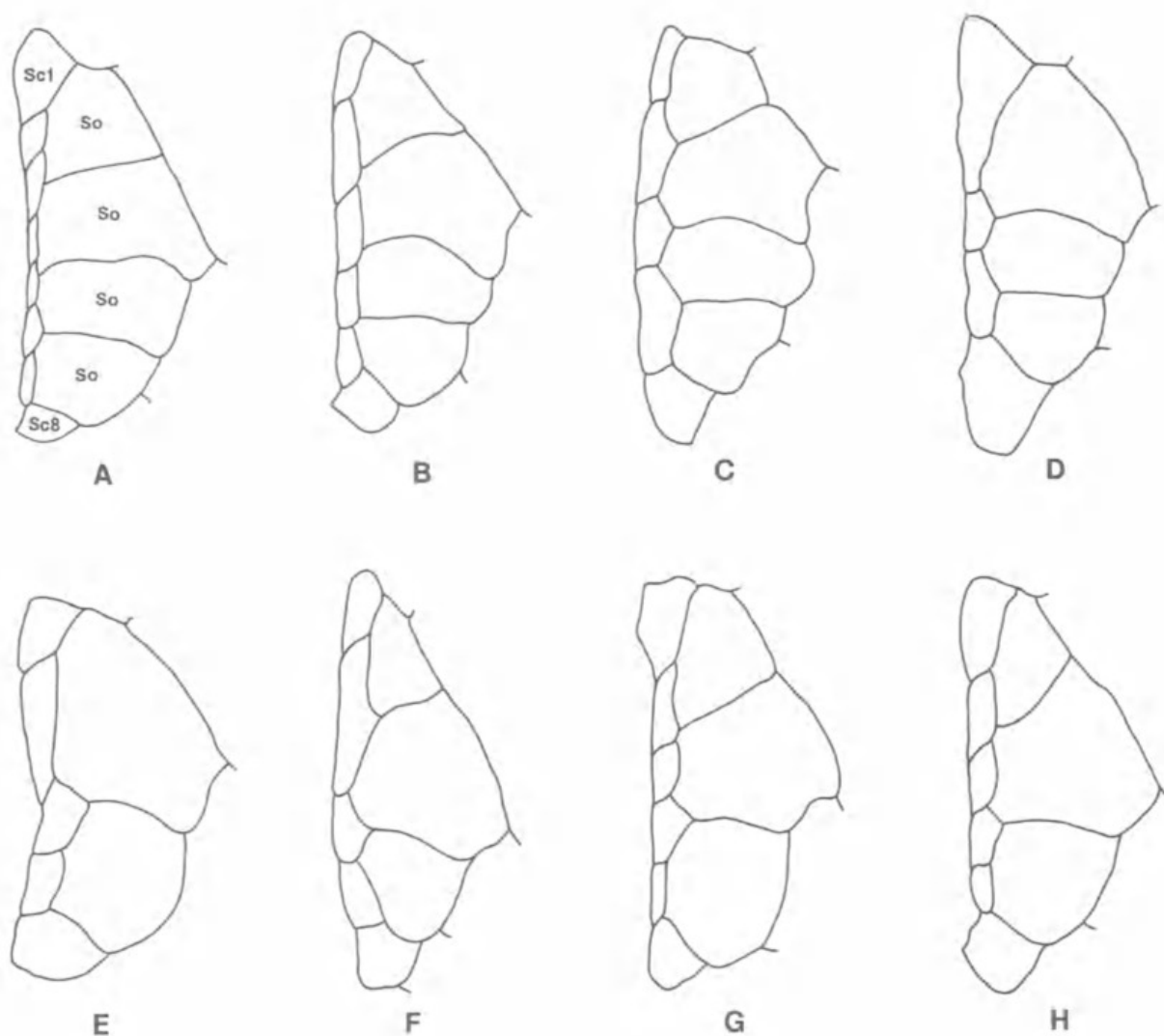


FIG. 7. Supraocular and supraciliary scales of A. *Egernia whitii* (AM R125299), B. *Tiliqua scincoides* (AM R123923), C. *T. nigrolutea* (AM R111500), D. *T. rugosa* (AM R102594), E. *T. multifasciata* (AM R10080), F. *T. adalaidensis* (South Australian Museum (SAM) R2227), G. *Cyclodomorphus gerrardii* (AM R50219), H. *C. casuarinae* (AM R112395). Sc1 = first supraciliary; Sc8 = eighth (last) supraciliary; So = supraoculars.

for *T. adalaidensis*, although long-preserved material shows no pigmentation on the tongue.

13. Colour pattern. Broad patterns of dorsal and lateral coloration have been frequently used in skink systematics at the generic level (Greer, 1970b, 1974, 1979b). The majority of taxa within the outgroups, including most *Eumeces*, *Mabuya* and *Egernia* species, show strong indications of a longitudinally striped pattern dorsally and laterally, generally with some or all of the following elements: continuous dark dorsal stripes, longitudinally aligned dark dorsal streaks, a broad dark upper lateral stripe and a pale midlateral stripe. In contrast, strongly

banded colour patterns are uncommon in all outgroups (Greer, 1970b, 1979b). A dominance of longitudinal elements of pattern is considered primitive, and strongly banded patterns derived. Most *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* have a dorsal and lateral body and tail pattern of strongly contrasting light and dark bands. Two species (*T. nigrolutea*, some *Trachydosaurus*) have the transverse elements obscured by expansion of the dark-pigmented areas, while *T. adalaidensis* has a back pattern of broken narrow dark vermiculations on a light background. *Cyclodomorphus* species have either narrow alternating light and dark bands

(most *C. casuarinae*) or a pattern of dark and light spots (*C. branchialis*, *C. maximus*), which in all species are most prominent in juveniles. However, even in *Cyclodomorphus* and *T. adelaidensis*, the dark markings are transversely aligned rather than longitudinal, and I believe that the pattern in these cases is most simply explained as a secondary reduction of the broad-banded motif.

14. Subocular scale row. The presence of a complete row of enlarged subocular scales, separating the lower eyelid from the supralabials, has variously been considered primitive (Fuhn, 1969; Greer and Cogger, 1985) or derived (Greer, 1982; Sadler, 1987). In attempting to survey this character, I have experienced occasional difficulties in differentiating subocular scales from enlarged granules on the ventral margin of the lower eyelid. In these instances, I have defined a complete subocular scale row as existing only when fewer than three moderate to large scales border the subocular supralabial between presubocular and postsubocular series. Within *Egernia*, a complete subocular row is present only in the *E. luctuosa* species group, *E. major*, *E. rugosa* and a few members of the *E. whitii* species group. In the second and third outgroups, a complete subocular row is consistently present in 16 genera or species groups, variably present in four (and then only in a few species), and absent in 39 genera or species groups. Most *Eumeces* and *Mabuya* species have an incomplete subocular row. The incomplete subocular scale row seen in *Cyclodomorphus* and *Hemisphaeriodon* is primitive and the complete, even subocular row, with 0-1 scales interposed between presubocular and postsubocular series, seen in *Tiliqua* and *Trachydosaurus* (Fig. 8) is derived.

15. Nuchal scales. In general, (transversely enlarged nuchal scales exhibit three patterns in skinks: absent (i.e., scales bordering the caudal margin of parietals not noticeably wider than succeeding scales, each scale overlapping three scales caudally), a single pair present (each nuchal overlapping four or more scales caudally), or a variable number of multiple pairs present (Fig. 9). The first condition is rare in the first three outgroups, and is considered derived. However, it is more difficult to determine the relative polarities of the other two conditions. In *Egernia*, a single pair of nuchals is characteristic of the *E. whitii* species group, while most other groups have multiple pairs of nuchal scales. Within the second outgroup, a single pair of

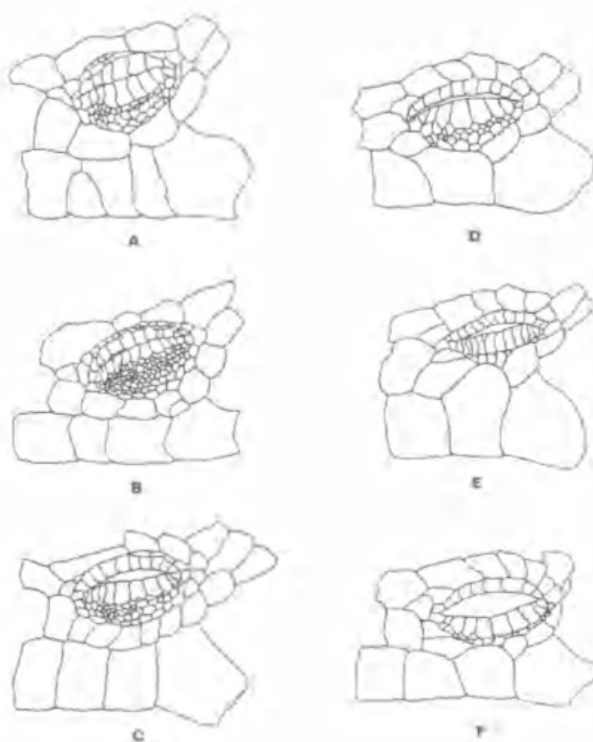


FIG. 8. Periorbital scalation of A. *T. nigrolutea* (AM R28494), B. *T. rugosa* (AM R102594), C. *T. multifasciata* (AM R123942), D. *C. branchialis* (AM R101805), E. *C. gerrardii* (AM R50219), F. *C. casuarinae* (AM R107594).

nuchals characterises most members of the *Eugongylus* group, *Mabuya*, *Macrosclincus* and *Dasia*, while multiple pairs of nuchals are characteristic of most members of the *Sphenomorphus* group and *Lamprolepis*. Within the third outgroup, *Eumeces*, *Scincus* and *Scincopus* have multiple pairs of nuchals, while *Janetaescincus* and *Pamelaescincus* lack nuchals. Because of the more widespread occurrence of multiple nuchals in *Egernia*, I am inclined to consider multiple nuchals primitive within the *Tiliqua* lineage. *Cyclodomorphus* and *Hemisphaeriodon* have multiple pairs of nuchals, while most *Tiliqua* and *Trachydosaurus* lack nuchals (Fig. 9). The exception, *T. adelaidensis*, has a variably expressed single pair of slightly enlarged nuchals generally separated by an internuchal.

16. Jugal bone. The dorsal process of the jugal is long and slender in all of the outgroups, generally much narrower than the adjoining jugal process of the maxilla, although in some *Egernia* species and a few other skinks the caudoventral angle bears a narrow spur to support the quadratojugal ligament. A narrow dorsal process, rounded in cross-section, as occurs in

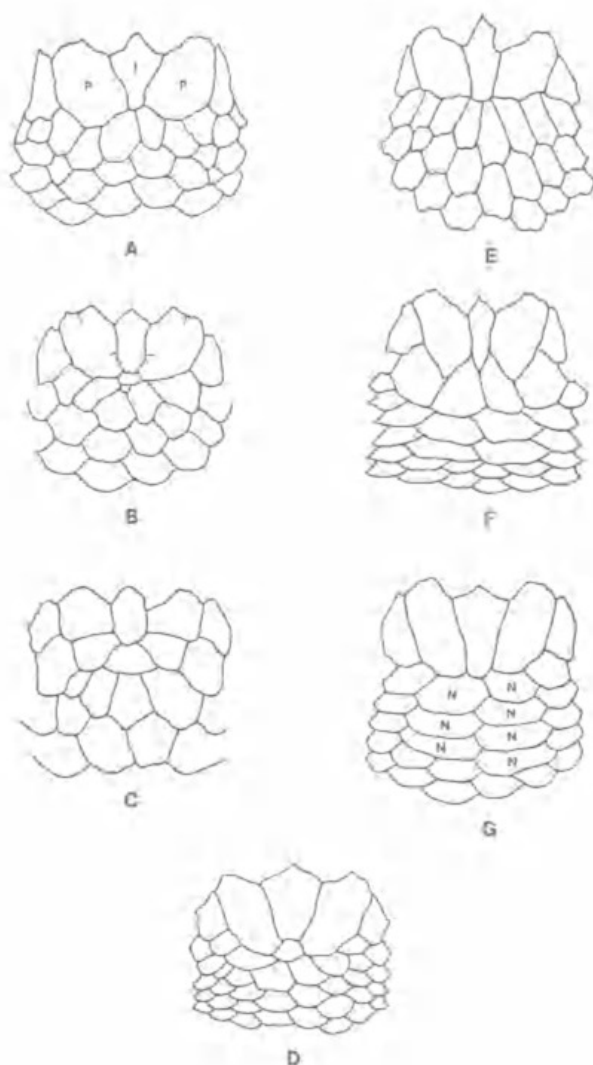


FIG. 9. Scales of nuchal region of A. *Tiliqua gigas* (United States National Museum 195733), B. *T. nigrolutea* (AM R111500), C. *T. rugosa* (AM R105622), D. *T. adelaidensis* (SAM R2227), E. *T. multifasciata* (AM R123942), F. *Cyclodomorphus gerrardii* (AM R47341), G. *C. casuarinae* (AM R112395). P = parietal; I = interparietal, N = nuchal.

Hemisphaeriodon and most *Cyclodomorphus*, is considered primitive. In *Tiliqua* and *Trachydosaurus*, the dorsal process is much more robust (Fig. 10), apparently largely due to expansion of its caudal free margin, producing a flattened cross-section. This expansion of the caudal margin is particularly evident at the dorsal and ventral extremities, which are expanded into two caudally-directed flanges. *C. branchialis* and *Hemisphaeriodon* show some trend in this direction, but in both the expansion

is less than in *Tiliqua* and *Trachydosaurus*, as is evidenced by the the lack of expansion of the caudoventral angle beyond the maxilla, and in *Hemisphaeriodon* by the rounded cross-section and the very narrow, straight dorsal extremity.

17. Rostral margin of frontal bone. In most skinks the frontal extends superficially a variable distance laterally along the nasals, forming lateral frontal processes between nasals, prefrontals and often the maxillae. These processes are consistently present, and usually long in the outgroups, and in *Tiliqua* and *Trachydosaurus*, although in *Eugongylus* they extend into the nasals rather than along their lateral border. In *Cyclodomorphus* and *Hemisphaeriodon* they are either completely absent, or when present in some individuals, short and less developed than the opposing caudomedial frontal processes of the maxillae. Consequently, I believe that the presence of superficial lateral rostral frontal processes, forming a W-shaped rostral frontal margin, is primitive, and their absence, replaced by caudomedial processes from the maxillae, and leaving a A-shaped frontal margin (Fig. 11), is derived.

18. Supraocular scales. Four supraoculars, the first two contacting the frontal, has been considered the primitive condition for skinks (Greer, 1974; Perret, 1975; Greer and Cogger, 1985). This configuration occurs in all *Egernia* species, and in at least some species in 46 of 51 genera and species groups in the second outgroup, although most *Mabuya* species have the first three supraoculars contacting the frontal. In the third outgroup, *Amphiglossus* (*Madascincus*), *Janetaescincus* and *Pamelaescincus* have four supraoculars (although fusion of frontoparietals and frontal makes it impossible to determine the pattern of frontal contact), *Scincus* and *Scincopus* have multiple supraoculars, and most *Eumeces* have four supraoculars with the first three contacting the frontal, although some species have the four-two configuration. The evidence suggests that the four-two configuration is primitive for lygosomines at least, and reduction either in total number or number contacting the frontal is derived. In *Tiliqua*, *T. gigas*, *T. nigrolutea* and *T. scincoides* usually have the primitive condition, while *T. multifasciata*, *T. occipitalis* and *T. rugosa* usually have the first and second supraoculars fused, leaving only a single supraocular contacting the frontal. *T. adelaidensis*, *Cyclodomorphus* and *Hemisphaeriodon* have only three supraoculars, but two contacting the frontal (Fig. 7). On the basis

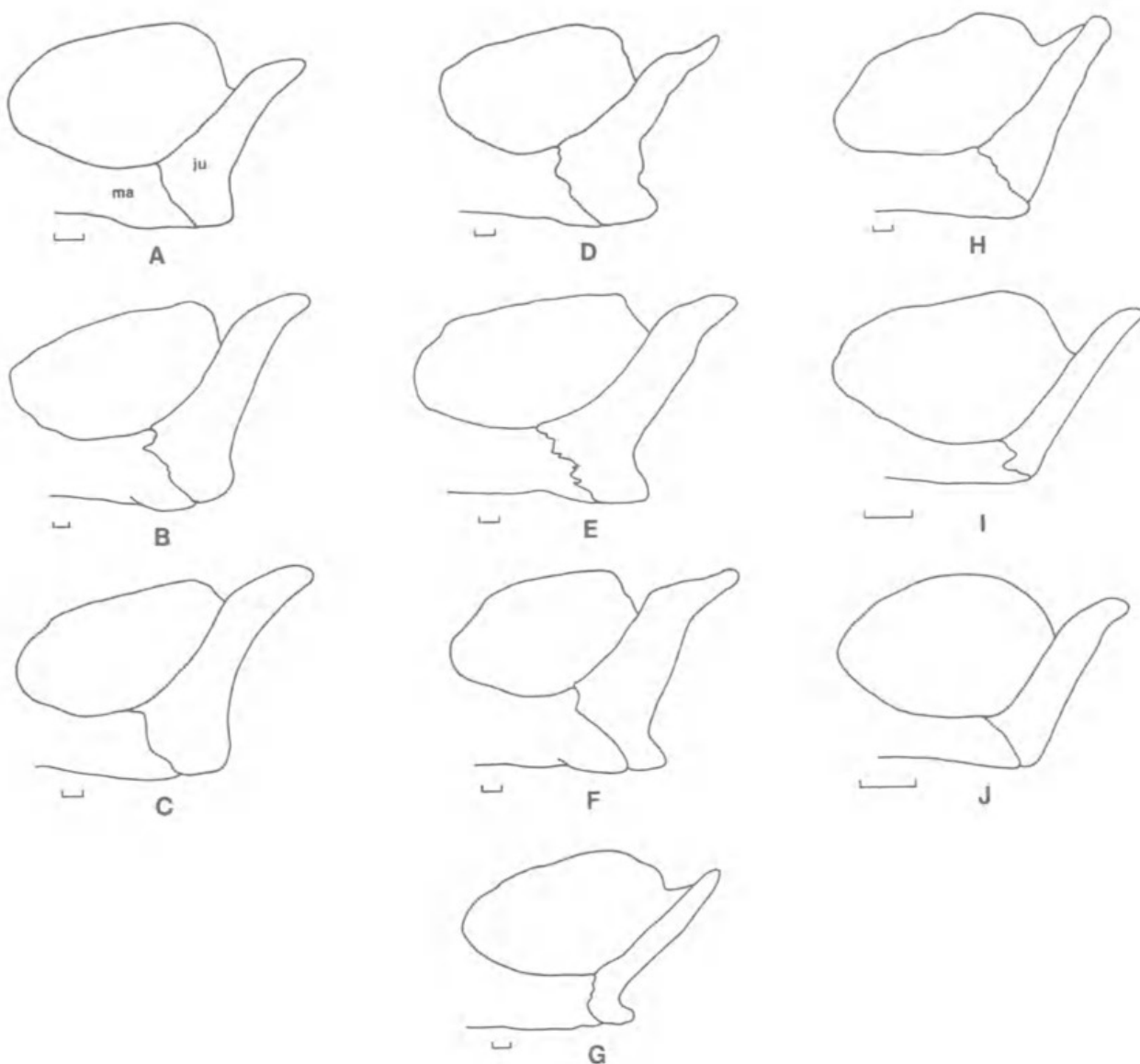


FIG. 10. Lateral view of jugal of A. *Tiliqua scincoides* (AM R127904; SVL = 95mm), B. *T. gigas* (AM R93222), C. *T. rugosa* (WAM R13162), D. *T. nigrolutea* (AM R127909), E. *T. occipitalis* (AM R127925), F. *T. multifasciata* (AM R100984), G. *Egernia cunninghami* (AM R66018), H. *Cyclodomorphus gerrardii* (AM R13084), I. *C. casuarinae* (AM R37706), J. *C. branchialis* (AM R127930). Ju = jugal; Ma = maxilla. Scale bar = 1mm.

of the supraciliary contact pattern, it appears that the second and third supraoculars have fused in these taxa. However, in that *T. adelaidensis* modally has only five supraciliaries, like most *Tiliqua*, while *Cyclodomorphus* and *Hemiphaeriodon* have the more primitive six, I believe that fusion of the second and third supraoculars has occurred independently in this species.

19. Ear lobules. Most generally primitive skinks have a moderate to large external ear, with

several rounded to acute lobules along the rostral margin (Perret, 1975; Greer, 1982), although lobules are generally lacking in those taxa which have a greatly reduced external ear. Of those taxa which have a moderate to large ear, several moderate to large lobules are present in all *Egernia* species and consistently present in half (24 of 48) of the genera and species groups in the second outgroup (including *Corucia*, most *Mabuya*, and most members of the *Eugongylus* group). In the third outgroup, ear lobules are

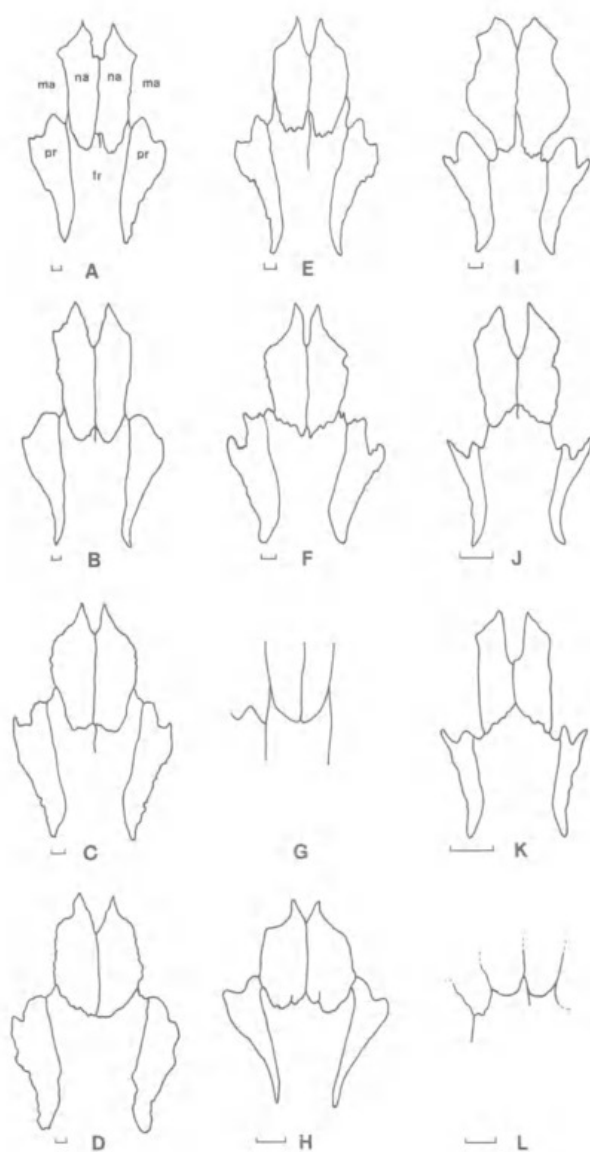


FIG. 11. Dorsal view of fronto-nasal region of skulls of A. *Tiliqua scincoides* (AM R127901), B. *T. gigas* (AM R93222), C. *T. nigrolutea* (AM R127911), D. *T. rugosa* (AM R127916), E. *T. occipitalis* (AM R127925), F. *T. multifasciata* (AM R100984), G. *T. adelaidensis* (SAM R4307A), H. *Egernia striata* (WAM R25402), I. *Cyclodomorphus gerrardii* (AM R13084), J. *C. casuarinae* (AM R37706), K. *C. branchialis* (AM R127930), L. *C. maximus* (WAM R77042). Fr = frontal; ma = maxilla; na = nasal; pr = prefrontal. Scale bar = 1mm.

generally present in *Eumeces* and *Scincopus*, but absent in *Janetaescincus* and *Pamelaescincus*. Although the evidence is not conclusive, the condition shown by *Egernia*, *Corucia*, *Mabuya* and *Eumeces*, several moderate to large lobules

along the rostral margin of the ear, is considered primitive, and the 0-2 small rounded lobules seen in *Cyclodomorphus*, *Hemisphaeriodon* and *T. adelaidensis*, derived. It is difficult to assess the condition of the rostral margin of the ear in *Trachydosaurus*, as the scales are thick and bony, and evenly grade into smaller bony scales deep within the external auditory meatus, but these thickened bony scales may be derived from the lobules of other *Tiliqua* species.

THE *TILIQUA* LINEAGE

The species variously assigned to *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* share the derived condition in characters 1-13, and constitute a lineage, which may be defined as follows:

Osteology: Prefrontal and postfrontal narrowly separated or in contact; jugal and squamosal in contact; lacrimal absent; medial palatine process of ectopterygoid strong, broadly contacting palatine; coronoid process of dentary laterally overlapping coronoid; single grossly enlarged tooth in maxilla (position 7 or 8) and dentary (position 10) in juveniles; presacral vertebrae 32-44; phalangeal formulae of manus and pes 2.3.4.4.3/2.3.4.4.3 or fewer.

Scalation: Caudalmost supralabial divided into an upper and a lower scale; supraciliaries modally six or fewer.

Coloration: tongue deeply pigmented, at least in juveniles, blue- black to bright blue; dorsal and lateral pattern on body and tail predominantly consists of narrow to broad bands or transversely aligned vermiculations or spots, at least in juveniles.

THE HOLOPHYLY AND RELATIONSHIPS OF THE *TILIQUA* LINEAGE

There seems little doubt that the *Tiliqua* lineage is holophyletic. Two characters seem particularly telling in this regard: the increase in number of presacral vertebrae and the pattern of phalangeal loss. Within the *Egernia* group, these characters readily separate the *Tiliqua* lineage from both *Egernia* and *Corucia*, with no evidence of intermediacy. The *Egernia luctuosa* species group is clearly not a member of the *Tiliqua* lineage on both characters, having the primitive number of presacral vertebrae and phalanges.

No skinks currently outside of the *Egernia*

group appear to be members of the *Tiliqua* lineage or likely close relatives. The cluster of genera closest to the *Egernia* group, the *Eugongylus* group, rarely show marked increases in number of presacral vertebrae or phalangeal loss, apart from the loss of the first finger in *Carlia*, *Lygisaurus*, *Menetia*, *Ristella* and *Saproscincus tetradactyla* (Greer, 1974, 1979a; pers. obs.), a derived state that does not occur within the *Egernia* group. The only two exceptions to this pattern are *Graciliscincus*, which has a similar number of presacral vertebrae to the *Tiliqua* lineage while still retaining the primitive phalangeal configuration, and *Nannoscincus*, in which there is a mosaic of taxa with elevated numbers of presacral vertebrae and phalangeal loss (Sadler, 1987, pers. comm.), including the combination seen in the *Tiliqua* lineage. However, it is apparent that this similarity between *Nannoscincus* and the *Tiliqua* lineage is due to convergence, as *Nannoscincus* is both monophyletic and clearly a member of the *Eugongylus* group rather than the *Egernia* group (Greer, 1974; Sadler, 1987), and otherwise shows little resemblance to *Tiliqua*.

Although *Egernia* has been shown to be the genetically closest genus to the *Tiliqua* lineage (Hutchinson, 1981), the nature of the relationship has not previously been determined. Three types of relationship are possible: *Egernia* and the *Tiliqua* lineage are sister-groups; *Egernia* is primitive, possibly ancestral to the *Tiliqua* lineage, or the *Tiliqua* lineage is primitive, possibly ancestral to *Egernia*. The latter hypothesis was favoured by Horton (1972). At first glance, the third hypothesis seems untenable, given the above argument for the holophyly of the *Tiliqua* lineage. However, given the high frequency of parallel evolution and character reversal within the Scincidae, if the third alternative were the case, use of *Egernia* as the primary outgroup would be inappropriate, potentially assigning erroneous character polarities. This is worrying, when it is remembered that in almost all characters used to define the *Tiliqua* lineage, either *Egernia* uniformly shows the 'primitive' condition, or only a few *Egernia* species show the 'derived' condition. However, exclusion of the first outgroup does not reverse the inferred polarity of any character, and hence confirms the highly derived nature of the *Tiliqua* lineage.

In contrast, I have been unable to identify any synapomorphies with which to diagnose *Egernia* vis-à-vis the *Tiliqua* lineage. Previous diagnoses

have also failed to demonstrate a sister-group relationship between the two groups. The modern concept of *Egernia* is derived from Boulenger (1887), who placed in one genus a range of species formerly spread over at least five genera. Boulenger's diagnosis utilises only two derived characters compared to generally primitive lygosomine skinks: pterygoid teeth 'few or absent' and lack of supranasal scales. Although Hoffstetter (1949) also records pterygoid teeth in *Egernia*, I have been able to identify them only in one specimen of *E. cunningghami*. Both characters are shared with *Tiliqua*, and the second also with *Corucia*. At best, the second character merely supports the monophyly of the *Egernia* group, and the first the monophyly of *Egernia* + *Tiliqua*. Mitchell (1950), Cogger (1975) and Storr (1978) have subsequently attempted to diagnose *Egernia*. However, none of these diagnoses offer any additional synapomorphies for *Egernia*.

On present knowledge, therefore, the second hypothesis, that *Egernia* is primitive, possibly ancestral to the *Tiliqua* lineage, and potentially a paraphyletic assemblage, seems to be the most likely. Although there are arguments for not recognising paraphyletic taxa (recently discussed by Hutchinson and Maxson, 1987), the interrelationships of the recognisable lineages within *Egernia* remain obscure (Horton, 1972; Storr, 1978; Wells and Wellington, 1984, 1985; Shea, in prep.) and in the absence of firm evidence relating the *Tiliqua* lineage to any one of these other lineages, I prefer to retain the *Egernia* assemblage as a generic unit distinct from the *Tiliqua* lineage.

GENERA WITHIN THE *TILIQUA* LINEAGE

On the basis of characters 14-19, I believe that two sister-taxa can be recognised within the *Tiliqua* lineage. The first of these, comprising the species formerly placed in *Tiliqua* (s.s.) and *Trachydosaurus* and for which the name *Tiliqua* is available, may be diagnosed as follows:

Tiliqua Gray, 1825

Tiliqua Gray, 1825: 201. Type species *Lacerta scincoides* Shaw, 1790, by subsequent designation (Cogger et al., 1983).

Trachydosaurus Gray, 1825: 201. Type species, by monotypy, *Trachydosaurus rugosus* Gray, 1825.

Trachysaurus Gray, 1827: 430. Unjustified emendation pro. *Trachydosaurus*.

Cyclodus Wagler, 1828: pl. 6. Type species, by monotypy, *Cyclodus flavigularis* Wagler, 1828 [= *T. gigas*].

Brachydactylus Smith, 1834: 144. Type species, by monotypy, *Brachydactylus typicus* Smith, 1834 [= *T. rugosa*].

Tiliqua Duméril, 1837: 16. Lapsus pro. *Tiliqua*.

Keneaux Duméril, 1837: 16. Nomen nudum. Originally proposed without included species, ex Cocteau MS.

Tachydosaurus Gray, 1838: 288. Lapsus pro. *Trachydosaurus*.

DIAGNOSIS

Moderate to very large skinks, with a complete subocular row of evenly enlarged scales separating supralabials from lower eyelid, nuchals either a single variably expressed pair or absent, and a broad, winglike jugal.

CONTENT

Cyclodus adelaidensis Peters, 1864, *Scincus gigas* Boddaert, 1783, *Tiliqua occipitalis multifasciata* Sternfeld, 1919, *Scincus nigroluteus* Quoy and Gaimard, 1824, *Cyclodus occipitalis* Peters, 1864, *Trachydosaurus rugosus* Gray, 1825, *Lacerta scincoides* Shaw, 1790. See Boulenger (1887) and Cogger et al. (1983) for species synonymies.

NOMENCLATURE

Although *Tiliqua* and *Trachydosaurus* were both erected by Gray (1825), Mitchell (1950), acting as first reviser in the sense of Article 24(b) of the Code of Zoological Nomenclature, selected *Tiliqua* to have precedence over *Trachydosaurus*.

The second taxon, comprising the species variably placed in *Omolepida*, *Cyclodomorphus* and *Hemisphaeriodon*, for which *Cyclodomorphus* is the earliest available name, may be diagnosed as:

***Cyclodomorphus* Fitzinger, 1843.**

Cyclodomorphus Fitzinger, 1843: 23. Type species, by original designation, *Cyclodus casuarinae* Duméril and Bibron, 1839.

Omolepida Gray, 1845: 71, 87. Type species, by monotypy, *Cyclodus casuarinae* Duméril and Bibron, 1839.

Hemisphaeriodon Peters, 1867: 24. Type species, by monotypy, *Hinulia gerrardii* Gray, 1845.

Homolepida Lütken, 1863: 294. Lapsus pro. *Omolepida*.

Omolepidota Frost and Lucas, 1894: 227. Lapsus pro. *Omolepida*.

DIAGNOSIS

Small to moderately large skinks lacking lateral rostral projections of frontal bone, or with them very reduced, leaving a Λ -shaped frontal margin; second and third supraoculars fused, leaving only three supraoculars, first two contacting the frontal; lobules along rostral margin of ear very reduced (both in size and number) or absent.

CONTENT

Hinulia branchialis Günther, 1867, *Cyclodus casuarinae* Duméril and Bibron, 1839, *Hinulia gerrardii* Gray, 1845, *Omolepida maxima* Storr, 1976. See Cogger et al. (1983) for species synonymies.

NOMENCLATURE

Although *Cyclodomorphus*, a senior objective synonym of *Omolepida*, has been formally used only six times in the 145 years since its erection (Fitzinger, 1860; Wells and Wellington, 1984, 1985; Shea and Wells, 1985; Czechura, 1986; Shea, 1988), while *Omolepida* (or its emendation *Homolepida*) has been frequently used as an available generic or subgeneric name over the same period, I do not believe that recognition of the priority of *Cyclodomorphus* over *Omolepida* disturbs stability or causes confusion (Articles 23(b) and 79(c) of the Code). Mitchell (1950), Hutchinson (1981) and Cogger (1983), while placing both names into the synonymy of *Tiliqua*, clearly recognised the priority of *Cyclodomorphus*. In the previous fifty years, *Omolepida* has been formally used only once in combination with the type species (Storr, 1976), although frequently used as the generic name for the *C. branchialis* complex and *C. maximus* in Western Australia. Use of *Cyclodomorphus* here recognises the rather different concept of the genus I have proposed, and clearly distinguishes this version from that to which the name *Omolepida* had formerly been applied.

Romer (1956) and Cogger et al. (1983) list three additional names in the synonymy of *Tiliqua* and *Trachydosaurus*: *Rachites*, *Homolepides* and *Silubolepis*. All are apparently derived from an unpublished manuscript, *Tabulae synopticae Scincoideorum*, by J.-T. Cocteau, submitted to the Académie des Sciences in Paris,

and described by Duméril (1837). All three names appear to be unavailable. *Rachites* was published without any included species or description (Duméril, 1837; Duméril and Bibron, 1839: 523). There appears to be no justification for associating *Rachites* with *Tiliqua* other than the inclusion of both, along with *Euprepis* Wagler, 1830, *Keneaux*, *Psammistes*, *Heremites* and *Arne* (the latter four similarly nomina nuda) as subgenera of the vernacular *Sclérobépharides* by Duméril (1837). *Keneaux* Duméril, 1837 was subsequently associated with *Tiliqua* by the inclusion of two of Cocteau's vernacular names, *Keneaux de l'Uranie* and *Keneaux de Boddaert*, in the synonymy of *Cyclodus nigroluteus* and *C. boddaertii* (Duméril and Bibron, 1839). *Homolepides* Agassiz, 1846 was based, again without included species, on Cocteau's vernacular *Omolépidés*. There is no indication provided by Duméril (1837) as to the status assigned to this name, other than that it was six divisions below a tribe and, in turn, three divisions above *Tiliqua*. Consequently, there appears to be no basis for associating *Homolepides* with the *Tiliqua* lineage. *Siluholepis* Duméril and Bibron, 1839, a name assigned to Cocteau, appears only in the synonymy of *Trachysaurus*, and is not therefore available (Article 11(c)).

An alternative classification reflecting the same relationships as defined here would be to recognise *Tiliqua* and *Cyclodomorphus* as subgenera within an expanded *Tiliqua*. This would emphasise the sister-group relationship between the two taxa. However, I prefer generic separation for three reasons. Firstly the larger *Tiliqua* are frequently used as experimental subjects in comparative physiological and biochemical research. Generic separation simplifies a nomenclature frequently used by non-taxonomists. Secondly, with the generic status of *Egernia* still undetermined, generic status adds two well-defined monophyletic groups to an *Egernia* group otherwise having *Corucia* as its only other definable genus. Finally, the two genera are also ecologically distinct. With the exception of *T. adalaidensis*, a small, probably extinct species of largely unknown habits (Ehmann, 1983), *Tiliqua* comprises large, mostly diurnally active species that forage widely in largely open habitats, while *Cyclodomorphus* species are mostly of small to moderate size and secretive habits in generally 'closed' habitats and microhabitats, from closed forest (*C. gerrardii*) to *Triodia* tussocks (*C. branchialis*).

PREVIOUS ARGUMENTS FOR THE SYNONYMY OF *CYCLODOMORPHUS* WITH *TILIQUA*

Arguments for the synonymy of *Cyclodomorphus* with *Tiliqua* are based on two lines of evidence: morphology (Duméril and Bibron, 1839; Duméril and Duméril, 1851; Strauch, 1866; Smith, 1937; Mitchell, 1950; Cogger, 1983) and immunology (Hutchinson, 1981).

Hutchinson (1981), using serum immunoelectrophoresis with a single *T. rugosa* antiserum, found little antigenic difference between *T. rugosa* and *T. scincoides*, a greater divergence between *T. rugosa* and *C. casuarinae*, and *C. gerrardii* the most divergent. Hence, he concluded, 'to separate *T. rugosa* or *T. casuarinae* [from *Tiliqua*], and not *T. gerrardii*, as has been suggested [by Storr, 1976], is quite inconsistent with the IEP results' (Hutchinson, 1981: 188). By comparison with *Egernia*, which showed greater intrageneric variation to *E. cunninghami* antiserum than occurred between *T. rugosa* and *C. gerrardii*, yet was still treated as a monophyletic unit, *Cyclodomorphus* was regarded as synonymous with *Tiliqua*.

However, as noted above, evidence for the monophyly of *Egernia* is wanting, and hence the comparison used by Hutchinson (1981) is invalid. The classification proposed here satisfies Hutchinson's other major criticism by separating both *C. gerrardii* and *C. casuarinae* from *Tiliqua*. Indeed, Hutchinson's criticism of Storr's (1976) concept of *Omolépida* is flawed. Although Storr did not specifically include *gerrardii* in *Omolépida* (perhaps due to lack of familiarity with the species), it possesses all of the diagnostic characters Storr proposed for the genus, and clearly should have been included.

Of the morphological arguments for the synonymy of *Cyclodomorphus* and *Tiliqua*, those of Duméril and Duméril (1851) and Strauch (1866) are not explicit, but appear to be largely based on a combination of overall phenetic similarity and the synapomorphy of enlarged, molariform teeth, while one of the two characters employed by Smith (1937), complete separation of the parietals by the interparietal, is a symplesiomorphy (Greer, 1979a) and hence of no use in inferring relationships. Most authors advocating synonymy on morphological grounds have recognised a basic division within *Tiliqua* (s.l.). Duméril and Bibron (1839) and Duméril and Duméril (1851) separated *C. casuarinae* from the two other *Cyclodus* species

then recognised in the first couplet of their keys, on the basis of lack of ear lobules. Strauch (1866) separated the subgenus *Omolepida* on the basis of lack of a postnarial groove. Smith (1937) and Mitchell (1950) separated *casuarinae* and the *branchialis* complex from other *Tiliqua* on the basis of a longer tail and incomplete subocular scale row. Using these criteria, *C. gerrardii* comes out with *C. casuarinae* (Mitchell, 1950). The generic separation advocated here does not contradict any of these proposed taxonomies, apart from the level at which the distinction is made.

Cogger (1983:8) introduced a more serious objection to the recognition of *Cyclodomorphus* by stating 'there is a continuum of character states linking the extreme expression of *Tiliqua* via *Hemisphaeriodon* with that of *Omolepida* (= *Cyclodomorphus*)'. I do not believe this to be the case. *Hemisphaeriodon* shows all of the synapomorphies used to diagnose *Cyclodomorphus* vis-à-vis *Tiliqua*, most notably the supraocular pattern and the shape of the suture between frontal, nasals, maxillae and prefrontals, and is plesiomorphic vis-à-vis *Tiliqua* in all diagnostic characters. Within *Cyclodomorphus*, *gerrardii* shares with *casuarinae* one synapomorphy unique within the *Tiliqua* lineage, loss of the postnarial groove, and another synapomorphy rare in other taxa, extreme reduction of the single ear lobule. A derived behavioural pattern also links the two species: tongue-flicking, used in both food location and defence (Shea, 1988, pers. obs.), in contrast to simple tongue protrusion in other species. Both species are primitive within the *Tiliqua* lineage in possessing a mode of eight premaxillary teeth (Greer, 1979a; Shea, pers. obs.). These characters in combination suggest to me that *C. casuarinae* and *C. gerrardii* are each other's closest relatives, and that any apparent phenetic similarity between *C. gerrardii* and *Tiliqua* is due to a position for *C. gerrardii* close to the basal stock of the lineage.

PREVIOUS ARGUMENTS FOR THE RECOGNITION OF *TRACHYDOSAUROS*

Trachydosaurus rugosus possesses all of the diagnostic characters listed above for *Tiliqua*, or further derivations from these, and is clearly a member of the *Tiliqua* (s.s.) radiation. *Trachydosaurus* has previously been differentiated from *Tiliqua* by only a few characters.

Gray (1825), in describing *Trachydosaurus*,

used two characters: thick, bony scales on head and body, and a short, depressed tail. Wagler (1830) added to these a difference in dentition: conical teeth in *Trachydosaurus* vs rounded, obtuse crowns in *Cyclodus*. These three characters were employed by all authors for over sixty years (Gray, 1827, 1831, 1838, 1845; Wiegmann, 1834; Duméril and Bibron, 1839; Duméril and Duméril, 1851; McCoy, 1885), although Peters (1864) noted that the teeth of *T. adalaidensis* had conical rather than rounded crowns. Boulenger (1887) recognised all three characters, and added a further two: the presence of an azygous occipital scale and mostly divided subdigital lamellae. Mitchell (1950), in synonymising *Trachydosaurus* with *Tiliqua*, considered only the difference in tail morphology to be of potential value for generic separation, stating 'the general scalation, dentition and osteology are identical with those typifying *Tiliqua*' (Mitchell, 1950: 277). The tail shape he dismissed as a character by using as a parallel the placement of the similarly short-tailed *depressa* and *stokesii* in *Egernia*. However, as noted above, this argument is invalid, as *Egernia* is plesiomorphic and may only be an assemblage. Copland (1953: xxi) wished to retain *Trachydosaurus* 'if only on the grounds of its gross scalation'. Mertens (1958) resurrected *Trachydosaurus* in describing the insular race *T. r. konowi*, but reserved his reasons for publication in a report on his 1957 Australian expedition. This appears not to have been published. Glauert (1960) used the blunt tail as a diagnosis for *Trachydosaurus*, while Worrell (1963) used both the tail and the rugose scalation. Cogger (1975) noted the short tail, rugose scalation, and mostly divided subdigital lamellae. Cogger (1983: 8) justified his continued recognition of *Trachydosaurus*, stating 'I believe ... that the available morphological, biological and geographic evidence suggests that the shingle-back/blue-tongue divergence was earlier than, rather than approximately contemporaneous with, the radiation of the blue-tongued lizards in Australia', apparently hypothesising a sister-group relationship with *Tiliqua* (inclusive of *Cyclodomorphus*). However, no evidence was advanced in support of this hypothesis.

In summary, previous arguments for the recognition of *Trachydosaurus* have rested on five morphological characters: a short, blunt tail, thickened, rugose scalation, divided subdigital lamellae, conical teeth and an azygous occipital scale.

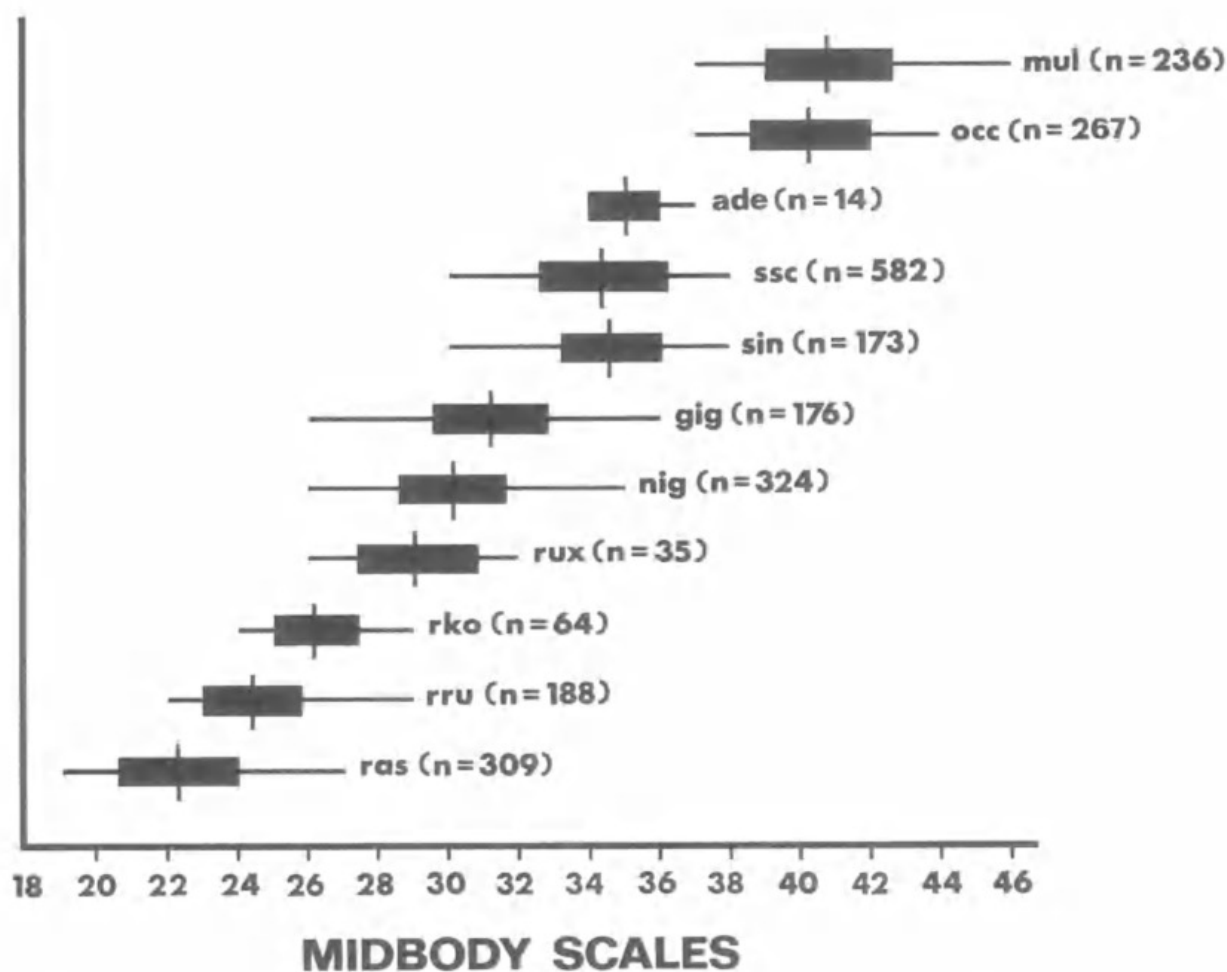


FIG. 12. Variation in number of midbody scales in *Tiliqua* species. Vertical bar is mean, solid rectangle is one standard deviation on each side of mean, horizontal line is range. Ade = *T. adelaidensis*, gig = *T. gigas*, mul = *T. multifasciata*, nig = *T. nigrolutea*, occ = *T. occipitalis*, ras = *T. rugosa asper*, rko = *T. r. konowi*, rru = *T. r. rugosa*, rux = *T. r. subsp. nov.*, sin = *T. scincoides intermedia*, ssc = *T. s. scincoides*.

The latter two characters are of no use in diagnosing *Trachydosaurus*, as they also occur in *Tiliqua* species. Within *Tiliqua*, there is marked interspecific and ontogenetic variation in tooth shape (Shea, pers obs.). Only *T. gigas* and *T. scincoides*, the first two described species, have the rounded tooth crowns noted by Wagler (1830). The other species have more conical crowns, those of *T. nigrolutea* being more conical than in *Trachydosaurus*.

The presence of a median occipital is variable in *Trachydosaurus*, although it is present in most individuals. A median scale caudal to the interparietal is a derived character in skinks (Greer, 1968), and has been previously used as a major diagnostic character in one genus, *Geomyersia*. However, the median occipital of *Trachydosaurus* also occurs in *T. adelaidensis* (Fig.

9D), and is frequently present in *T. nigrolutea*, occurring in 42.1% (n = 321) of specimens examined. Asymmetry in the scales bordering the caudal margin of the parietal/interparietal complex, a possible precursor to the differentiation of a median occipital, is common in other *Tiliqua* species.

Similarly, although the grossly enlarged, thickened osteoderms characteristic of *Trachydosaurus* are unique within the Scincidae, *T. nigrolutea* also displays a trend in this direction. Enlargement of body scales can also be expressed as a reduction in number of scales. If number of midbody scales, paravertebral scales and ventral scales are compared (Figs. 12-14), it can be seen that the values for *T. rugosa* overlap with *T. nigrolutea* in two cases (midbody and ventral scales) while *T. nigrolutea* also

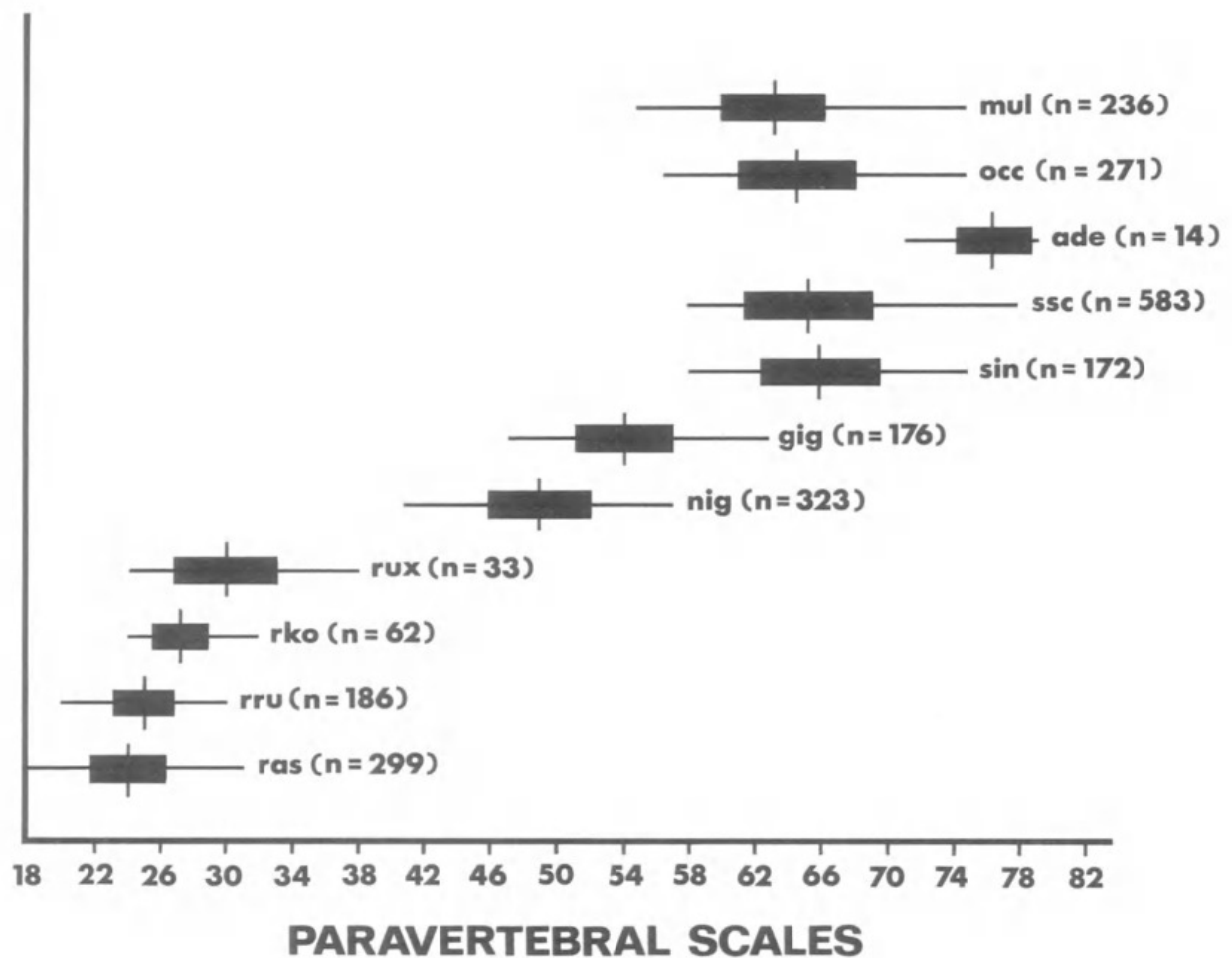


FIG. 13. Variation in number of paravertebral scales in *Tiliqua* species. Conventions as in Fig 12.

shows a trend towards *T. rugosa* in number of paravertebral scales.

The short, depressed, blunt-tipped tail of *Trachydosaurus* is also derived. However, there is geographic variation in tail length in *Trachydosaurus*, with the longest tails occurring in the south-west of Western Australia. Moreover, some Western Australian individuals have a distinctly conical tail tip (Fig. 15). *T. nigrolutea* again shows some trend in the direction of *Trachydosaurus*, having a short, thick tail which becomes depressed in emaciated individuals, in contrast to the compressed tail seen in *T. multifasciata* and *T. occipitalis*.

The division of subdigital lamellae seen in *Trachydosaurus* is uniquely derived within the *Egernia* group, with no trend in this direction, such as a median groove, seen in any other *Tiliqua* species.

A number of other differences between *T.*

rugosa and other *Tiliqua* (usually as represented by *T. scincoides*) have been noted in the course of more general comparative studies, though not previously utilised for formal taxonomic separation (Arnold, 1984; Camp, 1923; Cope, 1892b; Greer, 1979a; Hoffstetter, 1949; Lécure, 1968; Parker, 1868; Renous-Lécure, 1973; Siebenrock, 1892, 1895; Smith, 1976, 1982). I have re-examined all of these characters. In almost all cases, I find the purported differences to be less than diagnostic, either due to variation within *T. rugosa*, or *Tiliqua* species not previously examined having the condition reported for *T. rugosa*. Only in the further reduction of phalangeal formula (Siebenrock, 1895; Hoffstetter, 1949) is the difference clear-cut and consistent.

In summary, *T. rugosa* differs markedly and consistently from other *Tiliqua* species in having some subdigital lamellae divided and in further reduction in phalangeal formula. In two other

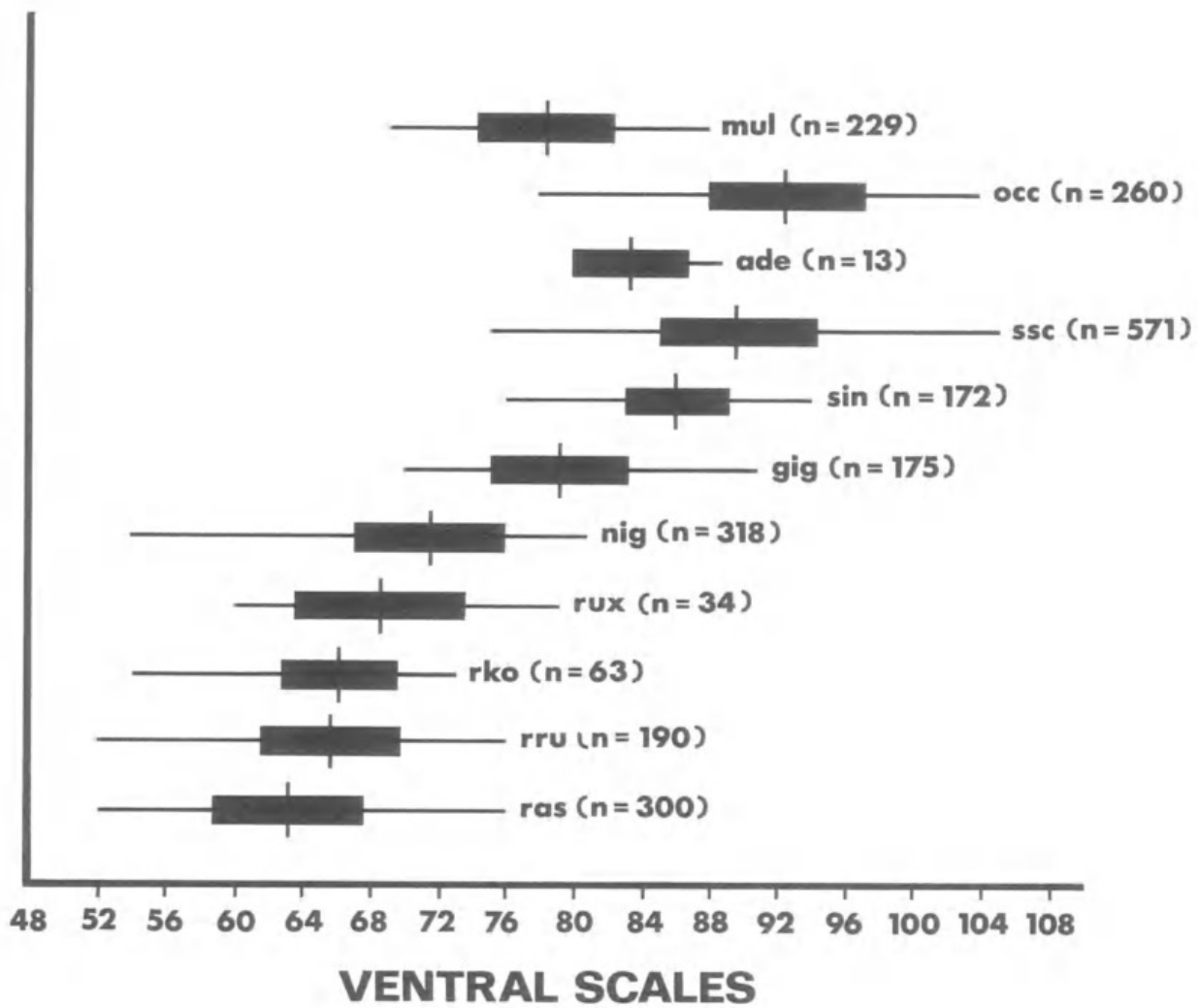


FIG. 14. Variation in number of ventral scales in *Tiliqua* species. Conventions as in Fig 12.

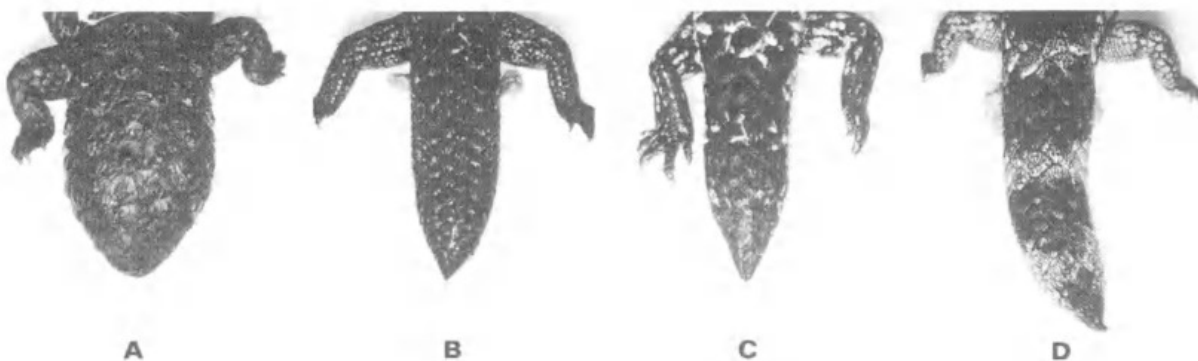


FIG. 15. Dorsal view of tails of A. *Tiliqua rugosa asper* (AM R123583), B. *T. rugosa* subsp. nov. (AM field series 15164), C. *T. rugosa* subsp. nov. (AM R102711), D. *T. r. rugosa* (AM R102594).

characters, tail shape and rugosity of body scalation, variation is largely non-overlapping with other *Tiliqua* species, although in both cases *T. nigrolutea* displays a trend in the direction of *T. rugosa*. In all of these characters, the state present in *T. rugosa* is derived. However, to generically separate *Trachydosaurus* on these characters would leave *Tiliqua* an undiagnosable entity vis-à-vis *Trachydosaurus*, as there are as yet no identifiable synapomorphies to link the remaining *Tiliqua* species independent of *T. rugosa*. On the available data, *T. rugosa* is merely a highly derived member of the genus, phenetically most similar to *T. nigrolutea*, and *Tiliqua* without *T. rugosa* is paraphyletic. Consequently, I retain *Trachydosaurus* in the synonymy of *Tiliqua*.

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