

Society for the Study of Amphibians and Reptiles

The Oldest Genus of Scincid Lizard (Squamata) from the Tertiary Etadunna Formation of South Australia

Author(s): James E. Martin, Mark N. Hutchinson, Robert Meredith, Judd A. Case and Neville S. Pledge

Reviewed work(s):

Source: *Journal of Herpetology*, Vol. 38, No. 2 (Jun., 2004), pp. 180-187

Published by: [Society for the Study of Amphibians and Reptiles](#)

Stable URL: <http://www.jstor.org/stable/1566212>

Accessed: 29/10/2012 11:56

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Society for the Study of Amphibians and Reptiles is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Herpetology*.

The Oldest Genus of Scincid Lizard (Squamata) from the Tertiary Etadunna Formation of South Australia

JAMES E. MARTIN,^{1,2} MARK N. HUTCHINSON,³ ROBERT MEREDITH,⁴
JUDD A. CASE,⁵ AND NEVILLE S. PLEDGE³

¹Museum of Geology, South Dakota School of Mines and Technology, Rapid City,
South Dakota 57701, USA; E-mail: james.martin@sdsmt.edu

³South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia

⁴Biology Department, University of California, Riverside, California 92521, USA

⁵Department of Biology, St. Mary's College of California, Moraga, California 94575, USA

ABSTRACT.—Recent expeditions to the Lake Palankarina area of South Australia resulted in the oldest and only known extinct skink genus in Australia. The holotype of a new genus and species, *Proegernia palankarinensis*, was collected from the basal portion of the Late Oligocene Etadunna Formation from the Minkina Local Fauna. Additional scincid fossils previously recovered from higher levels in the formation include material that may be referable to *Proegernia*. *Proegernia* is placed in the *Egernia* group within the Australian Lygosominae, based mainly on its closed Meckelian groove with the apex of the splenial notch low on the lingual surface. However, the apex is markedly more anterior in *Proegernia* than in any living *Egernia* group taxon. *Proegernia* possesses characters suggestive of its position as a stem taxon for later occurring skinks of the *Egernia* species groups. Even so, overall stage of evolution suggests that the Scincidae of Australia had a long evolutionary history prior to the Late Oligocene, a contention supported by previous molecular studies.

The Scincidae are the most abundant and diverse lizards in Australia. At least 38 genera and 378 species are recognized (Cogger, 2000) in Australia, and additional species are known but not yet described (e.g., Storr et al., 1999). Skink species range from 0.4 g and 35 mm snout–vent length (SVL) to 1000 g and 371 mm SVL (Hutchinson, 1993). The diversity of skink habitat preferences includes terrestrial, fossorial, arboreal, saxicoline, and semiaquatic. Skink diets are also diverse as reflected by various tooth morphologies, some of which are characteristic of lineages, whereas others are related to prey type (e.g., Estes and Williams, 1984).

Skink systematics emphasize cranial features and include a cranium covered with enlarged dermal plates, paired premaxillae, and parietals with a descending process that abuts against the epipterygoids (Estes et al., 1988). In fossil deposits, cranial material is often scarce or fragmentary (Smith, 1976), so most fossil skinks are identified by the peglike teeth and enlarged coronoid process of the dentary (Estes, 1983). Although these characters are shared with related groups (cordylids and anguoids; Lee, 1998), most skinks are distinguishable by mode of tooth replacement and tooth-crown shape (Edmund, 1969; Lang, 1991).

Given the diversity of Australian scincids, one might expect a long evolutionary history on the

continent. However, because of the isolation of Australia, one might also postulate rapid diversification caused by reduced competition and limited predators. Based upon immunological data, phylogenetic divergence of major scincid groups is postulated to have occurred during the earliest Tertiary, suggesting divergence of the family during the Cretaceous (Baverstock and Donnellan, 1990). Unfortunately, the fossil record is limited. A medial to late Eocene femur from the Rundle Formation, central east Queensland was reported by Hocknull (2000), who felt that the specimen warranted assignment to scinciforms but not enough morphological data were preserved for assignment to the Scincidae. Estes (1984) described skinks from the Late Oligocene Etadunna Formation, represented by dentary, maxillary, and parietal elements, which until now were the oldest well-documented skink fossils. Estes identified these specimens as *Egernia* and *Tiliqua*, but both were derived from higher in the stratigraphic section (Ditjimanka L.F.) than that described herein. Skinks from the early to medial Miocene Riversleigh assemblages were described by Hutchinson (1992) and include the *Egernia frerei* (= *Egernia major*) species group, the *Egernia striolata* species group, and *Tiliqua* (Hutchinson, 1992; Shea and Hutchinson, 1992). These *Egernia* comparisons were based upon plesiomorphic morphology or characters (especially dentition) that are phenetically similar to those of certain *Egernia* but of unclear

² Corresponding Author.

TABLE 1. Comparative species examined and *Egernia* species groups assignments.

Species group	Species included	Number specimens examined
<i>E. major</i>	<i>E. major</i>	2
	<i>E. frerei</i>	3
<i>E. whitii</i>	<i>E. whitii</i>	4
	<i>E. kintorei</i>	2
	<i>E. inornata</i>	2
	<i>E. margaretae</i>	3
	<i>E. multiscutata</i>	2
	<i>E. pulchra</i>	2
<i>E. cunninghami</i>	<i>E. striata</i>	2
	<i>E. cunninghami</i>	3
	<i>E. depressa</i>	1
	<i>E. hosmeri</i>	1
<i>E. striolata</i>	<i>E. stokesii</i>	4
	<i>E. striolata</i>	8
	<i>E. napoleonis</i>	2
	<i>E. richardi</i>	2
<i>E. luctuosa</i>	<i>E. saxatilis</i>	2
	<i>E. coventryi</i>	3
<i>E. kingii</i>	<i>E. kingii</i>	1

evolutionary polarity. Finally, Pledge (1992) described extant taxa from Plio-Pleistocene deposits. Because of the fragmentary nature of the scincid record, the occurrence of relatively well-preserved specimens from the late Oligocene, richly fossiliferous Etadunna Formation are important because they occur in some of the oldest Tertiary terrestrial deposits known from Australia.

MATERIALS AND METHODS

The fossil specimen described in this contribution was procured through field campaigns in cooperation among the institutions represented by the authors. Quarrying techniques of tuffaceous detrital layers from low in the preserved geological section produced the lower jaw. The jaw was then compared with 49 osteological specimens of the *Egernia* group (Greer, 1979) and, in particular, the *Egernia* species groups (Horton, 1972; Storr, 1978; Table 1). Specimens of the 19 *Egernia* species were measured and analyzed to quantify morphological characteristics of the splenial notch (49 specimens) and internal septum (24 specimens). Because of space limitations, these measurements and analyses are available from the authors.

STRATIGRAPHIC AND CHRONOLOGIC POSITION

The skink described herein was collected from the Lake Palankarinna area in the Tirari Desert of the eastern Lake Eyre Basin of South Australia. This fossiliferous region was discovered in 1953 by R. A. Stirton and R. H. Tedford from the

University of California, Berkeley, and their colleagues from the South Australian Museum, Adelaide. The major stratigraphic unit is the Etadunna Formation, named for the station (ranch) upon which the deposits and fossils were found (Stirton et al., 1961). The formation is approximately 40 m thick (Woodburne et al., 1993:484) and consists predominately of greenish tuffaceous siltstones and claystones interbedded with tan to white dolomitic units and some matrix-supported conglomerates grading into sandstones. These units represent lacustrine deposits interrupted by intervals of fluvial incursions in a somewhat rhythmical succession.

The Etadunna formational name was extended northward to include deposits at Lakes Kanunka, Pitikanta, and Ngapakaldi. As a result, the Ngapakaldi Fauna was an inclusive term for all vertebrates in the Etadunna Formation (e.g., Stirton et al., 1961, 1968; Rich et al., 1982). However, Woodburne, Tedford, and others (see Aplin and Archer, 1987, and articles in that volume) noted that the mammalian assemblages were distinct between the northern lakes and Lake Palankarinna. Consequently, the term Ngapakaldi Fauna was restricted to the northern assemblages above a dolomite marker bed, and the Ditjimanka Local Fauna was proposed for the vertebrates from Lake Palankarinna below a unit referred to as the "upper dolomite" (Woodburne et al., 1993). Pledge (1984) differentiated the Ngama L.F. at the northwestern corner of Lake Palankarinna from levels higher than those that produced the Ditjimanka L.F. Subsequent work (see Woodburne et al., 1993) indicated that an older local fauna occurred at the southwestern corner of Lake Palankarinna from the lowest stratigraphic levels. Consequently, Woodburne et al. (1993) subdivided the Etadunna Formation into five faunal "zones" (A-E) preliminarily based on stage of evolution of marsupial taxa, rather than first or last appearances of taxa: the Minkina, Ditjimanka, Ngapakaldi, Ngama, and Treasure local faunas. The lizard described here is from the oldest fossiliferous exposures at Lake Palankarinna, is part of the Minkina L.F. and was presumably deposited approximately 25–26 Ma (= late Oligocene).

SYSTEMATIC PALEONTOLOGY

Class: Reptilia

Order: Squamata

Family: Scincidae

Subfamily: Lygosominae

Proegernia palankarinensis
new genus and species

Holotype.—SAM (South Australian Museum) P39204, right dentary with 10 complete teeth and 12 alveoli or broken teeth for a total of at least 22

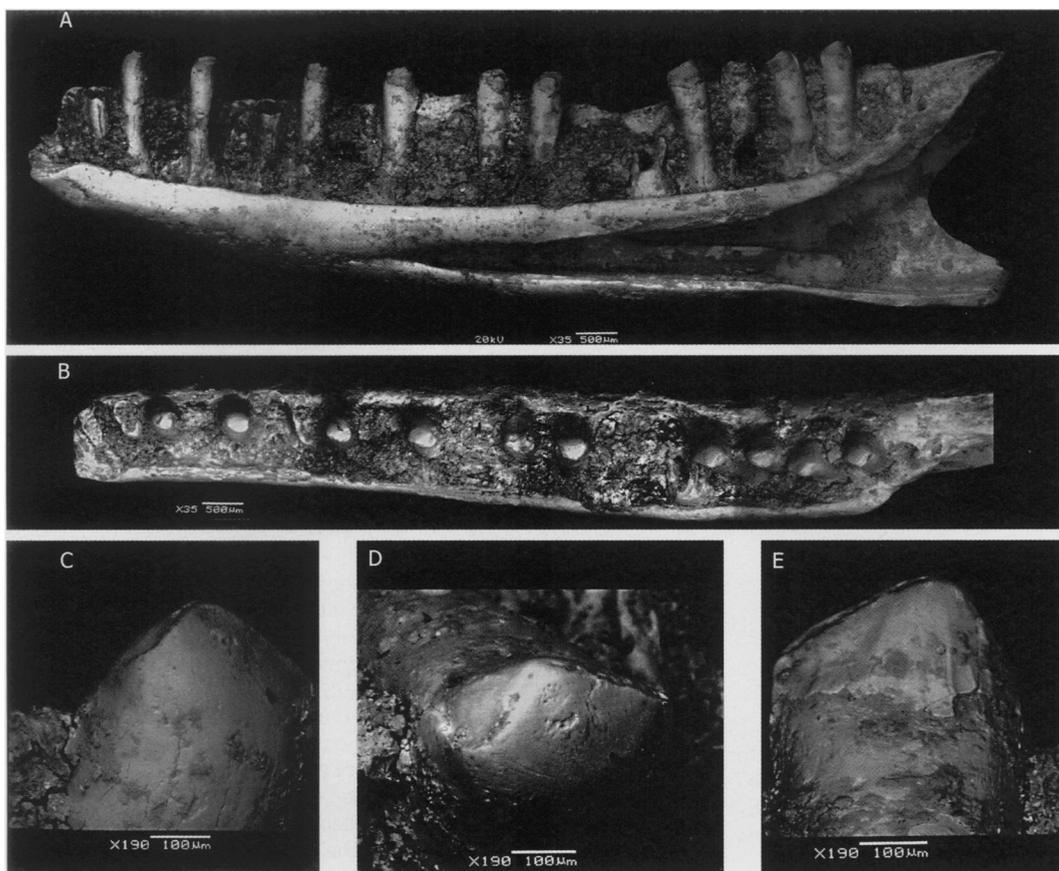


FIG. 1. Holotype of *Proegernia palankarinnensis* new genus and species, SAM P39204. (A) lingual view of right dentary; (B) dorsal (occlusal) view of dentary; (C) buccal view of 18th tooth from the anterior end; (D) occlusal view of 18th tooth; (E) lingual view of 18th tooth.

teeth (Fig. 1). Abrasion within the symphyseal region may have removed another alveolus, suggesting the possibility of a maximum of 23 teeth.

Etymology.—Derived from the Greek and Latin *pro*, meaning before or forward, indicating the early occurrence of an *Egernia*-like taxon. Named for the Lake Palankarinna area, source of the holotype; derived from Palankarinna, an aboriginal (Diyari) word, meaning place of intercourse, and the Latin suffix *ensis*, meaning native or resident in.

Type Locality.—Young Bucks Quarry (University of California, Riverside Locality RV-9002) in the Lake Palankarinna area, 30 km south of Etadunna Station; 28°47' S Latitude, 138°25' E Longitude; South Australia, Australia.

Stratigraphic Position.—Lower Etadunna Formation, Zone A (Woodburne et al., 1993).

Age.—Late Oligocene, 24–26 Ma (Woodburne et al., 1993).

Diagnosis.—The holotype is a member of the *Egernia* group (Greer 1979), with a closed Meckel-

ian groove and a large, elongate inferior alveolar foramen located relatively low and anterior. The genus is distinguished from other members of the *Egernia* group (*Egernia*, *Cyclodomorphus*, *Tiliqua*, and *Corucia*) by the anteriorly positioned apex of the splenial notch at 61% the anteroposterior length of the dentary; a patent suture of the Meckelian groove trending forward from the inferior alveolar foramen; and the anteriorly excavated caudal margin of the exposed internal septum.

Description.—The type specimen (Fig. 1A) is 10.05 mm from the anterior tip to the end of the angular process and exhibits several cycles of tooth replacement. The Meckelian canal is closed anterior to the inferior alveolar foramen by overgrowth of the dentary. However, a remnant millimeter-long groove occurs at the symphysis. The contact between the dentary and coronoid is robust and rises steeply as a distinct, posterodorsally directed coronoid process.

Lingually (Fig. 1A), the splenial notch is completely open 6.5 mm from the distal end of the angular process (5.3 mm from the indenture between the angular and coronoid processes and 6.1 mm from the end of the coronoid projection) to a position below the 12th preserved tooth from the anterior end (11th from the posterior end). At this point the dentary is 2.5 mm deep; its maximum height at the posterior end between the angular and coronoid processes is 2.8 mm. However, a patent groove extends anteriorly for a further 2.1 mm. The lower edge of the internal septum that separates the Meckelian groove and alveolar canal terminates at a point below the posterior end of the tooth row, but its margin is deeply excavated. The excavation reaches the 14th tooth, 4.25 mm from the distal end of the angular process (3.3 mm from the indenture between the coronoid and angular processes and 3.75 mm from the tip of the coronoid process). Labially, the jaw is smooth with eight nutrient foramina extending 4.1 mm from the anterior jaw tip to below the 13th preserved tooth from the anterior end.

The jaw has alveoli for 22 pleurodont teeth, although only 10 are preserved (Fig. 1B). However, a small portion of the symphyseal region has been abraded as the anterior opening of the Meckelian canal is visible. Perhaps a single tooth was lost during abrasion, suggesting that the maximum tooth number may have been 23. Some crowding of the first four teeth occurs. The teeth are seemingly more widely spaced than those of most *Egernia* species. All *Proegernia* teeth are wide at the bases and taper slightly upward. The tooth crowns are thumb-shaped, with curved lateral face and flattened medial face. The two surfaces meet and form an anteroposteriorly oriented apical ridge. In lateral view, the profile of the apical ridge forms a shallow, inverted asymmetrical vee, with the apex offset posteriorly (Fig. 1C–E). No distinct apical cusp occurs, nor any trace of the bicuspid crown morphology regarded as plesiomorphic for scincid lizards (Sumida and Murphy, 1987). Distinct striations trend vertically on both lingual and labial faces of SAM P39204. Relatively little differentiation of crown pattern exists along the tooth row.

Comparisons.—The majority of extant Australian skink species are part of the Lygosominae (Greer, 1970), which is characterized by fused frontals, a secondary palate formed by expanded ventral laminae of the palatines, and an angular contact between the ventrolateral ridge of the frontal or its ventral process and the prefrontal (Greer, 1970, 1986). Lygosomines comprise five major lineages (Honda et al., 2000), of which three are Australian (Greer, 1979, 1989): the *Sphenomorphus* group (13 genera), the *Egernia*

group (3 genera), and the *Eugongylus* group (16 genera). The *Sphenomorphus* group is characterized by the retained plesiomorphic open Meckelian groove occurring along the ventromedial margin of the dentary below the anterior half of the tooth row (lost several times within the group), as well as by an apomorphic parallel-sided retroarticular process. The *Egernia* group (following the restricted sense of Greer, 1979; see Hutchinson, 1993:278) exhibits an anteriorly closed Meckelian groove and a large, elongate inferior alveolar foramen but is otherwise plesiomorphic in having the foramen located relatively low and anterior, possessing a relatively large splenial, and exhibiting an inflected retroarticular. The *Eugongylus* group has a reduced or absent angular, reduced splenial, and an inflected retroarticular. Within the Lygosominae, *Proegernia* is excluded from the *Sphenomorphus* group owing to the anteriorly closed Meckelian canal and from the *Eugongylus* group because of its large splenial notch. *Proegernia* may be referred to the *Egernia* group because of its anteriorly closed Meckelian groove and large splenial.

The *Egernia* group includes approximately 50 species within three Australian genera (*Cyclodomorphus*, *Tiliqua*, and *Egernia*) and one in the Solomon Islands (*Corucia*). *Corucia* has laterally flattened teeth with fan-shaped crowns (Greer, 1976), unlike the columnar teeth of *Egernia* or *Proegernia* (Estes, 1984:339–340). *Cyclodomorphus* and *Tiliqua* are sister groups of large skinks with durophagous dentitions (Estes and Williams, 1984), again unlike *Egernia* or *Proegernia*. Within the *Egernia* group, the majority of species are placed in the genus *Egernia*. Members of this genus are currently defined by lacking the specializations of dentition and by the vertebral and cranial features that diagnose the other three genera (e.g., Shea, 1990). The species of *Egernia* have been placed into six species groups (Horton, 1972; Storr, 1978), based on external morphology and scalation: the *Egernia cunninghamii*, *Egernia major*, *Egernia striolata*, *Egernia kingii*, *Egernia whitii*, and *Egernia luctuosa* species-groups (See Table 1).

The size and shape of the holotype dentary compares favorably with members of several species groups of *Egernia*, particularly those in the *E. striolata* and *E. luctuosa* species groups that possess tooth crowns with slightly flared profiles, with a continuous lingual apical ridge lacking an apical cusp, and with only modest differentiation from the crowded anterior teeth to larger posterior teeth. The fossil specimen is approximately the size of most specimens of the *E. striolata*, *E. whitii*, and *E. luctuosa* species groups but much smaller (normally ~50%) than the *E. major*, *E. cunninghamii*, and *E. kingii* species groups. With 22 teeth represented in the

dentition, the fossil lies within the range of most dentitions of *Egernia*, except *E. cunninghami*, *E. kingii*, and some members of the *E. whitii* species groups, which normally possess more. Within *Egernia*, tooth morphology varies markedly. Members of the *E. whitii* species group have narrow-crowned teeth, with an apical cusp and angular rather than smoothly rounded corners at the anterior and posterior ends of the apical ridge where it meets the tooth shaft. The *E. luctuosa* species group has similar tooth morphology with an apical cusp, but the marginal corners are more rounded and the teeth are more laterally flattened. Largely herbivorous species of the *E. cunninghamii* species group have small, closely packed teeth with laterally compressed crowns having a sharp cutting edge. In some of the larger species, such as *E. kingii* and *E. frerei* (*E. major* species group), the teeth are robust with crowns expanded both anteroposteriorly and lingually. This morphology also develops later ontogenetically in *E. striolata* (Hutchinson, 1990), but in both *E. striolata* and the larger species mentioned, younger individuals show the same tooth morphology exhibited by the fossil specimen. The tooth crown shape of SAM P39204 is the basic pattern that has been modified within *Egernia*, as currently defined.

The splenial notch and the internal septum are distinctive in *P. palankarinnensis*, although the characteristics are approached by some members of the *Egernia* species groups. The anterior extent of the splenial notch and anterior position of the inferior alveolar foramen are more extreme than in any *Egernia* species we examined. Most species of *Egernia* show the anterior termination of the foramen/splenial notch at a point between 20 and 52% (average = 34%) from the posterior margin of the coronoid process, rather than the 61% as in the fossil. The closest approach to the condition in the fossil is seen in *Egernia coventryi* (*Egernia luctuosa* species group), in which the anterior alveolar foramen/splenial notch is 40% the dentary length measured from the posterior tip of the coronoid process and in *E. major* in which the splenial notch may be 52% of the dentary length; however, the latter species is three times the size of *P. palankarinnensis*. Moreover, the splenial notch length-overall jaw length ratio of *E. major* species group and *E. major* itself (exhibiting the largest noted ratio among extant species) is significantly smaller than that of *P. palankarinnensis* (probability 0.0001 at 95% Confidence Level). The internal septum dividing the Meckelian and alveolar canals is deeply excavated anteriorly on the holotype, and the ventral portion extends to near the end of the tooth row. In other species of *Egernia*, the anterior extent of the septum ranges from 14–32% (average 22%) of the dentary length measured

from the posterior end of the coronoid process. This compares with 37% of the dentary length in the fossil taxon. The extant species in which the extent of the septum is most similar to that of the fossil taxon is *E. frerei*. However, statistical analysis indicates that the length of the internal septum measured from the coronoid process to the septum apex compared to dentary length of this living species is significantly smaller than that of the fossil species (probability 0.0019 at 95% C.L.).

With greater sample size, two other characters may become important in differentiating *Proegernia* from other species groups. Observed specimens of *E. coventryi*, *E. kingii*, and some *E. stokesii* have a relatively longer, thin angular process compared to the short, stout process of *Proegernia* and most other *Egernia* species. Also, the holotype dentary exhibits eight mental foramina, whereas most other species exhibit six to seven.

Overall, the dental morphology and closure of the Meckelian groove indicate inclusion of the fossil taxon in the *Egernia* group, but the combination of features in the type specimen, especially the anteriorly extended splenial notch and the anteriorly positioned posterior margin of the internal septum differentiate this taxon from known Australian skinks. The anterior extent of the splenial notch may be plesiomorphic, representing a lesser extent of closure of the Meckelian groove than in living *Egernia*. The margins of the bone at the apex of the splenial notch are smooth, without articular facets for the surangular and splenial, and indicate the opening of the inferior alveolar foramen. This implied position for the inferior alveolar foramen is further forward compared to that of any living *Egernia*, and also compared to other skinks, even those without a closed Meckelian groove. Simple closure of the Meckelian groove would not be expected to leave the foramen in this topological position, implying that the anteriorly placed inferior alveolar foramen of *P. palankarinnensis* is an apomorphic character state.

DISCUSSION

Proegernia represents the oldest, unequivocal skink known from Australia, based upon the smoothly closed Meckelian groove, enlarged coronoid process, and dental morphology (Estes, 1983, 1984). Although a closed groove occurs in members of the Gekkonidae, relatively few, robust teeth differentiate *Proegernia*. Moreover, features such as the anteriorly open splenial notch, incomplete internal septum, generalized tooth crowns, and small size suggest this species could be ancestral to later skinks of the *Egernia* group. However, having more than 60% of the dentary exposed by the splenial notch, compared

to 50% or less for known species of *Egernia* and an incomplete internal septum separating the Meckelian canal from the alveolar canal suggests a lineage separated from the extant genus.

Estes (1984) considered specimens from the Etadunna Fm. (Ditjimanka L.F.) as skinks based on one apomorphic character state, closure of the Meckelian groove, combined with plesiomorphic character states, notably separation of the parietal scales by the interparietal, as evinced from the osteoderms adherent to the parietal, relatively unmodified teeth, and lack of obvious specializations. The holotype of *P. palankarinnensis* and Estes' specimens are distinguishable from any living *Egernia* species but strikingly similar to one another. We can assess this similarity only in a preliminary manner as Estes provided a single line drawing of each element (dentary in lingual view, maxilla in lateral view, and parietal in dorsal view), and these illustrations leave a number of characters indeterminable. He also did not provide meristic data aside from a scale bar accompanying the drawings. Moreover, searches of both the University of California, Riverside, and San Diego State University collections have failed to locate Estes' material. Given these limitations, the list of morphological similarities that can be gleaned from the single drawing is significant. The two are apparently identical in length (estimated 10 mm) and are immediately distinguished from extant *Egernia* species by the anteriorly placed inferior alveolar foramen situated near the midpoint of the tooth row (incomplete anteriorly in Estes' specimen). The foramen (apex of the splenial notch) terminates below the 11th tooth locus from the rear of the tooth row in both and is approximately 5 mm from the anterior limit of the indenture between the coronoid and angular processes. The depth of the jaw at the level of the inferior alveolar foramen (approximately 2 mm in Estes' specimen, 2.5 in SAM P39204) and at the posterior end of the tooth row (approximately 3 mm in Estes' specimen, 2.8 in SAM P39204) indicates that proportions as well as absolute size are comparable. Additional qualitative similarities include a dorsal groove for contact with the splenial above the inferior alveolar foramen, steeply rising contact facet for the coronoid, and relatively strong striations on the lingual faces of the tooth crowns. Other potential similarities, such as the morphology of the internal septum and detailed morphology of the tooth crowns are not determinable from Estes' illustrations. On current evidence, Estes' assignment to *Egernia* sp. should be regarded as *Proegernia* rather than *Egernia* (s.l.). Specific attribution is not advisable until the specimens are found, given that important distinguishing features of *P. palankarinnensis* are not yet known for Estes' younger specimens.

The occurrence of *P. palankarinnensis* in deposits of late Oligocene age sheds some light concerning possible ancestry and biogeography. As mentioned above, the closed Meckelian groove and dental morphology indicate the taxon is a basal member of the *Egernia* group. This occurrence confirms that this lineage dates to at least 25–26 Ma, and some time may have elapsed between the arrival of the scincid ancestor in Australia and the appearance of *Proegernia*. Living skinks are concentrated in the Southern Hemisphere, with most of the surviving stem-group "scincines" restricted to Gondwanan land masses (southern Africa, Madagascar, and India). The oldest fossils reported to be scincids are from North America, but the evidence for their familial assignments is weak. Estes (1969) described *Contogenys sloanei* from the Hell Creek Formation (Late Cretaceous) and Tongue River Formation (Medial Paleocene) of Montana as a scincid, but later (Estes, 1983) treated the scincid attribution of both *Contogenys* and *Paracontogenys* (Late Eocene) as tentative, mainly because of the paucity of characters provided by the material. Gao and Fox (1996) discussed these genera and concluded that *Paracontogenys* was most likely a xantusiid (probably congeneric with *Palaeoxantusia*) and *Contogenys* also was more similar to xantusiids than scincids. Gao and Fox (1996) also allocated one of their new taxa, *Penemabuya antecessor*, to the Scincidae, and identified two others, *Orthrioscincus mixtus* and *Aocnodromeus corrugatus* as probable scincids. In our view, familial assignment of any of the three genera is unwarranted, as the differential characters used are not restricted to the scincids, nor even typical of scincids in some cases. These taxa are best regarded only as scincomorphans and may be closer to cordylids than to scincids.

Molecular divergence among major skink lineages is profound (Baverstock and Donnellan, 1990; Honda et al., 2000) and suggests divergence of the family during the Paleocene or earlier. The likelihood is that this divergence occurred in Gondwana where great numbers of skinks now occur, although generally recognized less-derived skinks such as *Eumeces* and their relatives are from the Northern Hemisphere. The fossil record is becoming better known, and the recognition of extant lineages already differentiated 25 million years ago pushes the ultimate origin of these lineages, and therefore of skinks as a whole, further back in time. The possible existence of North American fossil scincids suggests that a northern origin is a persistent possibility, but much of the differentiation evidently occurred in the south. If a northern origin is substantiated, a corridor through Antarctica (Case et al., 2000) is now recognized

during the Late Cretaceous and may have provided the route by which skinks dispersed.

Acknowledgments.—We thank A. Greer and anonymous reviewers, who made valuable suggestions that resulted in a much better contribution. We also thank M. Gabel, Department of Biology, Black Hills State University, who spent a great amount of time and lent expertise to produce the SEM photographs for illustrations herein. The Royal Geographic Society of London/Discovery Channel-Europe provided partial field funding through a prize awarded to the first author. The National Science Foundation (OPP 0087972) provided ancillary funding for study of Gondwanan fossil reptiles through grants awarded to the first author. Additional funding through the Faculty Development Fund was provided by St. Mary's College to the fourth author. We thank K. Aplin, Western Australia Museum, for loan of Recent comparative specimens and M. O. Woodburne, University of California, Riverside, for loan of additional squamate specimens.

LITERATURE CITED

- APLIN, K. P., AND M. ARCHER. 1987. Recent advances in marsupial systematics with a new syncretic classification. *In* M. Archer (ed.), *Possums and Opossums: Studies in Evolution*, pp. xv–lxxi. Surrey Beatty and Sons, Sydney, New South Wales, Australia.
- BAVERSTOCK, P. R., AND S. C. DONNELLAN. 1990. Molecular evolution in Australian dragons and skinks: a progress report. *Memoirs Queensland Museum* 29:323–331.
- CASE, J. A., J. E. MARTIN, D. S. CHANEY, M. REGUERO, S. A. MARENSSI, S. M. SANTILLANA, AND M. O. WOODBURN. 2000. The first Duck-Billed Dinosaur (Family Hadrosauridae) from Antarctica. *Journal Vertebrate Paleontology* 20:612–614.
- COGGER, H. G. 2000. *Reptiles and Amphibians of Australia*. 6th ed. Reed New Holland, Sydney, New South Wales, Australia.
- EDMUND, G. 1969. Dentition. *In* C. Gans, A. d'A. Bellairs, and T. Parsons (eds.), *Biology of the Reptilia*, pp. 117–200. Academic Press, London.
- ESTES, R. 1969. A scincoid lizard from the Cretaceous and Paleocene of Montana. *Breviora* 331:1–9.
- . 1983. *Handbuch der paläoherpetologie*. *Encyclopedia of Palaeo-herpetology*. Part 10A. Sauria terrestria, Amphibia. Gustav Fischer Verlag, Stuttgart, Germany.
- . 1984. Fish, amphibians and reptiles from the Etadunna Formation, Miocene of South Australia. *Australian Zoologist* 21:335–343.
- ESTES, R., AND E. E. WILLIAMS. 1984. Ontogenetic variation of molariform teeth of lizards. *Journal of Vertebrate Paleontology* 4:96–107.
- ESTES, R., K. DE QUEIROZ, AND J. GAUTHIER. 1988. Phylogenetic relationships within Squamata. *In* R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp*. Stanford Univ. Press, Stanford, CA.
- GAO, K., AND R. C. FOX. 1996. Taxonomy of late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bulletin of Carnegie Museum of Natural History* 33:1–107.
- GREER, A. E. 1970. A subfamilial classification of scincoid lizards. *Bulletin Museum of Comparative Zoology, Harvard* 139:151–184.
- . 1976. On the evolution of the giant Cape Verde scincoid lizard *Macrosцинus coctei*. *Journal Natural History* 10:691–712.
- . 1979. A phylogenetic subdivision of Australian skinks. *Records Australian Museum* 32:339–371.
- . 1986. Lygosomine (Scincidae) monophyly: a third corroborating character and a reply to critics. *Journal of Herpetology* 20:123–126.
- . 1989. *The Biology and Evolution of Australian Lizards*. Surrey, Beatty and Sons, Pty. Limited, Chipping Norton, New South Wales, Australia.
- HOCKNULL, S. A. 2000. Remains of an Eocene skink from Queensland. *Alcheringa* 24:63–64.
- HONDA, M., H. OTA, M. KOBAYASHI, J. NABHITABHATA, H.-S. YONG, AND T. HIKIDA. 2000. Phylogenetic relationships, character evolution, and biogeography of the subfamily Lygosominae (Reptilia: Scincidae) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 15:452–461.
- HORTON, D. R. 1972. Evolution in the genus *Egernia*. *Journal Herpetology* 6:101–109.
- HUTCHINSON, M. N. 1992. Origins of the Australian scincoid lizards: a preliminary report on the skinks of Riversleigh. *Beagle, Records Northern Territory Museum of Arts and Sciences* 9:61–70.
- . 1993. Family Scincidae. *In* C. J. Glasby, G. J. B. Ross, and P. L. Beesley (eds.), *Fauna of Australia*. Vol. 2A. Amphibia and Reptilia, pp. 261–279. Australia Government Publishing Service, Canberra, Australian Capital Territory, Australia.
- LANG, M. 1991. Generic relationships within Cordyliformes (Reptilia: Squamata). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* 61:121–188.
- LEE, M. S. Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards [sic] resolution of squamate relationships. *Biological Journal Linnean Society* 65:369–453.
- PLEDGE, N. S. 1984. A new Miocene vertebrate faunal assemblage from the Lake Eyre Basin: a preliminary report. *Australian Zoologist* 21:345–355.
- . 1992. The Curramulka local fauna: a late Tertiary fossil assemblage from Yorke Peninsula, South Australia. *The Beagle* 9:115–142.
- RICH, T. H., M. ARCHER, M. PLANE, T. F. FLANNERY, N. S. PLEDGE, S. HAND, AND P. V. RICH. 1982. Australian Tertiary mammal localities. *In* P. V. Rich and E. M. Thompson (eds.), *The Fossil Vertebrate Record of Australasia*, pp. 526–572. Monash Univ. Offset Printing Unit, Clayton, Victoria, Australia.
- SHEA, G. M. 1990. The genera *Tiliqua* and *Cyclo-domorphus* (Lacertilia: Scincidae): generic diagnoses and systematic relationships. *Memoirs Queensland Museum* 29:495–520.
- SHEA, G. M., AND M. N. HUTCHINSON. 1992. A new species of *Tiliqua* (Lacertilia: Scincidae) from the

- Miocene of Riversleigh. *Memoirs Queensland Museum* 32:303–310.
- SMITH, M. J. 1976. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia IV. Reptiles. *Transactions of the Royal Society of South Australia* 100:39–51.
- STIRTON, R. A., R. H. TEDFORD, AND A. H. MILLER. 1961. Cenozoic stratigraphy and vertebrate paleontology of the Tirari Desert, South Australia. *Records South Australian Museum* 14:19–31.
- STIRTON, R. A., R. H. TEDFORD, AND M. O. WOODBURNE. 1968. Australian Tertiary deposits containing terrestrial mammals. *Univ. of California Publications Geological Sciences* 77:1–30.
- STORR, G. M. 1978. The genus *Egernia* (Lacertilia: Scincidae) in Western Australia. *Records of the South Australian Museum* 6:147–187.
- STORR, G. M., L. A. SMITH, AND R. E. JOHNSTONE. 1999. Lizards of Western Australia. I Skinks. *Western Australia Museum, Perth, Western Australia, Australia*.
- SUMIDA, S. S., AND R. W. MURPHY. 1987. Form and function of the tooth crown structure in gekkonid lizards (Reptilia, Squamata, Gekkonidae). *Canadian Journal of Zoology* 65:2886–2892.
- WOODBURNE, M. O., B. J. MACFADDEN, J. A. CASE, M. S. SPRINGER, N. S. PLEDGE, J. D. POWER, J. M. WOODBURNE, AND K. B. SPRINGER. 1993. Land mammal biostratigraphy and magnetostratigraphy of the Etadunna Formation (Late Oligocene) of South Australia. *Journal Vertebrate Paleontology* 13:483–515.

Accepted: .

Journal of Herpetology, Vol. 38, No. 2, pp. 187–196, 2004
Copyright 2004 Society of Amphibians and Reptiles

Taxonomy and Geographic Variation in the Leaf-Nosed Snake *Phyllorhynchus decurtatus* (Squamata: Colubridae)

STEPHANIE A. GARDNER AND JOSEPH R. MENDELSON III¹

Department of Biology, Utah State University, Logan, Utah 84322-5305, USA

ABSTRACT.—The previously recognized subspecies (used here as a heuristic tool) of *Phyllorhynchus decurtatus* artificially compartmentalize the inconsistent geographic variation in this species. Principal component analysis did not identify consistent geographic groupings of individuals. Regression Analysis revealed a longitudinal cline in number of ventral scales, as well as some weaker clinal trends in other characters. There is extensive overlap in all morphological and color-pattern characters examined between four subspecies of *P. decurtatus* and their intergrades. There are differences between mean scale and blotch counts between previously recognized subspecies, but they do not represent discrete differences among these taxa. Discriminant Analysis demonstrated the inconsistency in the observed geographic variation in this species. We conclude that *P. decurtatus* represents a geographically variable species lacking consistent geographic pattern classes.

Phyllorhynchus decurtatus was first described by Cope (1868) as *Phimothyra decurtata*. Stejneger (1890) later referred the taxon to the genus *Phyllorhynchus*. Five subspecies of *P. decurtatus* and their distributions have been described (Fig. 1; McCleary and McDiarmid, 1993). McCleary and McDiarmid (1993) suggested that most of these putative subspecies may actually be ecomorphs resulting from differences in incubation temperature. Similarly, Grismer (1999) compared *Phyllorhynchus decurtatus arenicola* to *Phyllorhyn-*

chus decurtatus decurtatus and found overlap in the diagnostic characters of these two subspecies; he placed *P. d. arenicola* as a junior synonym of *P. decurtatus*. Stebbins (2003) did not incorporate any subspecific designations for *P. decurtatus*, and Grismer (2002) referred all subspecific taxa on the Baja California Peninsula to simple pattern classes. However, neither of these two authors included explicit analyses of data.

Distinct evolutionary species may go unrecognized among the variation in widespread species, and closer evaluation of subspecific taxa may reveal the existence of species (see discussions by Burbrink et al., 2000). In any case, studies of geographic variation inform the discovery of

¹ Corresponding Author. E-mail: sapo@biology.usu.edu