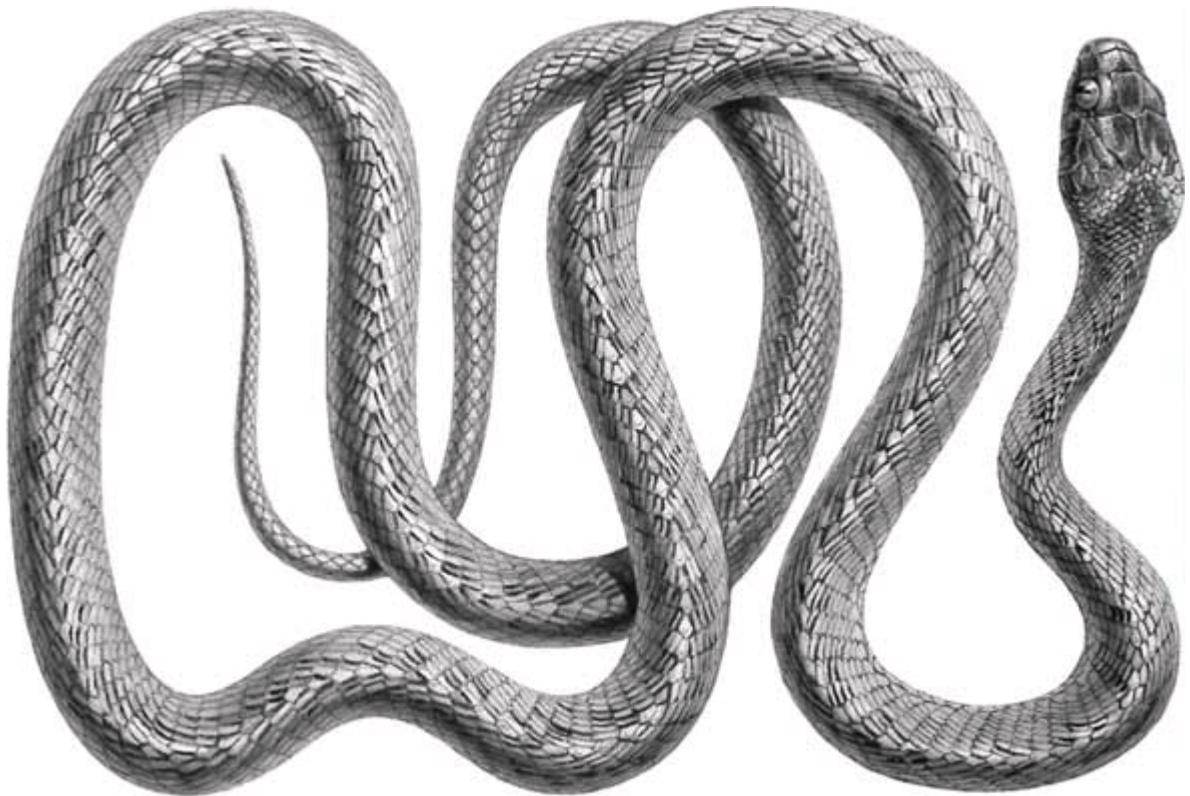


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## A CLADISTIC EVALUATION OF THE COSMOPOLITAN GENUS *Eumeces* WIEGMANN (REPTILIA, SQUAMATA, SCINCIDAE)

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A phylogenetic analysis of morphological characters shows that the scincid lizard genus *Eumeces* Wiegmann, 1834 is paraphyletic. East Asian and New World *Eumeces* form a clade referred to as the *Pariocela* section. A petition filed with the ICZN designates *Lacerta fasciata* Linnaeus 1758 as the type species of *Eumeces*, and, therefore, the *Pariocela* section retains the name *Eumeces*. Members of the *schneiderii* and *taeniolatus* species groups are more closely related to the genera *Scincopus* Peters and *Scincus* Laurenti than to other *Eumeces*. The *taeniolatus* species group is the sister group to the *schneiderii* species group plus *Scincopus* and *Scincus*, and requires generic status. *Eurylepis* Blyth, 1854 is the oldest available name for the *taeniolatus* group, and the *schneiderii* group is placed in a new genus. The three species of the Middle American *schwartzii* species group form a clade that cannot be associated with any other group of *Eumeces* and, therefore, they are also placed in a new genus.

**Key words:** *Eumeces*, *Eurylepis*, *Mesoscincus*, *Novoeumeces*, Scincidae, *Scincus*, *Scincopus*; Systematics.

The scincid genus *Eumeces* Wiegmann, 1834 is one of the most widely distributed squamate genera, occurring throughout much of the Holarctic region. The approximately 50 species display a considerable amount of morphological and ecological diversity. However, no known synapomorphies unite the species. *Eumeces* includes skinks that possess a scincine palate (Greer, 1970), a full complement of head scales, and lack structural reduction of limbs. Thus, the genus is defined by a combination of morphological character states that are plesiotypic for the Scincidae (e.g., Taylor, 1936).

At least one attempt has been made to split the genus *Eumeces*. Dunn (1933) placed two Central American species (*E. schwartzii* and *E. managuae*) and Southwest Asian *E. taeniolatus* in a separate genus, *Eurylepis* Blyth, 1854. However, this reclassification was rejected by Taylor (1936: 37), who doubted that *Eumeces* would ever be split up: “The

likelihood that further generic or subgeneric divisions of the genus will ever be considered for species now known is extremely remote.” Nevertheless, Arnold and Leviton (1977) suggested that the genera *Scincopus* Peters and *Scincus* Laurenti are descendants of *E. schneiderii*. Lieb (1985) followed Taylor’s (1936) classification in his review.

A re-evaluation of *Eumeces* is desired, not only to test the monophyly of the group, but also because members of the genus have been frequent subjects of numerous morphological, ecological and biogeographical studies. In order to develop strong hypotheses of evolutionary process, it is essential to differentiate among morphologies, behaviors, and other characteristics of taxa that are phylogenetically plesiotypic, and those characteristics that are novel and potentially have recent adaptive significance. The use of potentially paraphyletic taxa, such as *Eumeces*, in comparative studies may confuse rather than elucidate patterns of adaptation and historical biogeography.

Herein we phylogenetically analyze the major subgroups of *Eumeces*, as delineated by Lieb (1985), using relatively accessible anatomical characters. Because there is general anatomical and ecological similarity among the Old World forms of *Eumeces*, *Scincopus*, and *Scincus* are included in our ingroup. Notwithstanding, our ingroup might remain paraphyletic.

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Only a very extensive study including all scincid genera could address this problem.

## MATERIAL AND METHODS

### Ingroup

The ingroup consists of all species of *Eumeces* sensu Lieb (1985), plus the genera *Scincopus* and *Scincus*. Some species of *Eumeces* and *Scincus* were not available for examination, but their character states were obtainable from literature sources. We treated *Eumeces* as four operational groups, following the subgeneric classification of Lieb (1985). The *Pariocela* species group (39 species), in the *Pariocela* section, is widespread, ranging from North America to eastern Asia. The next three species groups comprise the *Eumeces* section. The *schneiderii* species group (5 species) occurs in northern Africa, Cyprus and southwestern Asia. The *taeniolatus* species group (2 species) is from Pakistan, Afghanistan and the bordering republics. Finally, the *schwarzei* species group (3 species) inhabits Central America. The four groups were a priori treated as being monophyletic, an assumption that would be supported by autapomorphies for those groups (representing synapomorphies among their component species). *Scincopus* is monotypic and includes only the species *S. fasciatus*. Autapomorphies include large head, large eyes with elliptical pupils, and nocturnal habit. The genus *Scincus* contains three species, *S. hemiprichii*, *S. mitranus*, and *S. scincus*. The latter species has several nominal subspecies, and has been considered to be a species complex by Arnold and Leviton (1977). Probable synapomorphies that support monophyly include a single premaxilla, spatulate rostrum with bony support, and extended auditory meatus (Arnold and Leviton, 1977).

After our initial analysis, specimens from other scincine and lygosomine genera were examined in order to determine distribution of character states (relative to the hypothetical ancestors within the cladogram). This was done to assess ingroup monophyly, and test the robustness of the relationships obtained. Specimens examined are listed in [Appendix](#).

### Outgroup

Because of the absence of knowledge about basal scincid phylogenetic relationships, and the possibility that *Eumeces* represents an assemblage of basal scin-

cid groups (Greer, 1970; Estes et al., 1988), no skink could be used in the outgroup. Estes et al. (1988) provided 11 synapomorphies for the family Scincidae. Two unambiguous synapomorphies for the Scincidae are compound osteoderms present both dorsally and ventrally (Camp, 1923), and serrated tongue scales (Schwenk, 1988). Nine characters are homoplastic with members of other families, but not in a congruent pattern. These include four cranial features, suturing of adjacent cervical centra and intercentra, loss of the quadrate process of the stapes, loss of femoral and preanal pores, presence of cycloid scales, and presence of the nucleus reticularis ventrolateralis of the spinal cord. Another, significant, but homoplastic, synapomorphy is the development of a secondary palate, consisting of medial extensions of the palatine bones, including the pterygoid bones in some groups (Greer, 1970). The Dibamidae, a small family consisting of specialized burrowing species, are the only other saurian group to develop a secondary palate. Rieppel (1984a) suggested that dibamids are most closely related to the scincid subfamily Acontinae, but they are usually placed with anguimorph groups (Estes et al., 1988).

According to Estes et al. (1988), the nearest outgroup taxon is the other major scincoid family, the Cordylidae, containing the Cordylinae plus the Gerrhosaurinae. Other authors (e.g., Camp, 1923) have placed cordylines with the Anguinae, and have suggested that the gerrhosaurines alone are the sister group of the scincids. However, Estes et al. (1988) argued strongly for cordylid monophyly, and for the purposes of this study, Cordylidae refers to both subfamilies. The next outgroup is the Lacertoidea, consisting of the Xantusiidae as the sister group to the Lacertidae plus the Teiioidea (Teiidae plus Gymnophthalmidae).

The genera included for outgroup comparison are listed in [Appendix](#), under [Cordylidae](#). Additional character state data were available in the text or figures of literature sources (Fitzsimons, 1943; Broadley, 1978; Brygoo and Böhme, 1985; Estes et al., 1988).

### Character Analysis

Characters were polarized using outgroup analysis (Watrout and Wheeler, 1981; Maddison et al., 1984). Among our 16 characters, 14 could be polarized unambiguously using cordylids as the outgroup. The two characters for which the states in the Cordy-

lidae are variable were coded as unknowns in the outgroup.

The data were heuristically evaluated using PAUP\* (ver. 4.0b1; Swofford, 1998). Heuristic searches involved keeping minimal length trees only, random stepwise addition, 50 repeats, and 20 equally parsimonious trees held for branch swapping. Branch swapping was performed using tree bisection-reconnection, steepest descent, and holding all most parsimonious trees (MPTs).

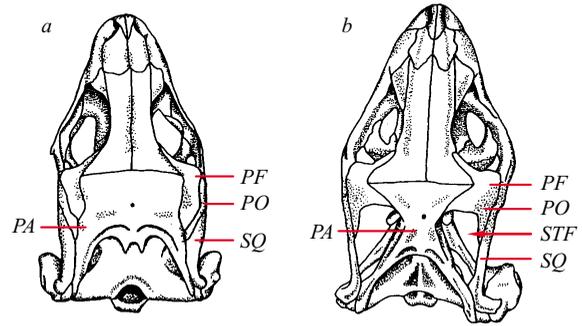
## RESULTS

### Character Analysis

A matrix of taxa and character states is given in Table 1. Terminology for osteology and myology follows Nash and Tanner (1970), and scalation terminology is based on Taylor (1936).

**1. General shape of Head.** State 0: The head is moderately flattened dorso-ventrally. The dorsal surface of the skull posterior to the rostrum is flat in lateral view, and in anterior view the head is significantly wider than high. State 1: The head is laterally compressed, especially anteriorly, and the dorsal surface is convex, producing a somewhat conical skull. In anterior view the head is higher than wide, or height and width are approximately equal.

**2. Parietal anatomy.** State 0: The portion of the parietal forming the skull roof is broad, and lacks deep, V-shaped lateral indentations. The lateral margins may have slight, irregular indentations, but are relatively straight, and subparallel in most individuals, diverging posteriorly (Fig. 1a). State 1: The parietal is constricted at its midpoint, contributing to a broad supratemporal fontanelle (Fig. 1b).



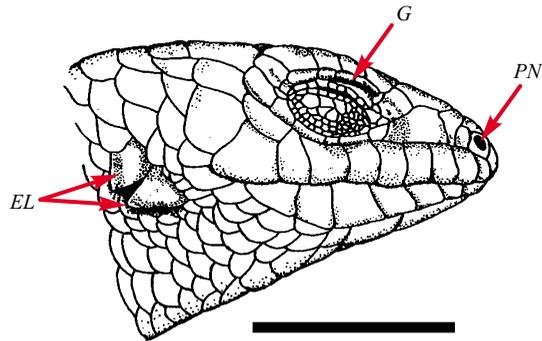
**Fig. 1.** Dorsal views of skulls of (a) *Eumeces obsoletus* (AMNH 68919), length = 24 mm (member of *Pariocela* section); (b) *Eumeces schneiderii* (AMNH 57864), length = 39 mm, showing morphology of the temporal region. PA) Parietal bone; PF) postfrontal bone; PO) postorbital bone; SQ) squamosal bone; STF) supratemporal fontanelle. Suture between postfrontal and postorbital not discernible in (b).

**3. Bones of supratemporal region.** State 0: The supratemporal region is extensively or fully covered by the postfrontal bones, plus the postorbital and squamosal bones (Fig. 1a). State 1: A broad supratemporal fontanelle occurs because the postfrontal and postorbital bones do not contact the parietal bone except anteriorly (Fig. 1b). In the cordylids, the supratemporal fontanelle is closed, although this is due mostly to the postorbital bone, rather than the postfrontal bone as above. Lacertids, the furthest outgroup, show closure by the postfrontal as in some skinks, but the xantusiids show closure by the postorbital, as in cordylids. The postfrontal is absent in xantusiids, which is recognized as a synapomorphy for that family (Estes et al., 1988). Thus, the tendency toward closure of the supratemporal fontanelle in the Cordylidae, plus the similarity of State 0 to the

**TABLE 1.** Character and State Matrix for Potentially Cladistically Informative Anatomical Data from the Skink Genus *Eumeces* Used to Estimate the Phylogenetic Relationships Among Groups of Species

Taxa	Character numbers														
	1	2	3	4	5	6	7	8	9	10	11	13	14	15	
<i>Eumeces</i>															
<i>Pariocela</i> section	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>schniderii</i> species group	1	1	1	1	1	0	0	1	1	1	1	1	1	0	0
<i>schwartzii</i> species group	0	1	1	1	0	0	1	1	1	1	2	0	0	0	0
<i>taeniolatus</i> species group	1	1	1	1	0	0	1	1	1	1	2	0	0	0	0
<i>Scincus</i>	1	1	1	1	1	1	0	1	1	2	1	1	1	1	1
<i>Scincopus</i>	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1
Outgroup	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0

**Note.** Synapomorphies supporting within group membership of species (group autapomorphies) are given in the text. The characters and states are described in the text.



**Fig. 2.** Lateral view of head of *Scincopus fasciatus* (MCZ 112193), showing: *EL* ear lobules; *PN* postnasal scale; *G* groove between upper palpebral and superciliary scales. Scale bar is 10 mm.

condition in the Lacertidae, State 0 is identified as being plesiomorphic within *Eumeces*. Effects of possible non-homology of the outgroup condition suggested by the different bones involved in closure are discussed below.

**4. Number of presacral vertebrae.** State 0: Relatively few (26 to 32) presacral vertebrae. State 1: 35 or more presacral vertebrae. Greer (1987) argued that 26 presacral vertebrae is the ancestral scincid condition, based on outgroup comparison with cordylids.

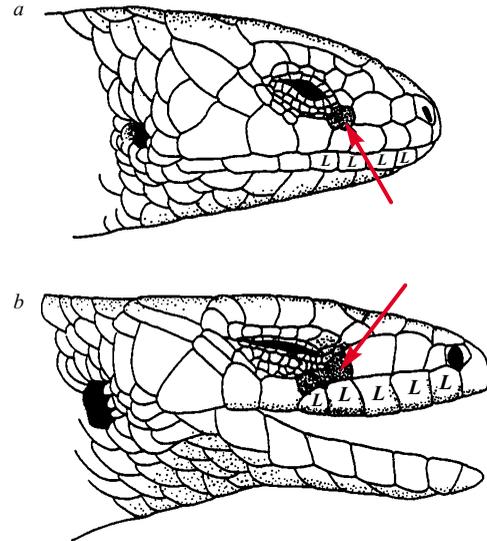
**5. Limb morphology.** State 0: Limbs slender, lamellae not expanded. State 1: Large, heavy limbs with robust pes, expanded lamellae on digits and phalanges. The outgroup is variable, with stout legs and loosely bound lamellae in *Cordylus*, and more slender limbs with unexpanded lamellae in others, so is coded as unknown.

**6. Tail length.** State 0: Relatively long, greater than snout-vent length. State 1: Short, approximately one-half snout-vent length.

**7. Postnasal scale present or absent.** State 0: Present (Fig. 2). State 1: Absent. This character is variable within the *Pariocela* Section, even within some species. It is coded as unknown for that group.

**8. Length of presubocular scale row.** State 0: Presubocular scale row short, the length of one labial scale, and consisting of one or two scales (Fig. 3a). State 1: Presubocular scale row longer, the length of two labial scales, and consisting of three scales (Fig. 3b). Cordylids have a short row consisting of a single scale, coded as State 0.

**9. Number of labial scales anterior to first subocular labial.** State 0: four labial scales in front



**Fig. 3.** Lateral views of heads of (a) *Eumeces copei* (ROM 10857), and (b) *Eumeces schwartzei* (ROM 10377), showing presubocular scales (arrows) and labial scales (*L*).

of first subocular (Fig. 3a); State 1: Five labial scales in front of first subocular labial (Fig. 3b). Outgroup genera have three or four.

**10. Ear lobule morphology.** State 0: Ear lobules small and not distinctly different from surrounding scales. State 1: Ear lobules enlarged, and heavier than surrounding scales; may cover much of ear opening. State 2: Two or three large, flap-like lobules, covering most of the ear opening (Fig. 2). Due to the unknown relationships of these states, this multistate character was evaluated as being unordered.

**11. Width and fusion of mid-dorsal scale rows.** State 0: Mid-dorsal rows not fused and approximately the same width as adjacent rows. State 1: Fusion of part or all of two median rows to produce a single row of enlarged scales. State 2: Mid-dorsal scale rows at least 1.5 times the breadth of adjacent rows. While it was clear that there is some relationship between fused and enlarged mid-dorsal scale rows, the relationship is not clear and this multistate character was evaluated as being unordered.

**12. Preanal scale row arrangement.** State 0: Medial preanal scales overlap adjacent lateral preanal scales. State 1: Medial preanal scales overlapped by lateral pair. Greer (1990) argued that if the Cordylidae (including Gerrhosaurinae) are the sister group to the scincids, then State 0 is primitive for the scincids, as it is typical of both cordylines and gerrhosaurines.

State 0 occurs in all ingroup members except the *Pariocela* section. A slightly different form of this state occurs in *Scincus*, in which the lateral preanal scales are quite small, and may protrude from the body adjacent to the medial preanals, rather than lie beneath them. However, the lateral preanals are situated on the distinctly keeled ventrolateral margins of the body, and scale orientation seems to be modified by their position. Because of this, *Scincus* is interpreted as showing a modification of State 0.

**13. Anterior palpebral scales.** State 0: In contact with superciliary scales. State 1: Separated from superciliary scales by a groove, which may be lined with small granular scales (Fig. 2).

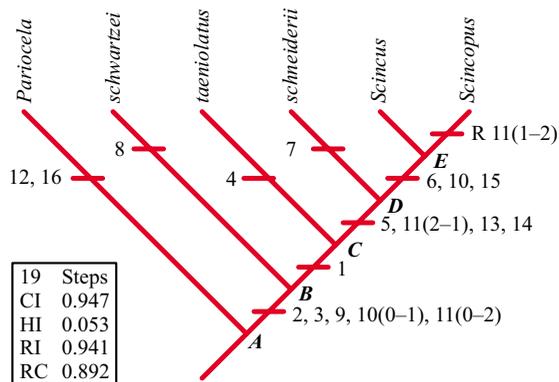
**14. Scale thickness.** State 0: Most taxa within the ingroup have thin, shiny scales separated by shallow sutures. State 1: In *Scincopus*, *Scincus*, and the *schneiderii* species group, the scales are heavy, dull, and separated by deep sutures.

**15. General color pattern.** State 0: Longitudinal striping. State 1: Broad black transverse bands, as found in *Scincopus* and typical of *Scincus* (see Arnold and Leviton, 1977, for variation within *Scincus*). Some variation occurs in the *schneiderii* species group, as recognized by Taylor (1936). *Eumeces algeriensis* typically has narrow, irregular, transverse orange or reddish stripes. Other species (*E. pavimentatus*, *E. blythianus*) have clear longitudinal stripes. Longitudinal striping is indistinct in *E. s. schneiderii* and *E. s. princeps*. Within the *schwartzzei* species group and the *Pariocela* section, color patterns generally show longitudinal striping.

**16. Color pattern ontogeny.** State 0: No major changes in color pattern during maturation. State 1: Significant change in coloration during maturation, consisting of loss of bright tail color (blue, violet, or red) and, in many species, especially in males, reduction or loss of longitudinal pale stripes.

### Relationships within the Ingroup

A single, fully resolved, most parsimonious tree of 19 steps was obtained (Fig. 4). The implied synapomorphies supporting Node A are the eleven derived features that define the Scincidae, as described by Estes et al. (1988) and palatal morphology. Two non-homoplastic characters support the clade: serrated tongue scales, and compound osteoderms present both dorsally and ventrally. The *Pariocela* section is monophyletic, supported by characters 12 (lateral preanal scales overlying medials) and 16 (color pattern ontogeny).



**Fig. 4.** Cladogram showing phylogenetic relationships implied by analysis of characters 1–16. Arrows indicate apomorphic states of characters. R indicates reversal.

Node B shows that *Eumeces* from the *schneiderii*, *schwartzzei*, and *taeniolatus* species groups are more closely related to one another and to at least two other genera (*Scincopus* and *Scincus*) than they are to the *Pariocela* section. This clade is supported by five synapomorphies: Character 2 (constricted parietal), Character 3 (open supratemporal fontanelle), Character 9 (five upper labials anterior to first subocular scale), Character 10 (conspicuous ear lobules), and Character 11 (fusion of adjacent mid-dorsal scale rows). Characters 2 and 3 are both expressions of skull roof morphology, and may be ontogenetically linked. Polarization of the states is uncertain owing to variation in the outgroup. However, if polarity was incorrectly assigned, then these characters would become synapomorphies for the *Pariocela* section and neither the cladogram topology, nor tree length would change.

Character 1 (conical head form) supports the monophyly of *Scincopus*, *Scincus*, and the *schneiderii* and *taeniolatus* species groups at Node C. Character 8 (presubocular scale row the length of two labial scales) supports the monophyly of the *schwartzzei* species group. Character 4 (35 or more presacral vertebrae) unites the two species of the *taeniolatus* species group.

Node D groups the *schneiderii* species group with *Scincopus* and *Scincus*. These forms are united by synapomorphies from characters 5 (heavy limbs), 13 (groove separating upper palpebral from superciliary scales), and 14 (heavy dull scales separated by deep sutures).

Node E represents the shared common ancestor of *Scincopus* and *Scincus*. Synapomorphies are

shown for Characters 6 (short tail), 10 (large flap-like ear lobules), and 15 (broad transverse color bands). Not all races of all species of *Scincus* are banded, but banded forms have a color pattern similar to that of *Scincopus*. These two genera also show much more conspicuous anterior tapering of the skull than is found in any other groups, and fusion of the second loreals with first presuboculars, which could be interpreted as a further derived states of Characters 1 and 9, respectively. The *schneiderii* species group is united by Character 7, absence of a postnasal scale.

## DISCUSSION

### Monophyly of the Subgroups

The monophyly of the four subsections of *Eumeces* is supported by our analysis. Minor homoplasy occurs in the *Pariocela* section; some large species have five labials anterior to the subocular scale (Character 9), and this group is variable for postnasal scale presence or absence (Character 8); the variant is apomorphic within the *Pariocela* section.

The *schwartzzei* species group is supported by a single synapomorphy (Character 7), as is the *taeniolatus* species group (Character 4). This latter group contains two nominal species, *E. taeniolatus* (Blyth) and *E. poonaensis* Sharma. Material of the latter species was not examined, but the description (Sharma, 1970) shows it to be extremely similar to *E. taeniolatus*, with differences not associated with degree of body elongation. Therefore, the numbers of presacral vertebrae are not expected to differ significantly. This species group is in need of basic revision; there is some doubt as to the validity of *E. poonaensis* (M. S. Khan, personal communication). Taylor (1936) suspected that more than one species may be included under the name *taeniolatus*.

Previous classifications (Taylor, 1936; Lieb, 1985) implied that the *schwartzzei* and *taeniolatus* species groups are sister taxa. In contrast, the similarity in dorsal scalation caused Dunn (1933) to suggest that these Southwest Asian and Central American forms, respectively, should be placed together in the genus *Eurylepis* Blyth, for which *Eurylepis taeniolatus* is the type-species. Taylor (1936: 110) suspected that *Eumeces taeniolatus* was most closely related to the *schneiderii* species group, sharing “more specialized features,” despite the superficial resemblance between the *schwartzzei* species group and *E. taeniolatus*, although his classification did not reflect this.

Subsequently, Lieb (1985) placed the *schwartzzei* species group within the *taeniolatus* species series, to the exclusion of all other *Eumeces*. Our cladogram (Fig. 4) corresponds to Taylor’s (1936: 110) interpretation, but not his classification. Only symplesiomorphic features “associate” the *schwartzzei* and *taeniolatus* species groups.

Character 7 supports the monophyly of the *schneiderii* species group. This arrangement contrasts with Arnold and Leviton (1977: 238), who noted that “...it is best to regard both *Scincus* and *Scincopus* as independent derivatives of *E. (s.) algeriensis*-like stock.” The only character of Arnold and Leviton (1977) that might support paraphyly of *E. schneiderii* is the shared possession of transverse color bars between *E. algeriensis* and the other two genera. However, the bars in *Scincus* and *Scincopus* are broad and dark, usually black. In *E. algeriensis*, the stripes are narrow and irregular, and bright orange or red, not suggestive of the same derived condition.

Taylor (1936) observed that members of the *schneiderii* group have a pocketed area posterior to the adducted hind limbs, lateral to the anus. However, in this respect we could not see how the *schneiderii* group species differed significantly from other taxa.

Although a few non-anatomical data have been collected for the genus, as a whole none can be polarized by outgroup comparison. Karyological data have been obtained for a few species from several species groups. Six species of the *Pariocela* section have 26 chromosomes each (Deweese and Wright, 1970). *Eumeces taeniolatus* has 28 chromosomes (Ivanov and Bogdanov, 1975). Karyotypes for members of the *schwartzzei* species group have not been published. Members of the *schneiderii* species group have 32 chromosomes (Gorman, 1973; Talliuri, 1975), which is the complement for *Scincus* (Gorman, 1973). Arnold and Leviton (1977) used the similarity in karyotypes between *Scincus* and *E. schneiderii* to support the hypothesis that they are nearest relatives. In the absence of karyotypic data for *Scincopus*, this interpretation does not contradict our analysis.

### Paraphyly in the Ingroup

Omission of ingroup taxa from analyses can be problematic, particularly when internal clades are supported by few synapomorphies, or when there are two or more equally parsimonious trees (Donoghue et al., 1989). Both situations are relatively sensitive to the addition of further characters and taxa, although,

the latter case does not apply to our study. However, because relatively few potentially informative characters were found, some of the more labile characters may have homoplastically linked distantly related taxa. Evaluating other genera can test this.

The subfamily Scincinae contains all of our ingroup taxa. Greer (1970) found that the other three subfamilies (Acontinae, Feylinae, Lygosominae) evolved independently from within the Scincinae, thus rendering the subfamily a paraphyletic taxon. The question of scincine monophyly is associated with the potential paraphyly of *Eumeces* (Estes et al., 1988), because all other scincines, and potentially all other skinks, may be descended from the same ancestor which is the most recent common ancestor of all *Eumeces*. Although we could have included any combination of scincid genera within the ingroup, we chose to limit the analysis to a relatively small, manageable group, primarily to test if *Eumeces* Wiegmann sensu Taylor and Lieb is monophyletic. Besides *Scincus* and *Scincopus*, other scincine genera not represented in the analysis contain highly specialized, elongate burrowing forms, with reduction in components of the appendicular skeleton, fusion and narrowing of cranial elements, and loss or fusion of head scales. All but three of the 21 other genera listed by Greer (1970) (*Brachymeles*, *Chalcides*, *Scelotes*) consist of a single or a few elongate species. The extensive reorientation of anatomy in these forms makes conventional anatomical comparisons with *Eumeces*, which is necessary for character analysis, very difficult. Nevertheless, it is possible that all other scincine genera, plus the other three subfamilies, fall within the original ingroup of this study.

Because of this problem, some additional taxa were examined. These included additional scincines, plus members of the Lygosominae. These groups are united by three skeletal synapomorphies (Greer, 1970, 1986; Estes et al., 1988), and thus members either belong to a single clade, or represent the sister group to all other taxa combined.

Head morphology (Characters 1 – 3) showed the *Pariocela* section to be the sister group of a clade consisting of the *schwartzii* species group and the remaining ingroup members. The distribution of character's states in other scincids does not change the trees' topology (Fig. 4). Character 1 is difficult to quantify, but no other skink examined possessed a conical skull as is found within all members of the clade united at Node C.

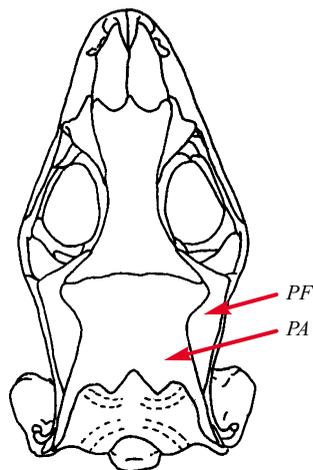
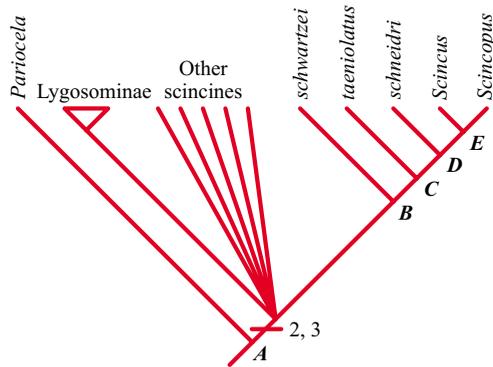


Fig. 5. Skull of *Mabuya multifasciata* (Lygosominae) (adapted from Greer, 1986) showing postfrontal bone (PF) filling supra-temporal fontanelle and constricted parietal bone (PA).

All other lacertiform scincines examined have an open supratemporal fontanelle. Some elongate scincines (*Brachymeles*, *Isopachys*, *Sepsina*, *Ophiomorus*) retain this opening, despite general lateral constriction of the skull. Others cannot exhibit this condition because of loss or reduction of the supratemporal arcade (*Barkudia*, *Fitzsimonsia*, *Nessia*, *Scolecoseps*, *Voeltzkowia*). Many lacertiform lygosomines possess an open supratemporal fontanelle, including *Apterygoida*, *Corucia*, *Eugongylus*, *Hemiergis*, *Lamprolepis*, *Lerista*, *Lobulia*, *Morethia*, *Prasinohaema*, and *Riopa*. Some lacertiform lygosomines have a partially closed supratemporal fontanelle, but it differs from the condition found in all species of the *Pariocela* section of *Eumeces* (e.g., *Ablepharus kitabellii*, *Cophoscincopus durus*, *Eumecia anchietae*, *Leiolopisma spenceri*, *Scincella bilineatum*, *S. laterale*, *Mabuya multifasciata*, *Sphenomorphus coxi*). In these lygosomines the postorbital bone makes little or no contribution to fontanelle closure. The postfrontal bone accomplishes closure almost entirely, and the postorbital bone is very small or absent (Fig. 5). This contrasts with species in the *Pariocela* section of *Eumeces*, where the postorbital bone is an important component of the skull roof. In addition, in the lygosomines the skull narrows posterior to the maximum breadth of the postfrontals, as in lygosomines and scincines with unclosed fontanelles. This condition differs from that in the *Pariocela* section, where the posterior of the skull has subparallel margins, as in cordylids. The differences in the posterior region of the skull suggest that the closed lygosomine fonta-



**Fig. 6.** Cladogram showing possible placement of other scincine taxa relative to original ingroup, based on interpretation of characters 2 and 3.

nelle is most likely homoplastic with that in the *Pariocela* section, and, thus, does not represent the same plesiomorphic state. It likely represents a synapomorphy for the Lygosominae.

Our interpretation of the cranial characters, particularly synapomorphies for characters 2 and 3, place the additional scincines, plus the Lygosominae as branches of a polychotomy radiating from the internode A – B (Fig. 6).

Characters of scalation primarily resolved the upper levels of the cladogram, but several also supported Node B. Character 12 (preanal scale arrangement) supported the monophyly of the *Pariocela* section. Unfortunately, scalation data for other skinks are incomplete, but on the basis of available data, only a few of these characters have homoplastic states.

Greer (1990) reviewed the distribution of character states for preanal scale row arrangement. The presumed derived state, characteristic of the *Pariocela* section, occurs nowhere else in the Scincinae, except in all of the Lygosominae excluding some members of the *Sphenomorphus* group. These sphenomorphines have either retained, or reversed to the condition found in other ingroup members. The shared possession of the derived state in the *Pariocela* section plus most lygosomines is convergent, given the monophyly of the Lygosominae, which seems well established (Greer, 1986).

No other skinks examined have three presubocular scales. We have not found fusion of the mid-dorsal scale rows (Node B) described in other scincines, including *Chalcides* (Pasteur, 1981; Pasteur et al., 1988), *Proscelotes*, *Scelotes*, and *Gongylo-*  
*morphus* (Brygoo, 1980a, 1980b, 1981a, 1981b,

1983a, 1983b, 1984, 1985) or described elsewhere for other scincids.

Well-developed ear lobules do not occur in scincines not included in our analysis, but they occur in some lygosomines, such as some members of the genera *Ctenotus* and *Egernia* (illustrated in Wilson and Knowles, 1988). This appears to be a homoplastic character, but does not contradict the cladogram, assuming the monophyly of those genera and the Lygosominae.

The relationships in Fig. 4 do not change after consideration of character state distributions among other skinks. Analyses of larger sets of both morphological and non-morphological characters for many taxa are needed to provide a reasonably complete, well-supported solution to intrafamilial scincid systematics. However, the characters used here represent a practical, easily examined set of data, which combined with Greer's (1970, 1986) osteological characters, may be examined in other scincids to test our best hypothesis of relationships (Fig. 6).

*Eumeces* is paraphyletic, and cannot be regarded as a single, basal scincid taxon. The largest subgroup, the *Pariocela* section, does not share ancestors with other taxa. This taxon appears to be the sister group to all other skinks, but this suggestion is made cautiously given that the placement of the extremely speciose Lygosominae is based on only two, possibly linked, characters, one of which is difficult to polarize. If the polarities for these characters were reversed, then the Lygosominae would become a branch of a polytomy radiating from Node A.

The question of the positions of Greer's (1970) other two subfamilies (Acontinae and Feylinae) has not been addressed here. Greer suggested that they arose independently from within the Scincinae, which may be true, but the relationships of these burrowing taxa probably cannot be determined using conventional anatomical characters, because of reduction in skeletal and external features, and convergent modification of the skull in these burrowing forms (Rieppel, 1984b).

### Taxonomic Recommendations

Given the paraphyly, and that taxonomic nomenclature must reflect genealogical associations, the genus *Eumeces* must be revised to reflect the independent origins of the four groups. *Eumeces*, *Eurylepis*, and *Scincopus* could be included within *Scincus* Laurenti. This would eliminate some potentially monotypic genera. However, given the uncertainty about the numbers of species in at least two of these groups,

and the considerable morphological and ecological variation among them, we believe that this is undesirable. Thus, we recommended that *Eumeces* be divided into four genera. The *schneiderii* species group would retain the name *Eumeces* Wiegmann, 1834, with the type-species *E. pavimentatus* (I. Geoffroy-Saint-Hilaire, 1827), which may be a subspecies of *E. schneiderii*. However, a petition has been filed with the ICZN (Murphy et al., submitted) to designate *Lacerta fasciata* Linnaeus 1758 as the type species of *Eumeces* therein preserving the genus for most of the species, those in the *Pariocela* section, and the vast majority literature.

The *schneiderii* group is assigned a new genus, and given that no names are available for this group, a new name is given below. The number of nominal species within the *schneiderii* group is uncertain because of the questionable validity of several taxa (Taylor, 1936; Eiselt, 1940 Mertens, 1946; Lieb, 1985). However, the broad distribution and extensive morphological variability strongly suggests that more than one species is present in the group. The *taeniolatus* species group is referred to the genus *Eurylepis* Blyth, 1854. The genus contains two nominal species, and one of these (*E. taeniolatus*) may contain more than one species. Finally, the *schwartzii* species group is given generic status. No name is available, and thus a new genus is described below.

### Taxonomy

Diagnoses contain plesiomorphic and apomorphic characters. Generic autapomorphies are italicized, and indications of convergence with other taxa are given. Given that our data reveal that the subfamily Lygosominae branches off from within the Scincinae, and that the genus *Eumeces* is basal to this clade, we also propose a new subfamily to maintain a monophyletic association of the genera.

### *Eumecinae*, subfam. nov.

**Diagnosis.** Same as for the genus *Eumeces*.

**Content.** The subfamily contains one genus, with 39 species.

### *Eumeces* Wiegmann, 1834

#### Synonymy.

*Lacerta* Linnaeus (in part).

*Eumeces* Wiegmann, 1834 (in part). Type-species, *Lacerta fasciata* Linnaeus, 1758 (Murphy et al., pending).

*Plestiodon* Duméril and Bibron, 1839. Type-species, *Plestiodon quinquelineatum* Duméril and Bi-

bron [= *P. fasciatus* (Linnaeus)], by subsequent designation (Fitzinger, 1843).

*Plestiodon* Fitzinger, 1843 [*lapsus calami*].

*Pariocela* Fitzinger, 1843. Type-species, *Pariocela laticeps* (Schneider).

*Lamprosaurus* Hallowell, 1852(1854). Type-species, *Lamprosaurus guttulatus* Hallowell, 1852 (1854) [= *Eumeces obsoletus* (Baird and Girard)].

*Mabouia* Günther, 1864, by synonymy of *Eumeces quadrivirgatus* Hallowell [= *P. quadrilineatus* (Blyth)].

**Definition.** The common ancestor of the species listed below, plus all its descendents.

**Diagnosis.** 26 – 34 presacral vertebrae. Limbs relatively slender, lamellae not expanded. Head somewhat depressed in lateral view. Skull with undented parietal bones and near-complete or full closure of supratemporal fontanelle. Conspicuous sexual dimorphism (except in *E. egregius*, *E. longirostris*); males with proportionally larger, broader heads, due to expansion of quadrate bones and adductor mandibularis muscles. Scales of head smooth and shiny, not separated by deep sutures. Two loreals, followed by two presuboculars. Postnasal present or absent. Palpebral and superciliary scales not separated by groove. One to two pairs of nuchal scales. Mid-dorsal scales not broadened, not fused. Lateral preanal scales overlies medial preanal scales (convergent with some sphenomorphine lygosomines). Ear lobules inconspicuous. Juveniles dark, usually strongly striped, tails brilliantly colored, adults show reduction or loss of striping and tail coloration. From temperate North America south to northern Central America, Bermuda, and eastern Asia.

**Content.** *Eumeces anthracinus* (Baird), *E. barbouri* Van Denburgh, *E. brevirostris* (Günther), *E. capito* Bocourt, *E. chinensis* (Gray), *E. colimensis* (Taylor), *E. copei* Taylor, *E. coreensis* Doi and Komita, *E. dicei* Ruthven and Gaige, *E. dugesii* Thominot, *E. egregius* (Baird), *E. elegans* Boulenger, *E. fasciatus* (Linnaeus), *E. gilberti* Van Denburgh, *E. inexpectatus* Taylor, *E. kishinouyei* Stejneger, *E. lagunensis* Van Denburgh, *E. laticeps* (Schneider), *E. laticutatus* (Hallowell), *E. liui* Hikida and Zhao, *E. longirostris* (Cope), *E. lynxe* (Wiegmann), *E. marginatus* (Hallowell), *E. multilineatus* Tanner, *E. multivirgatus* (Hallowell), *E. obsoletus* (Baird and Girard), *E. ochoterenae* Taylor, *E. okadae* (Stejneger), *E. oshimensis* Thompson, *E. parviauriculatus* Taylor, *E. parvulus* Taylor, *E. popei* Hikida, *E. quadrilineatus* (Blyth), *E. septentrionalis* (Baird), *E. skiltonianus* (Baird and Girard), *E. stimsonii* Thompson,

*E. sumichrasti* (Cope), *E. tamdaoensis* Bourret, and *E. tunganus* Stejneger.

**Remarks.** The name *Plestiodon* was widely used for this group during the early part of the twentieth century, apparently in deference to the classification of Duméril and Bibron (1839). The type for the genus (*quinquelineatus* = *fasciatus*) was designated by Fitzinger (1843: 22), but preceding this was the designation of *Eumeces laticeps* Schneider as the type for the new genus *Pariocela*. As the oldest name referring to an identifiable type, this latter name would be applied to the group if the petition to ICZN is unsuccessful.

### Subfamily Scincinae

#### *Mesoscincus* gen. nov.

**Type-species.** *Eumeces schwartzei* Fischer, 1884.

#### **Synonymy.**

*Eumeces* Wiegmann, 1834, in part.

*Platypholis* Dugès, 1891 (not of Boulenger, 1890). Type-species, *Platypholis altamirani* Dugès, 1891.

**Definition.** The common ancestor of *Mesoscincus altamirani* (Dugès, 1891), *Mesoscincus managuae* (Dunn, 1933), *Mesoscincus schwartzei* (Fischer, 1884) plus all of its descendents.

**Diagnosis.** 27 presacral vertebrae. Limbs relatively slender, lamellae not expanded. Dorsal surface of head somewhat depressed in lateral view, parietal bone with clear lateral indentations and supratemporal fontanelle open. Sexual dimorphism not distinct. Scales shiny, separated by shallow sutures. Two loreals, followed by three presubocular scales. Post-nasal scales present. Palpebral and superciliary scales not separated by groove. Elevated numbers (4 or 5 pairs) of nuchal scales, followed by several pairs of broadened mid-dorsal scales and broad row of fused mid-dorsal scales. Large medial preanal scales overlie small lateral pair. Ear lobules small and rounded, but conspicuous. Color pattern variable, but generally consists of irregular spots and longitudinal striping.

From lowlands of southern Mexico (Michoacan, Yucatan Peninsula), northern and Pacific coastal Honduras, Pacific coastal Nicaragua and Costa Rica.

**Content.** *Mesoscincus altamirani* (Dugès, 1891), *Mesoscincus managuae* (Dunn, 1933), and *Mesoscincus schwartzei* (Fischer, 1884).

**Remarks.** This genus is equivalent in content to the *schwartzei* species group of Taylor (1936). Members are poorly known in most respects, particularly *P. altamirani*, which is not well represented in collec-

tions. The generic name *Platypholis* Dugès, 1891 is preoccupied by *Platypholis* Boulenger 1890, a genus of gecko, and, thus, is unavailable.

**Etymology.** The name refers to the Middle American distribution of this group, and its current position as a middle group within the scincid cladogram. It is masculine in gender.

#### *Eurylepis* Blyth, 1854

#### **Synonymy.**

*Eumeces* Wiegmann, 1834 (in part).

*Eurylepis* Blyth, 1854. Type-species *E. taeniolatus* Blyth, 1854.

*Plestiodon* Theobald, 1866, by synonymy of *E. taeniolatus* Blyth.

*Mabouia* Anderson, 1871 in part, by synonymy of *E. taeniolatus* Blyth.

**Definition.** The common ancestor of *E. poonaensis* (Sharma) and *E. taeniolatus* Blyth and all of its descendents.

**Diagnosis.** Elongate, 35 or more presacral vertebrae (convergent with many other scincid groups). Limbs relatively slender, lamellae not expanded. Head somewhat conical, dorsal surface convex in lateral view, parietal bone with clear lateral indentations and supratemporal fontanelle open. Sexual dimorphism in head proportions not distinct. Scales shiny, separated by shallow sutures. Two loreals, followed by two presuboculars. Post-nasal scales present. Palpebral scales and superciliaries not separated by groove. Four or five pairs of nuchal scales, followed by several pairs of broadened mid-dorsal scales and broad row of fused mid-dorsal scales. Large medial preanal scales overlie small lateral pair. Ear lobules conspicuous, but not covering ear opening. Color pattern consists of gray-brown background, with pale, broad dorsolateral stripes, more distinct anteriorly, brown rectangular spots dominating posteriorly. Northern extent of range poorly known; southern portion of distribution includes Iran, Afghanistan, Pakistan, and northwestern India.

**Content.** *Eurylepis poonaensis* (Sharma), *Eurylepis taeniolatus* Blyth.

**Remarks.** M. S. Khan (personal communication) has suggested that *E. poonaensis* may be a junior synonym of *taeniolatus*, which would render the genus monotypic. However, Taylor (1936: 110) believed that more than one species might be included within *E. taeniolatus*, and recommended further investigation of the systematics of the *taeniolatus* group.

***Novoeumeces* gen. nov.**

**Type-species.** *Scincus pavimentatus* I. Geoffroy-Saint-Hilaire, 1827.

**Synonymy.**

*Scincus* Harlan 1824 by synonymy of *N. algeriensis* and *N. schneiderii*.

*Euprepis* Wagler 1830 by synonymy of *N. princeps*.

*Eumeces* Wiegmann, 1834 (in part). Type-species *Scincus pavimentatus* (= *Eumeces pavimentatus* I. Geoffroy-Saint-Hilaire, 1827) by subsequent designation (Wiegmann, 1835).

*Mabouia* Günther 1864 (in part) by synonymy of *M. blythiana* Anderson [= *N. blythianus* (Anderson)].

**Definition.** The common ancestor of *N. algeriensis* (Peters), *N. indothalensis* (Khan and Khan), *N. pavimentatus* (I. Geoffroy-Saint-Hilaire, 1827), *N. princeps* (Eichwald), and *N. schneiderii* (Daudin) plus all of its descendents.

**Diagnosis.** 26–28 presacral vertebrae. Relatively heavy limbs with robust pes, expanded lamellae on digits and phalanges. Head conical, dorsally convex in lateral view, parietal bone with clear lateral indentations and supratemporal fontanelle open. Sexual dimorphism in head proportions not distinct. Scales thick, separated by deep sutures. Two loreals, followed by two presuboculars. Postnasal absent. Palpebral scales separated from superciliary scales by deep groove containing small granular scales. Three or four pairs of nuchal scales. Two mid-dorsal scale rows broadened, not fused. Medial preanal scales overlie lateral preanal scales. Ear lobules conspicuous, but ear opening not fully covered. Color pattern usually consisting of small spots, broken longitudinal stripes or irregular narrow bars on brown or olive background. From northern Africa, Cyprus, Middle East to Iraq.

**Content.** *Novoeumeces indothalensis* Khan and Khan, *Novoeumeces schneiderii* (Daudin); see remarks.

**Remarks.** Taylor (1936) recognized six species within the *schneiderii* species group: *N. algeriensis* (Peters), *N. blythianus* (Anderson), *N. pavimentatus* (I. Geoffroy-Saint-Hilaire, 1827), *N. princeps* (Eichwald), *N. schneiderii* (Daudin), and *N. zarudnyi* (Nikolsky). Eiselt (1940) and Mertens (1946) argued that only a single, variable species is represented. Lieb (1985) tentatively recognized four species: *N. algeriensis* (Peters), *N. pavimentatus* (I. Geoffroy-Saint-Hilaire, 1827), *N. princeps* (Eichwald), and *N. schneiderii* (Daudin). Schleich et al. (1996)

tentatively recognized *N. meridionalis* (Doumergue, 1900), although noting that it might be a subspecies of *N. schneiderii*.

Subsequently, a new species, *N. indothalensis* (Khan and Khan, 1997) was described and assigned to the *schneiderii* group.

***Scincopus* Peters, 1864****Synonymy.**

*Scincus* Laurenti 1768 (in part). Type-species *Lacerta stincus* [*lapsus calami* for *scincus*] Linnaeus, 1758.

*Scincopus* Peters, 1864. Type-species *S. fasciatus* Peters.

**Definition.** Monotypic; sister taxon to *Scincus*.

**Diagnosis.** 26 presacral vertebrae. Heavy limbs with robust pes, expanded lamellae on digits and phalanges, short tail. Head large and conical, dorsally convex in lateral view, parietal bone with clear lateral indentations and supratemporal fontanelle open. Sexual dimorphism in head proportions not distinct. Large eye with vertically elliptical pupil. Scales thick, separated by deep sutures. Two loreals, two presuboculars (first fused with second loreal). Postnasal present. Palpebral and superciliary scales separated by groove. Four pairs of nuchal scales. Fused mid-dorsal scale rows, may be interrupted by one or a few pairs of broadened, paired scales. Medial preanal scales overlie lateral preanal scales. Two large, triangular ear lobules cover ear opening. Yellow or orange dorsally, with seven or eight broad black bands, equally spaced from nuchal region to tip of tail. From Saharan Africa.

**Content.** *Scincopus fasciatus* Peters.

***Scincus* Laurenti, 1768****Synonymy.**

*Scincus* Laurenti, 1768. Type-species *Lacerta stincus* [*lapsus calami* for *scincus*], Linnaeus, 1758.

*Pedorychus* Wiegmann, 1837.

**Definition.** The common ancestor of *S. scincus* (Linnaeus), *S. mitranus* J. Anderson, and *S. hemiprichii* Wiegmann, plus all its descendents.

**Diagnosis.** Heavy limbs with robust pes, expanded lamellae on digits and phalanges, short-tailed. Conical head, convex in lateral view, parietal bone with clear lateral indentations and supratemporal fontanelle open. Sexual dimorphism in head proportions not distinct. Spatulate rostrum supported by extended fused premaxillae. Strong ventrolateral keels running

from upper labial scales to sacral region (convergent with other genera of sand-swimming lizards). Scales thick, separated by deep sutures. Two loreals, second fused with first of two presuboculars. Postnasal present. Palpebral and superciliary scales separated by groove. Usually four or five pairs of nuchal scales. Broadened mid-dorsal scales, mid-dorsal rows not fused. Medial preanal scales enlarged, lateral edges coincide with ventrolateral keels. Small, ventrally directed ear opening covered by several overlapping lobules. Color pattern variable, but generally consisting of transverse stripes or bars on pale background. From Saharan Africa, eastward to southern Iran.

**Content.** *Scincus scincus* (Linnaeus), *Scincus mitranus* J. Anderson, *Scincus hemiprichii* Wiegmann.

**Remarks.** The genus *Scincus* was revised by Arnold and Leviton (1977). Their classification is followed here. They recognized four races of *S. scincus*, but refrained from identifying them as subspecies because of inadequate sampling over the geographic range of the species.

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## APPENDIX

Specimens examined for phylogenetic analysis, using “*Eumeces*” as currently recognized. Institutional abbreviations are: **AMNH**) American Museum of Natural History; **CAS**) California Academy of Sciences; **FMNH**) Field Museum of Natural History; **MCZ**) Museum of Comparative Zoology, Harvard University; **ROM**) Royal Ontario Museum; **UMMZ**) University of Michigan Museum of Zoology; **USNM**) National Museum of Natural History, Smithsonian Institution; **UTA**) University of Texas at Arlington, Zoological Collection. **Dry**) skeletonized; **C&S**) cleared and stained.

### *Eumeces*:

*Eumeces altamirani*: CAS 143083;  
*E. anthracinus*: MCZ 29312 (dry);

*E. brevirostris*: UTA 5799, 6649, 6650, 7857, 11948, 11949;  
*E. chinensis*: MCZ 29005 (skull), USNM 22300, 31720, 65344–65357, 65361–65362, 65364–65367, 65372–65374, 66374, 66438, 66439, 67034, 67608, 67700, 72916, 73187, 78208–78210, 78212, 78214–78218, 140023–140027, 152390;  
*E. copei*: AMNH 107039, 118416–118418, 118422, 118423, 118426, 119293, 17 unnumbered, ROM 10857–10859, USNM 113532–113535, 113536 (C&S), 113537–113540, 113541 (C&S), 113542–113569, 113571–113573;  
*E. dicei*: USNM 244667, 244668;  
*E. dugesii*: UTA 4023–4025, 4636, 6363, 7919, 11953, 11954;  
*E. egregius*: AMNH 22423, MCZ 852, 978, 10065, 10771, 12851–12853, 14464, 28386, 61200–61202, USNM 12002 (3 spec.), 12851, 13700, 19980, 19981, 26309, 32097, 32098, 48744, 49738, 56982 (C&S), 59418, 60515, 60516 (C&S), 61692, 69657, 75294, 85258–85260, 95752, 95753, 103512, 125130, 252434;  
*E. elegans*: CAS 25058, 25063, 25064, 25067, 25068, MCZ 28983 (dry), 28992 (dry), USNM 60574 (C&S), 64126, 67611, 67614, 67617, 78211, 78218–78227;  
*E. fasciatus*: FMNH 2214, 5829, 62045, 69340, 94849, 110510, 110513, 110539, 110540, 116806, 116839, 118843, 118858, 118870, 118884, 123758, 162961, 162971, 176934, 194356, 194359, 194362, 194364, 194366, MCZ 54126 (skull), UMMZ 97457, 97458, 97459 (19 spec.);  
*E. gilberti*: CAS 87805, 87929–87931, 87942, 89360–89363, 89407, USNM 3318, 5310 (3 spec.), 9229 (2 spec.), 11756 (3 spec.), 11799, 15714, 18598, 18599, 18601, 18603, 18604, 20341, 20385, 21999, 22653, 44771, 44891, 45053, 118631, 222716, 222717, 222719;  
*E. humilis*: CAS 114446, 114598; *E. inexpectatus*: USNM 231228 (C&S), 234191, 234193, 234194, 23400, FMNH 853(2 spec.), 946, 1882 (2 spec.), 2034 (2 spec.), 3357 (2 spec.), 4826, 4831, 5893, 5894, 194327, 194330, 194332, 194334, 194335, 194412, MCZ 45497 (skull), 55506 (dry), 45498 (dry), UMMZ 95578 (21 spec.);  
*E. kishinouyei*: CAS 21719–21721, MCZ 55935 (skull), USNM 34080, 34081;  
*E. laticeps*: AMNH 118587, 119461, 119464, 119467–119470, 119474, 119479, 119481, 120188, 120190, 120192, 120193, 120228, FMNH 2707, 5565, 8118, 8139, 23726, 23727, 26344, 26345, 33713, 37513, 41960, 44225, 46751, 46752, 53198, 53200, 55061, 69307, 104172, 162969, 164025, 194323, 194351, 228418, 228149, MCZ 4418 (dry), 55505 (skull), 132882 (skull), UMMZ 57716–57718, 56607, 64164, 64165, 72774 (2 spec.), 72776, 72777, 72780 (3 spec.), 77199, 77200, 95579 (4 spec.), 95580 (2 spec.), USNM 9242 (skull), 110470, 220260 (dry), 234382, 234384, 234385;  
*E. laticutatus*: CAS 33027, 33029, 33031–33033, USNM 12715, 13750, 31804, 31832, 31834–31836, 31879–

- 31881, 31883, 31890–31893, 34120, 34121 (C&S), 34122, 34124, 34126, 34128, 34130, 34131, 34133 (C&S), 34135, 34137, 34139, 245048–245051;
- E. longirostris*: MCZ 8223 (C&S), 20503 (skull), 20508, USNM 10392–10397, 11021, 11022, 12129, 58157, 67126, 67127, 137302, 137303, 217505 (dry), 217507 (dry), 217517;
- E. lynxe*: USNM 113590, 113595 (C&S), 113598, 113599 (C&S), 113600, MCZ 19086 (dry), 19087 (dry), 24533 (dry), 24534 (dry), UTA 4183–4185, 4204, 5940, 11955–11968;
- E. marginatus*: CAS 21640, 21641, 24251, 24253, 24255, MCZ 7409 (dry), 57111 (dry), 57112 (dry), USNM 36522 (C&S), 36523, 36524 (C&S);
- E. multivirgatus*: CAS 102222, 102229, 102236, 102245, 102246, USNM 4139 (2 spec.);
- E. obsoletus*: CAS 54742 (*guttulatus*), MCZ 35547 (dry), 61366 (dry), 61367 (dry), USNM 5049, 5247, 8170, 8176 (2 spec.), 8180, 9048 (2 spec.), 9220–9224, 9226, 11598, 14244, 15649, 15862, 17083, 17088, 22271, 25408, 32829, 32832, 44806, 51597, 53401, 53402, 53416, 56899, 56900, 58154, 58584, 58585, 71501, 89962–89964, 89967, 89969, 90717–90727, 90761, 90762 (C&S), 197505, 197508, 197509, 220269 (dry), 220270 (skull only), 22271, 231229 (C&S), 51587, 53416, 56899, 56900, 58154, 56902;
- E. ochoteranae*: USNM 113602, UTA 4079–4083, 4100, 4107, 4113, 4152 4415, 4574, 4575, 5554–5556, 5864, 5835, 5836, 7016–7020;
- E. okadae*: CAS 27229 (Paratype of *E. laticutatus okadae*);
- E. pavimentatus*: CAS 105279;
- E. parviauriculatus*: CAS 155914–155919;
- E. parvulus*: CAS 104981, 104982, 114321, USNM 47667 51395 (C&S);
- E. princeps*: CAS 105423–105425;
- E. schneiderii*: MCZ 9869, USNM 37290, 37291, 113432, 113433, 130374, 130375–130378, 134784, 134786, 134788, 135329, 135330;
- E. schwartzei*: USNM 113603 (dry), 113604 (C&S), 113605–113608, ROM 10337;
- E. septentrionalis*: USNM 10970, 10971, 11840, 13920, 13921 (spec.), 15685, 44969, 45293–49297, 49605, 53044, 53045, 58164, 71503, 89961, 90709, 100648, 129519, 131680;
- E. skiltonianus*: MCZ 6617A (dry), 6617B (dry), 8887 (dry), 131883 (dry), USNM 9227 (21 spec.), 9053, 11795 (3 spec.), 16176, 16177, 52083–52085, 56892–56895, 56897, 56898, 131682, 131683;
- E. sumichrasti*: USNM 113609, 113610 (C&S), 113612, 113616, 113617, UTA 3154, 3155, 3194;
- E. stimsonii*: CAS 21651, 21658–21660, 21663, 21673;
- E. taeniolatus*: CAS 94309, 120997, 140393, USNM 194971;
- E. tunganus*: USNM 82751 (skull), 107435, 107440, 107445, 107447 (C&S), 107450 (C&S),

**Other Scincinae**

- Barkudia insularis*: MCZ 54712;
- Brachymeles bonitae*: CAS 25891–25899;
- B. boulengeri*: CAS 24868–24871;
- B. gracilis*: CAS 28992–28998;
- B. schadenbergi*: CAS 26272–26287;
- B. talinus*: CAS 127584–12758, 127663–127668;
- B. tridactylus*: CAS 153817–153826;
- Chalcides chalcides*: CAS 92379, 92380, 138485, 138486;
- C. guentheri*: CAS 87436;
- C. ocellatus*: CAS 138487–138502, 136512, 142001, ROM R59 (skull);
- C. polylepis*: CAS 92386, 92387;
- C. thierryi*: CAS 104553;
- Fitzsimonsia brevipes*: MCZ 96702 (skull);
- Gongylomorphus bojeri*: MCZ 46677 (skull);
- Isopachys roulei*: MCZ 74099 (skull);
- Melanoseps ater*: MCZ 50955 (skull);
- Neoseps reynoldsi*: CAS 50188–50191, MCZ 131884 (skull);
- Proscelotes arnoldi*: MCZ 55145 (skull), 67856 (skull);
- P. eggeri*: CAS 168959–168961;
- Ophiomorus brevipes*: CAS 101792;
- O. latastei*: CAS 87417;
- O. persicus*: CAS 101794–101796;
- O. raithmai*: CAS 99835–99844;
- O. streeti*: CAS 100024;
- O. tridactylus*: CAS 84669–84671, 84673–84675, ROM noncataloged (C&S);
- Proscelotes eggeri*: CAS 16890, 16891;
- Scelotes angolensis*: CAS 85971, 85972;
- S. anguina*: CAS 173259–173260;
- S. arenicola*: CAS 106021;
- S. astrolabi*: CAS 13949, 13967, MCZ 20955 (skull);
- S. brevipes*: CAS 135467;
- S. caffer*: CAS 113507;
- S. capensis*: CAS 85929;
- S. gardneri*: CAS 159490, 159491;
- S. gastrostictus*: CAS 123191;
- S. gronovii*: CAS 173923;
- S. limpopoensis*: CAS 125790;
- Scincopus fasciatus*: AMNH 96096, MCZ 112193;
- Scincus scincus*: MCZ 27456 (skull) ROM 15502, 15503;
- Scolecoseps boulengeri*: MCZ 170057 (skull);
- Sepsina arenicola*: MCZ 14205 (skull);
- S. tetradactylus*: MCZ 56965 (skull).

**Lygosominae**

- Ablepharus kitaibelii*: MCZ 3961 (skull);
- Anomalopus larutense*: MCZ 39265 (skull);
- Apterygodon vittata*: MCZ 11261 (skull);
- Ateuchosaurus pellopleurus*: MCZ 55925 (skull);
- Cophoscincopus durus*: MCZ 131802 (skull);
- Corucia zebrata*: MCZ 72918 (skull);
- Emoia kordoana*: MCZ 248603 (skull);
- Eumecia anchietae*: MCZ 41562 (skull);
- Eugongylus albofasciata*: MCZ 72703 (skull);

*Hemiergis descreiensis*: CAS 77527, 77528;  
*H. tridactylum*: MCZ 24595 (skull);  
*Lamprolepis smaragdina*: MCZ 26429 (skull);  
*Lerista bipes*: CAS 104395;  
*L. miopa*: MCZ 33260 (skull);  
*L. punctatovittata*: CAS 83730–83734;  
*Leiopolisma spenceri*: MCZ 13453 (skull), 33212 (skull);  
*Lipinia pulchella*: MCZ 26440 (skull);  
*Lobulia elegans*: MCZ 80111 (skull);  
*Mabuya multifasciatus*: MCZ 25198 (skull);  
*Morethia layardi*: MCZ 4122 (skull);  
*Prasinohaema prehensicauda*: MCZ 21656 (skull);  
*Riopa fernandi*: MCZ 49696 (skull);  
*Scincella bilineata*: MCZ 7183;  
*Sphenomorphus coxi*: MCZ 26331.

### Cordylidae

*Angolosaurus skoogi*: CAS 106012;  
*Chamaesaurus anguina*: CAS 10456;  
*Cordylus subtesellatus*: CAS 173424;  
*C. trivittatus australis*: CAS 85930;  
*C. t. trivittatus*: CAS 104576;  
*Cordylus cataphractus*: CAS 12088;  
*C. coeruleopunctatus*: CAS 175052;  
*C. cordylus*: CAS 17885–7887;  
*C. jonesii*: CAS 135155;  
*C. mclachlani*: CAS 165757;  
*C. niger*: CAS 104348, 104349;  
*C. oelofseni*: CAS 173349–173360;  
*C. polyzonus*: CAS 165658;  
*C. vittifer*: CAS 85837;  
*Gerrhosaurus major major*: CAS 151090, 151091;  
*G. major*: CAS 162651;  
*G. nigrolineatus*: CAS 165467;  
*Platysaurus capensis*: CAS 12089, 12090;  
*P. intermedius intermedius*: CAS 106016;  
*Pseudocordylus melanotus*: CAS 156374, 156381–156385;  
*P. microlepidotes*: CAS 165760;  
*P. subviridis transvaalensis*: CAS 85843;  
*Tetradactylus seps seps*: CAS 175102;  
*T. tetradactylus tetradactylus*: CAS 111649;  
*Zonosaurus laticaudatus*: CAS 138031;  
*Z. madagascariensis*: CAS 156826, 156827;  
*Z. rufipes*: CAS 156896, 156897.

### REFERENCES

- Anderson J.** (1871), “On two saurian genera, *Eurylepis* and *Plocederma* Blyth, with a description of a new species of *Mabouia*, Fitzinger,” *Proc. Asiatic Soc. Bengal*, **1871**, 186 – 187.
- Arnold E. N. and Leviton A. E.** (1977), “A revision of the lizard genus *Scincus* (Reptilia: Scincidae),” *Bull. Br. Mus. Nat. Hist.*, **31**, 187 – 248.
- Blyth E.** (1854), “Report of Curator, Zoological Department, for September, 1854,” *J. Asiatic Soc. Bengal*, **23**, 729 – 740.
- Boulenger G. A.** (1890), “First report on additions of the lizard collection in the British Museum (Natural History),” *Proc. Zool. Soc. (London)*, **1890**, 77 – 86, pls. 8 – 11.
- Broadley D. G.** (1978), “A revision of the genus *Platysaurus* A. Smith (Sauria: Cordylidae),” *Occ. Pap. Natl. Mus. Rhodesia B. Nat. Sci.*, **6**, 129 – 185.
- Brygoo E. R.** (1980a), “Système des lézards scincidés de la région malgache. II. *Amphiglossus astrolabi* Duméril and Bibron, 1839; *Gongylus polleni* Grandidier, 1869; *Gongylus stumpffi* Boettger, 1882, et *Scelotes waterloti* Angel, 1930,” *Bull. Mus. Natn. Hist. Nat. Paris 4<sup>e</sup> Ser. 2. Sect. A*, No. 2, 525 – 539.
- Brygoo E. R.** (1980b), “Système des lézards scincidés de la région malgache. V. *Scelotes praeornatus* Angel, 1938, synonyme de *Scelotes s. l. frontoparietalis* (Boulenger, 1889),” *Bull. Mus. Natn. Hist. Nat. Paris 4<sup>e</sup> Ser. 2. Sect. A*, No. 4, 1155 – 1160.
- Brygoo E. R.** (1981a), “Système des lézards scincidés de la région malgache. VI. Deux scincines nouveaux,” *Bull. Mus. Natn. Hist. Nat. Paris 4<sup>e</sup> Ser. 3. Sect. A*, No. 1, 261 – 268.
- Brygoo E. R.** (1981b), “Système des lézards scincidés de la région malgache. VIII. Les *Mabuya* des îles de l’océan Indien occidental: Comores, Europa, Sechelles,” *Bull. Mus. Natn. Hist. Nat. Paris 4<sup>e</sup> Ser. 3. Sect. A*, No. 3, 911 – 930.
- Brygoo E. R.** (1983a), “Système des lézards scincidés de la région malgache X. Rapports de *Gongylus johanna* Günther, 1880, des Comores, et de *Sepsina valhallae* Boulenger, 1909, des Glorieuses, avec les espèces malgaches,” *Bull. Mus. Natn. Hist. Nat. Paris 4<sup>e</sup> Ser. 5. Sect. A*, No. 2, 651 – 660.
- Brygoo E. R.** (1983b), “Système des lézards scincidés de la région malgache. XI. Les *Mabuya* de Madagascar,” *Bull. Mus. Natn. Hist. Nat. Paris 4<sup>e</sup> Ser. 5. Sect. A*, No. 4, 1079 – 1108.
- Brygoo E. R.** (1984), “Système des lézards scincidés de la région malgache. XV. *Gongylus igneocaudatus* A. Grandidier, 1867, et *Scelotes intermedius* Boettger, 1913. Les *Amphiglossus* du groupe *igneocaudatus*,” *Bull. Mus. Natn. Hist. Nat. Paris 4<sup>e</sup> Ser. 6. Sect. A*, No. 3, 779 – 789.
- Brygoo E. R.** (1985), “Système des lézards scincidés de la région malgache. XVII. *Gongylus splendidus* A. Grandidier, 1872, *Scelotes macrolepis* Boulenger, 1888, et *Scelotes decaryi* Angel, 1930,” *Bull. Mus. Natn. Hist. Nat. Paris 4<sup>e</sup> Ser. 7. Sect. A*, No. 1, 235 – 247.
- Brygoo E. R. and Böhme W.** (1985), “Un *Zonosaurus* nouveau de la région d’Antseranana (= Diégo-Suarez, Madagascar) (Reptilia: Cordylidae),” *Rev. Fr. Aquariol.*, **12**, 31 – 32.
- Camp C. L.** (1923), “Classification of the lizards,” *Bull. Am. Mus. Nat. Hist.*, **48**, 290 – 491.

- Deweese J. E. and Wright J. W.** (1970), "A preliminary karyological analysis of scincid lizards," *Mamm. Chromosomes Newsl.*, **11**, 95 – 96.
- Donoghue M. J., Doyle J. A., Gauthier J., Kluge A. G., and Rowe T.** (1989), "The importance of fossils in phylogeny reconstruction," *Ann. Rev. Ecol. Syst.*, **20**, 431 – 460.
- Doumergue F.** (1900[1901]), *Essai sur la faune erpétologique de l'Oraine*, Imp. Typogr. Fouque, Oran.
- Dugès A.** (1891), *La Natureza*. (2) I, **1887–1890**, 485 – 486.
- Duméril A. M. C. and Bibron G.** (1839), *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles*. V, 1839, viii + 1–855.
- Dunn E. R.** (1933), "A new lizard from Nicaragua," *Proc. Biol. Soc. Wash.*, **46**, 67 – 68.
- Eiselt J.** (1940), "Der Rassenkreis *Eumeces schneiderii* Daudin (Scincidae, Rept.)," *Zool. Anz.*, **131**, 209 – 228.
- Estes R., de Queiroz K., and Gauthier J.** (1988), "Phylogenetic relationships within the Squamata," in: R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families. Essays Commemorating Charles L. Camp*, Stanford Univ. Press, Stanford (California), pp. 118 – 228.
- Fischer J. G.** (1884), "Herpetologische Bemerkungen," *Abh. Geb. Naturw. herausg. Naturw. Ver. Hamburg VIII*, **2**, 1 – 6.
- Fitzinger L. J. F. J.** (1843), *Systema reptilium. Fasciculus primus. Amblyglossae*. Vindobonae, Braumuller und Seide.
- Fitzsimons V. F.** (1943), "The lizards of South Africa," *Tansvaal Mus. Mem.*, **1**, 1 – 528.
- Geoffroy-Saint-Hilaire É. and Geoffroy-Saint-Hilaire I.** (1827), "Description des Reptiles qui se Trouvent en Égypte," in: *Description de l'Égypte, ou Recueil des Observations et des Recherches qui ont été faites en Égypte pendant l'expédition de l'Armée Française. Histoire Naturelle. Tome Premier* [Volume 1, part 1], Imprimerie Impériale, Paris, pp. 115 – 160, 118 plates.
- Gorman G. C.** (1973), "The chromosomes of the Reptilia, a cytotaxonomic interpretation," in: A. B. Chirelli and E. Campagna (eds.), *Cytotaxonomy and Vertebrate Evolution*, Acad. Press, New York, pp. 349 – 424.
- Greer A. E.** (1970), "A subfamilial classification of scincid lizards," *Bull. Mus. Comp. Zool.*, **139**, 151 – 184.
- Greer A. E.** (1986), "Lygosominae monophyly: a third, corroborating character and a reply to critics," *J. Herpetol.*, **20**, 123 – 126.
- Greer A. E.** (1987), "Limb reduction in the lizard genus *Lerista*. I. Variation in the number of phalanges and presacral vertebrae," *J. Herpetol.*, **21**, 267 – 276.
- Greer A. E.** (1990), "Overlap pattern in the preanal scale row: an important systematic character in skinks," *J. Herpetol.*, **24**, 328 – 330.
- Günther A.** (1864), *The Reptiles of British India*, London.
- Hallowell E.** (1852 [1854]), "On a new genus and three new species of reptiles inhabiting North America," *Proc. Acad. Nat. Sci. Philadelphia*, **1852**, 206 – 209.
- Harlan R.** (1824), "Description of a new species of *Scincus*," *J. Acad. Nat. Sci. Philadelphia* **4**, Pt. 2, **1824**, 286 – 288.
- Ivanov V. G. and Bogdanov O. P.** (1975), "Karyotype of *Eumeces taeniolatus* Blyth," *Tsitologiya*, **17**, 861 – 863 [in Russian].
- Khan M. S. and Khan R. Z.** (1997), "A New skink from the Thal Desert of Pakistan," *Asiatic Herpetol. Res.*, **7**, 61 – 67.
- Laurenti J. N.** (1768), *Specimen medicum, exhibens synopsia reptilium emendatum cum experimentis circa venena et antidota reptilium austriacarum*, Vienna.
- Lieb C. S.** (1985), "Systematics and distribution of the skinks allied to *Eumeces tetragrammus* (Sauria: Scincidae)," *Contrib. Sci. Los Angeles Co. Nat. Hist. Mus.*, No. 357, 1 – 19.
- Linnaeus C.** (1758), *Systema naturae*, 10th ed., Vol. I, Stockholm.
- Maddison W. P., Donoghue M. J., and Maddison D. R.** (1984), "Outgroup analysis and parsimony," *Syst. Zool.*, **33**, 83 – 103.
- Mertens R.** (1946), "Dritte Mitteilung über die Rassen der Glattechse *Eumeces schneiderii*," *Senckenbergiana*, **27**, 53 – 62.
- Murphy R. W., Smith H. M., Chiszar D., Griffith H., Ngo A., Ananjeva N., Darevsky I. S., Orlov N. L., Aguirre G., Morafka D. J., Reeder T. W., and Adler K.** (1999: in review), "*Eumeces* Wiegmann, 1834: designation of *Lacerta fasciata* Linnaeus, 1758, as type," *Bull. Zool. Nomencl.*
- Nash D. F. and Tanner W. W.** (1970), "A comparative study of the head and thoracic osteology and myology of the skinks *Eumeces gilberti* Van Denburgh and *Eumeces skiltonianus* (Baird and Girard)," *Brigham Young Univ. Sci. Bull. Biol. Ser.*, **12**, 1 – 32.
- Pasteur G.** (1981), "A survey of the species groups of the Old World scincid genus *Chalcides*," *J. Herpetol.*, **15**, 1 – 16.
- Pasteur G., Keymar P. F., and Perret J.-L.** (1988), "Canarian skink systematics. Contrasting insular diversifications within a species subgroup," *Ecol. Prat. Haute Etud. 3<sup>e</sup> Sect. Mem Trav. Inst. Montpellier*, **18**, 1 – 42.
- Peters W.** (1864), "Über die Eidechsenfamilie der Scincoiden insbesondere über die Schneider'schen Wiegmann'schen und neue Arten des zoologischen Museums," *Mber. K. Preuss. Akad. Wiss.*, **1864**, 44 – 58.
- Rieppel O.** (1984a), "The cranial morphology of the fossorial lizard genus *Dibamus* with a consideration of its phylogenetic relationships," *J. Zool. Lond.*, **204**, 289 – 327.

- Rieppel O.** (1984b), "Miniaturization of the lizard skull: its functional and evolutionary implications," *Symp. Zool. Soc. Lond.*, No. 52, 503 – 520.
- Schleich H. H., Kästle W., and Kabisch K.** (1996), *Amphibians and Reptiles of North Africa*, Koeltz, Koenigstein (Germany).
- Schwenk K.** (1988), "Tongue morphology and squamate relationships: a phylogenetic analysis," in: R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families. Essays Commemorating Charles L. Camp*, Stanford Univ. Press, Stanford (California), pp. 568 – 596.
- Sharma R. C.** (1970), "A new lizard, *Eumeces poonaensis* (Scincidae) from India," *Rec. Zool. Survey India*, **62**, 239 – 241.
- Swofford D. L.** (1998), "PAUP\*: phylogenetic analysis using parsimony and other methods, version 4.0b2a," Sinauer Assoc., Sunderland (Mass.).
- Talliuri V. M.** (1975), "*Eumeces schneiderii* algeriensis," in: M. L. Becak, W. Becak, T. R. Chen, and R. N. Shoffner (eds.), *The Chromosome Atlas: Fish Amphibians, Reptiles, Birds*, Vol. 3, R-42.
- Taylor E. H.** (1936), "A taxonomic study of the cosmopolitan scincoid lizards of the genus *Eumeces* with an account of the distribution and relationships of its species," *Univ. Kansas Sci. Bull.*, **23**, 1 – 643.
- Theobald W.** (1866), "Catalogue of reptiles in the museums of the Asiatic Society of Bengal," *Extra No. J. Asiatic Soc. Bengal*, No. 146, 1 – 88.
- Wagler J. G.** (1830), *Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vögel. Ein Beitrag zur vergleichenden Zoologie*, J. G. Cotta, München – Stuttgart – Tübingen.
- Watrous L. E. and Wheeler Q. D.** (1981), "The outgroup comparison method of character analysis," *Syst. Zool.*, **30**, 1 – 11.
- Wiegmann A. F. A.** (1834), *Herpetologia Mexicana, seu Descriptio Amphibiorum Novae Hispaniae, quae Itineribus Comitibus de Sack, Ferdinandi Deppe et Chr. Guil. Schiede in Museum Zoologicum Berolinense Pervenirunt*, C. G. Lüderitz, Berlin.
- Wiegmann A. F. A.** (1835), "Bericht über die Fortschritte der Zoologie in Jahre 1834 vom Herausgeber (Schlufs)," *Arch. für Naturg.*, **I**, 255 – 348.
- Wiegmann A. F. A.** (1837), "Herpetologische Notizen vom Herausgeber," *Arch. für Naturg.*, **III**, 123 – 136.
- Wilson S. K. and Knowles D. G.** (1988), *Australia's Reptiles. A Photographic Reference to the Terrestrial Reptiles of Australia*, Collins Publishers, Sydney.