Zootaxa 3490: 1–29 (2012)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Article

urn:lsid:zoobank.org:pub:A0DB5E47-3CBC-44D7-83A1-5235E9EE289D

On the identity of the type species of *Sphenomorphus* (Squamata: Scincidae): *Lygosoma melanopogon* Duméril and Bibron 1839, with a note on a new scalation character of the pes in *Sphenomorphus*

GLENN M. SHEA
Faculty of Veterinary Science B01, University of Sydney, NSW 2006 and The Australian Museum, 6 College St, Sydney, NSW 2000, Australia. E-mail: glenn.shea@sydney.edu.au

Abstract

The type series of *Lygosoma melanopogon* Duméril and Bibron 1839, the type species of the scincid lizard genus *Sphenomorphus* Fitzinger 1843, consists of four specimens representing three species, all of which have available junior synonyms. A lectotype is designated, and *Lygosoma melanopogon* becomes a senior synonym of *Lygosoma florense* Weber 1891 (= *Sphenomorphus florensis*) and that species is redefined based on specimens from throughout its distribution for the first time. Based on a lack of consistent differences in morphology and coloration, previously named subspecies of *Sphenomorphus florensis* are placed in synonymy, leaving a single wide-ranging species *S. melanopogon*. *Lygosoma Kühnei* Roux 1910 is also placed in the synonymy of *S. melanopogon*, and the nomenclatural status of the name *Scincus naevius* Duméril and Bibron 1839 resolved. *Lygosoma Meyeri* Doria 1874 is raised from synonymy to become the name for the New Guinean *Sphenomorphus* species to which the name *S. melanopogon* has sometimes previously been applied, and *Hinulia papuensis* Macleay 1877 synonymised with it. *Sphenomorphus melanopogon* is identified as a member of a group of *Sphenomorphus* species which show an extension of the imbricate dorsal scalation onto the solar surface of the pes.

Key words: *Sphenomorphus*, Indonesia, New Guinea, taxonomy, nomenclature, foot morphology

Introduction

As currently understood, the genus *Sphenomorphus* Fitzinger 1843 is a large and diverse polyphyletic assemblage of lygosomine skinks centered over Australasia. In encompassing many species and several poorly understood lineages, the genus is the current conceptual heir to the genus *Lygosoma* of the Boulengerian era. Resolution of these lineages is an area of current research (Greer 1979, 1983, 1991, 1997; Böhme 1981; Ferner *et al*. 1997; Mecke *et al*. 2009; Reeder & Reichert 2011; Linkem *et al*. 2011) and is approaching the point where the identity of the type species of the genus *Sphenomorphus* is important. The purpose of this paper is to solve this problem, to discuss some of the taxonomic consequences that follow from it, and to note the existence of a character of the pes that characterises this species and several other species of *Sphenomorphus*.

Materials and methods

Specimens, including all primary type material, were examined from the following collections: American Museum of Natural History, New York (AMNH), Australian Museum, Sydney (AM), Natural History Museum, London (BMNH), Bernice P. Bishop Museum, Honolulu (BPBM), Field Museum of Natural History (FMNH), Museum of Comparative Zoology, Harvard University, Cambridge (MCZ), Museum National d'Histoire Naturelle, Paris (MNHN), Museo Civico di Storia Naturale, Genoa (MSNG), Naturhistorisches Museum, Basel (NMBA), Naturhistorisches Museum, Vienna (NHMW), Papua New Guinea National Museum, Port Moresby (PNGNM), Naturalis, Nationaal Natuurhistorisches Museum, Leiden (RMNH.RENA), South Australian Museum (SAM),

Accepted by L. Grismer: 26 Jul. 2012; published: 19 Sept. 2012

Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt (SMF), University of Papua New Guinea, Port Moresby (UPNG), National Museum of Natural History, Smithsonian Institution, Washington (USNM), Vietnam National Museum of Nature, Hanoi (VNMN),Western Australian Museum, Perth (WAM), Zoologisches Museum, Universitei van Amsterdam, Amsterdam, now in Naturalis, Leiden (ZMA), Museum für Naturkunde der Humboldt-Universität, Berlin (ZMB), Zoologisches Sammlung des Bayerischen Staates, Munich (ZSM). In addition to specimens directly examined, I was provided with additional data and counts for some specimens examined by Dr. Allen Greer, formerly of the Australian Museum. In only a few cases did we examine the same specimens.

Nomenclature for head shields follows Taylor (1935). Head scales present bilaterally and not in median contact were counted on both sides of the head — hence sample sizes for such counts are approximately double the number of specimens examined.

Midbody scales (longitudinal rows of scales at midbody) were counted at the middle of the axilla–groin interval. Greer and I counted paravertebral scales and subdigital lamellae using different definitions, and hence these counts are presented in two categories. I counted paravertebral scales from the first scale behind the parietal to the last scale anterior to the level of the anterior margin of the hind limb (herein referred to as paravertebral scales A), while Greer took the limit as anterior to the level of the posterior margin of the hind limb (paravertebral scales B). For lamellae below the fourth toe, I began my count at the junction of the third and fourth toes (subdigital lamellae A), while Greer began more distally, including only those differentiated lamellae beginning basally at the level of the metatarsophalangeal joint (subdigital lamellae B) — this difference is due to the unusual feature in *Sphenomorphus melanopogon* of the free digit incorporating about a third of the distal end of the metatarsals. This basal portion of the digit is covered ventrally by imbricate scales, which more distally become differentiated into discrete lamellae.

Subdigital lamellae counts are averaged across both sides to maintain parity in sample sizes (a single value per specimen), although when presenting ranges, the extreme values are listed. Where two counts are provided for an individual, the first count is for the left side, the second for the right side.

The measurements snout–vent length (SVL), axilla–groin length (AGL), fore limb length (FLL), hind limb length (HLL) and tail length (TL) follow Cogger (2000), with the addition of head length (HL: from tip of snout to anterior margin of ear), head width (HW: maximum width of head across temporal region) and head depth (HD: maximum depth of head over parietal table, including the lower jaw). Non-cephalic measurements were made with the structure gently stretched along a metal ruler, and were made to the nearest 0.5 mm, while cephalic measurements were made with dial callipers to the nearest 0.1 mm.

Specimens were sexed by direct examination of gonads by a short incision, either midventrally or lateroventrally. Not all individuals were able to be dissected to examine gonads.

For orthography of specific epithets, I use the original form when citing the original combination, and the emended form, according with the Code of Zoological Nomenclature, in subsequent combinations.

Systematics

The identity of *Lygosoma melanopogon*. The type species of *Sphenomorphus* Fitzinger, by original nomination, is *Lygosoma melanopogon* Duméril and Bibron, 1839. The original description of the species emphasised the presence of six or seven supraoculars, a feature unique in their concept of the genus *Lygosoma*, but now known to occur in a number of *Sphenomorphus* species (Greer & Parker 1967). Other features noted in the description and useful in *Sphenomorphus* systematics are a high number of midbody scales (50), a high number (30–40) of single or smooth (the French "unies" can mean either) subdigital lamellae, prefrontals in contact (as "fronto-nasale"), seven supralabials, a tall narrow anterior loreal, and the dark throat to which the specific epithet draws attention.

Duméril and Bibron (1839) did not clearly indicate the extent of the type series, but mentioned three localities, New Guinea, Australia (as Nouvelle-Hollande) and Timor, and stated that specimens from all three were present in the MNHN collection, represented by material received from Péron and Lesueur, and from Quoy and Gaimard. They also listed in their description three names, *Scincus naevius*, *Scincus Erythrolamus* and *Scincus melanopogon*, the first proposed by "Péron, Mus. Par.", the latter two by "Müller, Mus. de Leyde". I have not been able to trace any published use of these three names prior to Duméril and Bibron's description. They seem to be unpublished names associated with the specimens examined, and the inclusion of the latter two names in synonymy suggests that Duméril and Bibron examined material obtained from Leiden.

The MNHN material was subsequently listed by Duméril and Duméril (1851), who reported specimens from New Holland obtained from Péron and Lesueur, from New Ireland obtained from Quoy and Gaimard, and from Timor, donated by the Musée de Leyde (now Naturalis, RMNH), but did not specify numbers of specimens.

Guibé (1954) listed only a holotype, MNHN 1245, registered with the locality Nouvelle-Hollande, and obtained from Péron. Roux-Esteve (1979) also listed this specimen as the "type" of *Lygosoma melanopogon*. Brygoo (1985) listed four syntypes, MNHN 1245, New Holland (Péron and Lesueur), 1244 and 7110, Timor (Musée de Leyde), and 2974, New Ireland (Quoy and Gaimard), corresponding to the localities and collectors listed earlier by Duméril and Duméril (1851). Brygoo also noted that Guibé's listing of a single specimen as holotype might qualify as a lectotype designation ("On peut admettre qu'il a alors désigné le lectotype de l'espèce").

Under the Third Edition of the Code of Zoological Nomenclature in force at the time of Brygoo's comment, listing of a holotype or "type" for a species based on syntypes qualified as a lectotype designation (Article 74(b)), and hence Brygoo's comment could be interpreted as formally recognising such a lectotype designation. However, the current Code (2000) alters this provision, and it only now applies when the original description "neither implies nor requires that there were syntypes" (Article 74.6). As Brygoo did not state clearly that he interpreted Guibé's listing in this fashion (indeed, he still listed all four types as syntypes), and as the original description clearly indicates that more than one specimen was involved, then it could equally be interpreted that no lectotype designation has been made yet.

All four specimens listed by Brygoo (1985) were presumably available to Duméril and Bibron (1839) as all had been collected well before this date. Francois Péron and Charles-Alexandre Lesueur collected together only on the Baudin expedition of 1800–1804, which visited both Australia and Timor (Baudin 1974; Brown 2004; Duyker 2006). Jean René Constant Quoy and Joseph Paul Gaimard visited New Ireland only during the 1826–1829 voyage of the Astrolabe, commanded by Dumont D'Urville (Dunmore 1969). Salomon Müller and Heinrich Christian Macklot collected in Timor and New Guinea during1828–1829, as members of the Triton expedition, with their collections being sent to Leiden (Wichmann 1910; Fransen *et al.* 1997). These four specimens also have the prime diagnostic character of six or seven supraocular scales stressed by Duméril and Bibron.

The first hint that the type series might be composite came from Boulenger (1887), who listed *Lygosoma melanopogon* both as a distinct species and in the synonymy of *L. variegatum* Peters 1867 (although it is apparent from other evidence that Boulenger's action was based on material in London, and not the type series; see below). Boulenger (1887, 1914) referred material from New Guinea to *L. melanopogon*, and the application of the name to this New Guinea species was subsequently followed by most authors (de Rooij 1915; de Jong 1930; Loveridge 1948; Capocaccia 1961; Scott *et al*. 1977; Whitaker *et al*. 1982; Welch *et al*. 1990; Allison *et al*. 1998).

Lidth de Jeude (1895) explicitly stated that Duméril and Bibron's (1839) original concept of *Lygosoma melanopogon* included three species, all of which had been subsequently described: *L. variegatum* Peters 1867, *L. Meyeri* Doria 1874 and *L. florense* Weber 1891. Lidth de Jeude further recommended that the name *L. Meyeri* should be resurrected for the New Guinean species to which Boulenger had applied the name *melanopogon*.

Having examined all four syntypes, I concur with Lidth de Jeude that the four specimens represent three distinct species, but disagree in part with his identification of the species involved.

Two of the syntypes, MNHN 1245 and 7110 (Figs. 1–2), represent the species which has usually been referred to as *S. florensis*. This is the only one of the three species possessing a black throat (present in many individuals/populations). While the other two species may have some dark streaking on the throat in some individuals, it never forms a predominantly black throat. *Sphenomorphus florensis* also has a high number of scale rows at midbody (38–47), a high number (25–34, method A) of undivided, smoothly rounded lamellae below the fourth toe, a mode of seven supralabials, medially contacting prefrontals, and a tall narrow anterior loreal. However, it does not attain the size listed by Duméril and Bibron for *L. melanopogon* (maximum snout-vent length 80 mm, n = 195, vs. 103 mm, the sum of Duméril and Bibron's measurements for head + neck + body). This species occurs in Timor, agreeing with the locality for MNHN 7110, but does not occur in Australia, *contra* the locality for MNHN 1245. However, the Baudin expedition, on which MNHN 1245 was collected, visited both Australia and Timor (Duyker 2006), and there are a number of similar swapped localities for other specimens collected during this expedition (Hellmayr 1916; Stresemann 1951). Hence, I consider the registered locality for this specimen to be in error for Timor, the only locality within the range of this species that was visited by Péron (Duyker 2006).

MNHN 7110, obtained from the Leyden Museum, is presumably derived from a series of 11 extant specimens of *S. florensis* (RMNH.RENA 2535) in the latter collection labelled as *Scincus melanopogon* and collected in

Timor by Salomon Müller and Heinrich Christian Macklot. A second series of 12 *S. florensis* (RMNH.RENA 2534), was collected by the same collectors from Samao (= Pulau Semau, a small island close to Kupang, the main settlement and port on the western end of Timor), but from the different nominal locality this is less likely to have been the source of the MNHN specimen. Brongersma (1942) published a colour drawing of *S. florensis* prepared in 1829 by the artist Pieter van Oort, who accompanied Müller and Macklot, and which clearly shows the black throat of this species. It is clear that Müller's manuscript name *Scincus melanopogon*, which prompted Duméril and Bibron to apply the specific epithet *melanopogon* to this species, was based on *S. florensis*.

The second species in the type series of *L. melanopogon* represents the New Guinean species to which the name has generally been applied, and for which two subsequent names, *Lygosoma Meyeri* Doria 1874 and *Hinulia papuensis* Macleay 1877, are available. MNHN 1244 (Fig. 3A) has 50 midbody scales, contacting prefrontals, a tall narrow anterior loreal, seven supralabials and a snout–vent length (101 mm) approximating the value given by Duméril and Bibron. The number of lamellae below the fourth toe is not determinable on this specimen, but the species has a range of 14–22 (n = 187, method A) subdigital lamellae, well below the range provided by Duméril and Bibron. Further, this species consistently has a predominantly pale throat. The specimen is similar in state of preservation to an extant series of three specimens (RMNH.RENA 3830) collected from New Guinea by Müller and Macklot, and associated with the jar label *Scincus erythrolaimus*. This presumably accounts for the other Müller name listed by Duméril and Bibron (1839). The locality Timor associated with the Paris member of this series does not agree with knowledge of the distribution of this species. However, Müller and Macklot had also visited New Guinea earlier on the same expedition (Wichmann 1910; Fransen *et al*. 1997), and the locality New Guinea associated with the Leiden series suggests that localities have become confused.

The final specimen in the type series, MNHN 2974 (Fig. 3B), is typical of the Bismark Archipelago form of *Sphenomorphus jobiensis* (Meyer 1874). Of the characters emphasised by Duméril and Bibron (1839), this specimen has contacting prefrontals, but differs from the type description of *L. melanopogon* in having a pale throat, fewer scales at midbody (43), fewer lamellae below the fourth toe (24/25, method A), an anterior loreal divided into an upper and lower scale, and eight supralabials.

It is not possible to nominate a lectotype that is fully compatible with the type description and original diagnosis of *Lygosoma melanopogon*. However, choosing one of the *S. florensis* specimens as lectotype will link the name *melanopogon* with the species to which the name was first applied in manuscript, will agree with the only previous specific discussion of the application of the name (Lidth de Jeude 1895), will most closely fit the original diagnosis of the species, and will link the name with the species that is best represented in the type series. As MNHN 1245, the earliest-collected specimen in the type series, has previously been identified as the primary type of *L. melanopogon* (Guibé 1954; Roux-Esteve 1979), and it has previously been suggested that this could qualify as a lectotype designation (Brygoo 1985), I believe that continuing stability is best served by formally nominating MNHN 1245 as the lectotype of *Lygosoma melanopogon*.

I also nominate ZMA 11060 as lectotype of *Lygosoma florense* Weber 1891, the largest and least bleached of the identifiable members of the syntype series.

There remain three problems associated with *Lygosoma melanopogon*: the status of *Scincus naevius*; the status of *Sphenomorphus kuehnei*; and the subspecies within *S. melanopogon*.

The status of *Scincus naevius*. The first of these concerns the name *Scincus naevius*, proposed by Péron for MNHN material. The basis for this name would appear to be the lectotype of *L. melanopogon*, collected by Péron and the only extant specimen available prior to Péron's death on 14 December 1810 (Whittell 1954; Duyker 2006). Although this is generally considered an unavailable name as first appearing in synonymy, it was used as an available name in five subsequent publications (Gray 1841, as *Tiliqua naevia* Péron; Gray 1845, as *Hinulia naevia*, with the specific epithet again attributed to Péron; Günther 1876, as *Hinulia naevia*; O'Shaughnessy 1877, as *Hinulia naevia* Gray, and Peters and Doria 1878, as *Lygosoma* (*Hinulia*) *naevium* Gray), with the name explicitly given priority over *melanopogon* by Gray and by Peters and Doria. Gray (1845) and Peters and Doria (1878) also provide a description. This adoption of a previously unavailable name as the name of a taxon validates and makes available the name (Article 11.6.1 of the Code of Zoological Nomenclature). The author and date of publication of the validated name is Duméril and Bibron (1839) (Article 50.7). As Duméril and Bibron (1839) did not explicitly state that only a single specimen was associated with the name, and as the type series of *L. melanopogon*, the name under which *naevius* first appears, consists of four specimens, a lectotype designation is required for *Scincus naevius*. I accordingly nominate MNHN 1245, the specimen on which Péron based the name in manuscript, as the lectotype of *Scincus naevius* Duméril and Bibron (1839), thereby permanently making this name a junior synonym of *Lygosoma melanopogon.*

Although Duméril and Bibron (1839) must be credited with the name *naevius*, it is Gray (1845) who is responsible for the subsequent history of this name. Gray referred two specimens in the British Museum (now in BMNH) to *Hinulia naevia*: one from New Guinea (BMNH 44.2.22.110, now 1937.12.6.7) obtained from the Leyden Museum (and probably derived from the same Müller and Macklot series as MNHN 1244), the other from the Philippines, obtained from Mr. Cuming (possibly BMNH xv.2b, Philippines, Mr. Cuming; the shelf number allocated to this specimen indicates that it was available to Gray for his catalogue; current identification *S. jagori* Peters 1864). When describing *Lygosoma* (*Hinulia*) *variegatum* from the Philippines, Peters (1867) noted that it was very similar to *L. melanopogon*. Günther (1873), mentioning Peters' description, obliquely implied that Philippines records of *L. melanopogon* were referrable to *L. variegatum*. It was presumably Gray's two specimens and Günther's subsequent restriction that led Boulenger (1887) to continue to apply the name *L. melanopogon* to the New Guinea species, while also listing the name in the synonymy of *L. variegatum*.

The status of *Sphenomorphus kuehnei*. The second problem relates to the status of the species *Lygosoma Kühnei* [= *kuehnei*] described from six specimens from an unspecified locality in the Kei Islands [= Kepulauan Kai] by Roux (1910). Roux compared his new species with *L. melanopogon*, but it is evident from the character states described that Roux followed Boulenger (1887) in applying the latter name to *S. meyeri*. Roux provided no comparison with the taxon then known as *S. florensis*. Additional specimens from Lontoor (= Palau Banda Besar), Palau Teun and Tepa, all to the west of the type locality, were referred to this species by Kopstein (1926, 1927). The species was next mentioned by Loveridge (1948), who treated it as a subspecies of *Lygosoma striolatum* Weber due to the shared presence of fine striations on the scales, combined with a difference in throat colour (dark in *kuehnei*, white in *striolatum*). This synonymy is the only evidence I can identify for the subsequent listing (Scott *et al*. 1977) of *Sphenomorphus striolatus* among the New Guinea herpetofauna. *Sphenomorphus kuehnei* was more recently listed as distinct by Welch *et al*. (1990). Loveridge's action is flawed, as finely striate scales are present in several Indonesian *Sphenomorphus*, including *S. melanopogon*. I have examined the lectotype (NMBA 5514; designated by Kramer 1979) and one paralectotype (MCZ 27945) of *L. Kühnei* and Greer has provided me with notes on the remaining paralectotypes (NMBA 5513, 5515–17), and they agree in all respects with *S. melanopogon*. All of the scalational features described by Roux (1910) occur within the *S. melanopogon* samples I have examined from Timor, the restricted type locality of the latter species.

Subspecies within *S. melanopogon*. The final problem relates to the application of subspecies names within *Sphenomorphus melanopogon* (= *S. florensis* auctorum). Dunn (1927) recognised four subspecies within *S. florensis*: the nominate subspecies from Padar and Flores, *S. f. nitidus* from Komodo (Fig. 8A), *S. f. barbouri* from Wetar (Fig. 8B) and *S. f. weberi* from Damar. Dunn differentiated his subspecies only on coloration, noting that he could find no scalational differences between the five islands. With larger and more geographically spread samples, I agree that there are no clear scalational differences between different island populations (Table 1).

As noted by Dunn, and other authors, there is much individual variation in coloration in *S. florensis*, even within populations. Some of this variation is ontogenetic, some has been suggested to be sexual or seasonal (Dunn 1927; Auffenberg 1980). The complex nature of the variation in coloration makes analysis of the geographic distribution of the colour patterns difficult. Dunn (1927), although describing coloration of "young", "medium" and "adult" lizards, did not provide any indication of the size at maturity; nor have most subsequent authors. Auffenberg (1980) stated that sexual maturity in the material available to him from Komodo, Padar and western Flores was attained at an SVL of about 58 mm. However, only one of the 12 females I examined from Komodo had an SVL of greater than 52 mm.

The material available to me indicates that maturity in females is reached at a much smaller size — of 19 females with either shelled oviductal eggs or enlarged yolking follicles (from Flores, Timor, Wetar, Damar, Tuan, Banda Besar and Babar), the range of SVL was 45.5–61 mm, with six (from Flores and Banda Besar) having an SVL of 50 mm or less. In the 17 individuals for which the number of eggs or follicles could be counted, the clutch size was a constant two. However, Auffenberg (1980) reported one female from Komodo with yolking follicles (hence more than one) in the right ovary, and one yolking follicle in the left ovary; the specimen he cites is not included in the list of specimens examined, nor is it allocated to specimens of any of the other species listed. I am suspicious of Auffenberg's (1980) estimate of size at maturity, although it is possible that western populations attain larger sizes — I did not examine reproductively active females from west of Flores.

Size of mature males is more difficult to infer. However, my data suggest that males are larger than females. Of 30 individuals with SVL greater than 62 mm that could be sexed, from throughout the range of the species, all but two were males, and the largest five of these were all males. The two females with an SVL greater than 62 mm came from Komodo (71 mm) and Deli (64 mm).

Dunn examined only a single specimen from Flores, the nominotypic population of *S. florensis*, when erecting his three new subspecies, and that individual was stated to be "young" (I have examined the specimen — it is a female with SVL 46 mm, with non-convoluted oviducts and hence presumably immature, but about the size of the smallest ovigerous female). Mertens (1930), working with larger samples from Flores, synonymised *S. f. nitidus* with the nominate subspecies, a synonymy accepted by Auffenberg (1980) who also had large samples from Komodo and Flores. Combining the coloration features described by Dunn (1927) for *florensis* and *nitidus*, *S. f. barbouri* is reported to differ from *S. f. florensis* in lacking a pale dorsolateral line in "young" lizards, and in possessing in adults both light and dark post-tympanic streaks, and a dark throat. Auffenberg (1980) noted that his Flores material, from the western end of the island, generally had unpigmented throats, with at most some dark flecking on the infralabials (present only at one locality, Ruteng, the easternmost locality he sampled).

I have examined ten of the eleven types of *Lygosoma florense* Weber, from Maumere (ZMA 11059–64; BMNH 1946.8.15.50) and Sika (ZMA 11056–58), both in eastern Flores. Of the seven individuals from Maumere, six (SVL 45.5–61 mm for three ovigerous females and 54.5–68 mm for three mature males with enlarged testes) have large dark blotches or clouding that largely covers the infralabial and gular regions while a single male (SVL 61 mm) has an unpigmented throat. Two females have both a light and dark post-tympanic streak, while the four males lack any post-tympanic markings. The smallest of the seven, a female with SVL 45.5 mm, lacks any pale dorsolateral line, while a distinct pale dorsolateral line is present in one larger lizard (the largest female). Of the three lizards from Sika, all female, the two larger (SVL 46–55 mm) had dark throats, while one (SVL 46 mm) had a pale throat. Hence, the diagnostic coloration features present in adults for *florensis* and *barbouri* are both present in the type series of *florensis*, from a single locality (Maumere) on Flores.

Further, there is evidence for a cline from west to east for increasing degree of development of a dark throat. The following discussion presents observations on samples from islands, in approximate order from west to east (Fig. 9).

Small islands off west Java. Mertens (1957) reported *S. florensis florensis* from two small islands, Pulau Deli and Pulau Tinjil, off the south coast of west Java, and noted that dark flecks were lacking on the throat. Greer examined some of Mertens' material from Pulau Deli, and confirmed that both males and females consistently have a pale throat. The sample includes males and females with SVL > 60 mm.

Sumbawa. Mertens (1930) reported *S. florensis florensis* from Sumbawa, noting that some individuals had dark flecking on the throat. Of the four individuals examined, two (female, SVL 49 mm; unsexed, SVL 60 mm) had a faint grey suffusion on the throat.

Komodo. An unpigmented throat was reported for this population by Dunn (1927) and Auffenberg (1980). I examined 19 members of the type series of *S. f. nitidus*, with SVL 36.5–80 mm, and all had pale throats.

Padar. Dunn (1927) examined five individuals from Padar, and reported that "adults" had the throat flecked with black. Auffenberg (1980) examined three different Padar specimens, and did not mention any dark pigmentation on the throat. I examined six Padar animals, including four of those examined by Dunn (1927), and all had pale throats, including four adult-sized animals with SVL 57–64 mm.

Sumba. I have not examined material from this island, but Forcart (1953) referred his material from this island to the nominate subspecies. Hence, large individuals presumably had dark flecking on the throat.

Flores. Nine individuals from the western half of Flores (Sita, Rana Mese, Riung, Ende, Welowaru; six males SVL 44–77 mm; one female SVL 61 mm; two unsexed juveniles SVL 29, 32 mm) all had unpigmented throats. Immediately to the east, the type series of *Lygosoma florensis* (see above) had dark throats on most adult-sized individuals. Still further east, 23 individuals from Laruntuka, Riangkamie and Ili Mandiri (one male SVL 57 mm; four females SVL 46–50 mm; 18 unsexed SVL 32–50 mm, only six of which had SVL > 46 mm) mostly had unpigmented throats; one small individual (SVL 35.5 mm) had traces of dark pigmentation.

Pulau Adonara. Both of the specimens from Adonara (SVL 45, 57 mm) had pale throats. The smaller individual is, from the size, possibly immature.

TABLE 1. Geographic variation in scalation in *Sphenomorphus melanopogon*. Islands are listed approximately from west to east.

	Deli	Sumbawa	Komodo	Padar	Flores
Midbody Scales					
Range	43–47	39–45	41–47	42–45	36–47
Mean (SD)	45.2 (1.19)	42.3 (2.50)	44.7 (1.84)	43.8 (0.98)	41.6 (2.99)
Mode	46		44,46	44	43
N	12	4	20	6	29
Paravertebral Scales A					
Range			71–83	70–75	70–84
Mean (SD)			78.3 (3.56)	72.8 (2.06)	75.0 (4.69)
N			15	4	8
Paravertebral Scales B					
Range	76–84	78–82	82–91	77–82	69–91
Mean (SD)	79.7 (2.42)	80.0 (2.00)	87.2 (3.22)	80.0 (1.87)	79.3 (4.95)
N	12	3	13	5	29
Subdigital Lamellae A					
Range			28–34	25–31	26–32
Mean (SD)			30.4 (1.42)	27.4 (2.17)	27.1 (2.21)
N			19	4	7
Subdigital Lamellae B					
Range	27–31	27–30	28–30	26–28	24–30
Mean (SD)	29.9 (1.30)	28.5 (1.29)	29.0	27.0	27.1 (1.43)
N	11	4	2	2	17
Prefrontals					
Contact	9	3	21	6	16
Separated	3	1			
Supraoculars contacting frontal					
3			4	2	7
4	24	7	38	8	27
5		1			
Supraciliaries					
Range			12–15	12–15	12–14
Mean (SD)			13.8 (1.00)	13.0 (0.71)	13.1 (0.62)
n			32	5	16
Supralabials					
6					
7	21	6	31	11	34
8	3	2	11		

TABLE 1. (continued)

	Adonara	Semau	Timor	Alor	Wetar	Damar
Midbody Scales						
Range	40–47	40–44	38–45	42–48	40–46	39–43
Mean (SD)	43.5	42.5 (1.31)	42.1 (1.82)	44.3 (2.63)	43.3 (1.54)	41.0 (1.20)
Mode		42	42		44	41
N	2	12	19	4	23	8
Paravertebral Scales A						
Range	68–79	67–78	66–77		66–75	73
Mean (SD)	73.5	72.8 (3.40)	72.4 (2.67)		71.2 (2.67)	73.0
N	2	12	17		19	1
Paravertebral Scales B						
Range	73–86	82	76–81	80–86	69–84	73–78
Mean (SD)	79.5	82	79.0 (1.73)	83.0 (2.45)	76.9 (4.05)	76.1 (2.10)
N	2	1	7	4	14	8
Subdigital Lamellae A						
Range	27–31	26–32	27–34		25–32	32–34
Mean (SD)	29.3	29.1 (1.77)	29.4 (1.59)		29.3 (1.60)	
N	2	12	17		21	1
Subdigital Lamellae B						
Range	28–32		26–30	26–30	31–32	26–32
Mean (SD)	30.0		28.3 (2.08)	28.0 (1.83)	31.3 (0.50)	28.8 (1.83)
N	2		3	4	4	8
Prefrontals						
Contact	2	12	20		25	9
Separated						
Supraoculars contacting frontal						
3		1		2	7	5
4	4	22	40	6	42	13
5		1			1	
Supraciliaries						
Range	12–14	12–15	12–15		11–15	14
Mean (SD)	13.3 (0.96)	14.3 (0.68)	13.7 (0.91)		13.2 (0.94)	14.0
n	4	24	24		37	2
Supralabials						
6						
7	4	22	37	8	40	18
8		2	3		2	

TABLE 1. (continued)

	Teun	Babar	Banda Besar	Kepulauan Kai
Midbody Scales				
Range	42–45	41–42	40–43	40–42
Mean (SD)	43.3 (1.50)	41.8 (0.41)	41.5	40.7 (0.82)
Mode	42	42		40
N	4	6	2	6
Paravertebral Scales A				
Range	69–71	65–69	71	67
Mean (SD)	70.0 (1.00)	66.8 (1.60)	71	67.0
N	3	6	2	1
Paravertebral Scales B				
Range	77			71–77
Mean (SD)	77.0			74.7 (2.25)
N	1			6
Subdigital Lamellae A				
Range	27–31	27–32	25–27	30
Mean (SD)	29.5 (1.80)	28.8 (1.51)	26.0	30.0
N	3	6	2	1
Subdigital Lamellae B				
Range	30			26–32
Mean (SD)	30.0			29.7 (2.25)
N	1			6
Prefrontals				
Contact	4	6	2	6
Separated				
Supraoculars contacting frontal				
3	1		2	
4	7	10	2	12
5				
Supraciliaries				
Range	12–14	12–15	13–14	13–14
Mean (SD)	13.2 (0.98)	13.5 (0.90)	13.3 (0.50)	13.5
n	6	12	4	2
Supralabials				
6		2		
7	8	10	4	12
8				

Pulau Semau. Of 12 individuals examined, dark throats were present on six adult-sized lizards (three females 57–62 mm, three males 65–66 mm), faint dark markings were present on two adult-sized females with SVL 58–61 mm, while four immature individuals (SVL 38–46 mm) had pale throats. None of the adults appeared to have reproductively active gonads.

Timor. Of 17 individuals for which throat colour could be assessed, a dark throat was present in five mature males (SVL 53–64 mm) and three mature, but non-reproductive females (SVL 52–60 mm). An additional male (SVL 60 mm) and two females (SVL 52–54 mm) had dark pigmentation restricted to the sides of the throat, while two males of similar size (SVL 53–57 mm) and two unsexed juveniles (SVL 38–43 mm) had pale throats.

Pulau Alor. Of four individuals examined, the two larger (SVL 63, 66 mm) had black throats, while the two smaller (SVL 48 mm male, 55 mm female) lacked dark pigmentation.

Wetar. Of 32 individuals scored for throat colour, a strongly dark throat was present in 11 males (SVL 57–63 mm) and two females (SVL 53, 56 mm, the latter ovigerous). An additional five females (SVL 52–56 mm, two of which were ovigerous) had a faint grey suffusion over the throat. Six smaller and presumably immature males (SVL 33–46 mm) had pale throats, as did seven females, five small (SVL 30–42 mm) and two larger (SVL 48, 53 mm).

Pulau Damar. Three males (SVL 57–65 mm) and the unsexed holotype of *S. f. weberi* (SVL 65 mm) have heavily pigmented throats and body venters. Four females (SVL 53–57 mm) have dark throats, while one smaller unsexed individual (SVL 49 mm) has a weakly pigmented throat

Palau Teun. All four specimens (three males, SVL 56.5–62 mm; one ovigerous female SVL 55 mm) from this island near Damar have dark throats and body venters, although in the female the belly is blotched rather than solidly dark.

Pulau Babar. Three males (SVL 59–64 mm), two of which had small testes but convoluted epididymides, suggesting they were mature but reproductively inactive, had dark throat and body venter. One female (SVL 51 mm) had a dark throat only, while two other females (SVL 52, 53 mm) had a pale throat.

Pulau Banda Besar. Both of the lizards examined are small (male SVL 44 mm, female SVL 48.5 mm), although the female is mature (enlarged follicles). Both have a dark throat but pale venters.

Kepulauan Kai. The type series of *Lygosoma Kühnei* consists of four males (SVL 59–66 mm), all of which have dark throats and body venters, and two females (SVL 52, 57 mm), both with a dark throat only.

Four conclusions are apparent from these observations. Firstly, a dark throat can be present in both sexes, although there is some suggestion that it is more common and often more heavily pigmented in males. This suggests that the presence or absence of dark pigmentation is not a simple sex-linked character, although the intensity of its expression may be sex-related. Secondly, a dark throat can be present in both ovigerous and non-reproductive females, and in males with enlarged turgid testes as well as those with regressed testes. Although dates of collection are available for few specimens, and the seasonality of reproduction not able to be assessed as yet, it is unlikely that the dark throat marks reproductive activity. Thirdly, although a dark throat, when it occurs in a population, occurs in most adult-sized individuals, there often remain a few adult-sized individuals that do not show it — both dark and light throats can be present in a sample from a single locality. Finally, it is clear that there is a geographic component to the occurrence of dark ventral pigmentation, and its intensity and extent, with western populations lacking any ventral melanisation, central populations showing variable expression of throat melanisation, and eastern populations showing variable melanisation of throat and body venter.

Because of the evidence for a cline in the development of dark ventral pigmentation, and the occurrence of the purported diagnostic characters differentiating *S. f. florensis* and *S. f. barbouri* within the type series of the former, I do not at present recognise subspecies within *S. melanopogon*. However, further work on the variation in coloration of *S. melanopogon*, particularly on Flores and further east, and preferably incorporating genetic data, is warranted. Kaiser *et al*. (2011) suggested that multiple species within the complex occur on Timor, although my examination of other specimens suggests that some of the differences they note reflect sexual dichromatism and ontogenetic change.

Hence, in the absence of analyses of variation in new character systems throughout the distribution of the species that might support alternative conclusions, I propose the following synonymies and diagnoses:

Sphenomorphus melanopogon (Duméril & Bibron 1839)

Lygosoma melanopogon Duméril and Bibron 1839: 723.
Lectotype: MNHN 1245 (designated herein, and according with previous restrictions on the type series by Guibé 1954); type locality Nouvelle Hollande (in error for Timor).
Scincus naevius Duméril and Bibron 1839: 724. (Junior objective synonym made available by subsequent recognition as a valid taxon prior to 1961).
Lectotype: MNHN 1245, designated herein; type locality Nouvelle-Hollande (in error for Timor).
Lygosoma florense Weber 1891: 173, plate 14, figs 2–3.
Lectotype: ZMA 11060, designated herein; restricted type locality (due to lectotype selection) Maumere, Flores.
Lygosoma (*Hinulia*) *Kühnei* Roux 1910: 237, plate 13, fig. 2.
Lectotype: NHMB 5514 (designated by Kramer 1979); type locality Kei Islands [= Kepulauan Kai].
Sphenomorphus florensis nitidus Dunn 1927: 5.
Holotype: AMNH 32068; type locality Komodo.
Sphenomorphus florensis barbouri Dunn 1927: 5.
Holotype: AMNH 32203; type locality north coast of Wetar, near Uhak.
Sphenomorphus florensis weberi Dunn 1927: 6.
Holotype: MCZ 20996 [erroneously cited as 2099 in description]; type locality Damma Island [= Pulau Damar].
Sphenomorphus kuehnei Kramer 1979: 163.
Emendation of *Kühnei* Roux (Article 32.5.2.1 of the Code of Zoological Nomenclature).

Diagnosis. This species can be readily differentiated from the majority of *Sphenomorphus* species by the combination of finely striate dorsal scales, the imbricate scales on the dorsal surface of the pes extending onto the plantar surface between the fourth and fifth digits, and three or more supraoculars contacting the frontal. It can be further differentiated from the few *Sphenomorphus* (all members of the *variegatus* group) with all of these character states by the combination of smoothly rounded subdigital lamellae, presence of auricular lobules and the postmental modally only contacting a single infralabial on each side. When present, the black throat is also a useful diagnostic character.

Distribution. Known from the Lesser Sunda Islands, specifically from west to east: Pulau Deli, Pulau Tinjil, Sumbawa, Sumba, Komodo, Padar, Flores, Pulau Adonara, Pulau Semau, Timor, Pulau Alor, Wetar, Pulau Babar, Pulau Damar, Pulau Teun, Pulau Banda Besar and Kepulauan Kei (Fig. 9). Auffenberg (1980) also lists the species from Pulau Rinca and Pulau Besar, although I am unaware of any specimen-based records to support this. Although the type series of *Lygosoma Kühnei* was purportedly collected from the Kei Islands, there are no other records of the species from this easternmost extremity of the species' distribution. The monograph by Roux (1910) is largely based on material collected by Jean Roux and his colleague Hugo Merton in the Kei and Aru Islands in 1907–08. However, two species, *Lygosoma Kühnei* and the agamid *Lophognathus temporalis* Günther, were not collected by Roux and Merton, but were reported solely on the basis of specimens purchased from the natural history dealer Hermann Rolle in Berlin in 1905, with the specimens said to have been collected by the late Herrn Kühne. Rolle's Kühne is presumably the ornithological and entomological collector Heinrich Kühn (8.ii.1860 Erlbach–26.vii.1906 Surabaya), who lived at Toeal [= Tual] in the Kei Islands for several years, but who also collected extensively in the surrounding islands, including Damar (1898), Banda Besar (1898), Wetar (1902) and Baber (1905) (Hartert, 1900a–b, 1901, 1904, 1906, 1907), all of which are within the confirmed distribution of *S. melanopogon*. There are specimens of *Sphenomorphus melanopogon* purchased from H. Rolle in 1900 in the BMNH collection (BMNH 1900.2.9.5–10) which bear the locality Damar I., a locality from which *S. melanopogon* was independently collected by the Siboga expedition (Dunn, 1927). These are likely to have been collected by Kühn. *Lophognathus temporalis* has also been reported from Damar and Baber (de Rooij, 1915), localities visited by Kühn. Hence it is possible that the type locality for *L. Kühnei* is incorrect.

Redescriptions of Lectotypes. The lectotype of *Lygosoma melanopogon* (MNHN 1245; Figs. 1A–B, 2) has the following character states: dorsal lobe of rostral with a slightly concave posterior border; nasals broadly separated; nostril central in nasal; supranasals absent; prefrontals in broad contact; supraoculars seven, first four in contact with frontal, last four in contact with frontoparietal; supraciliaries 14/14, first separated from frontal; frontoparietals in broad median contact; parietal eye spot at junction of second third and last third of interparietal length; parietals in broad contact behind interparietal; anterior loreal taller than wide and taller than posterior loreal; posterior loreal squarish, a little wider than tall, and narrowest ventrally; presuboculars two, first largest, last interdigitating with supralabials; suboculars 4/3; postsuboculars 7/8, first interdigitating with supralabials;

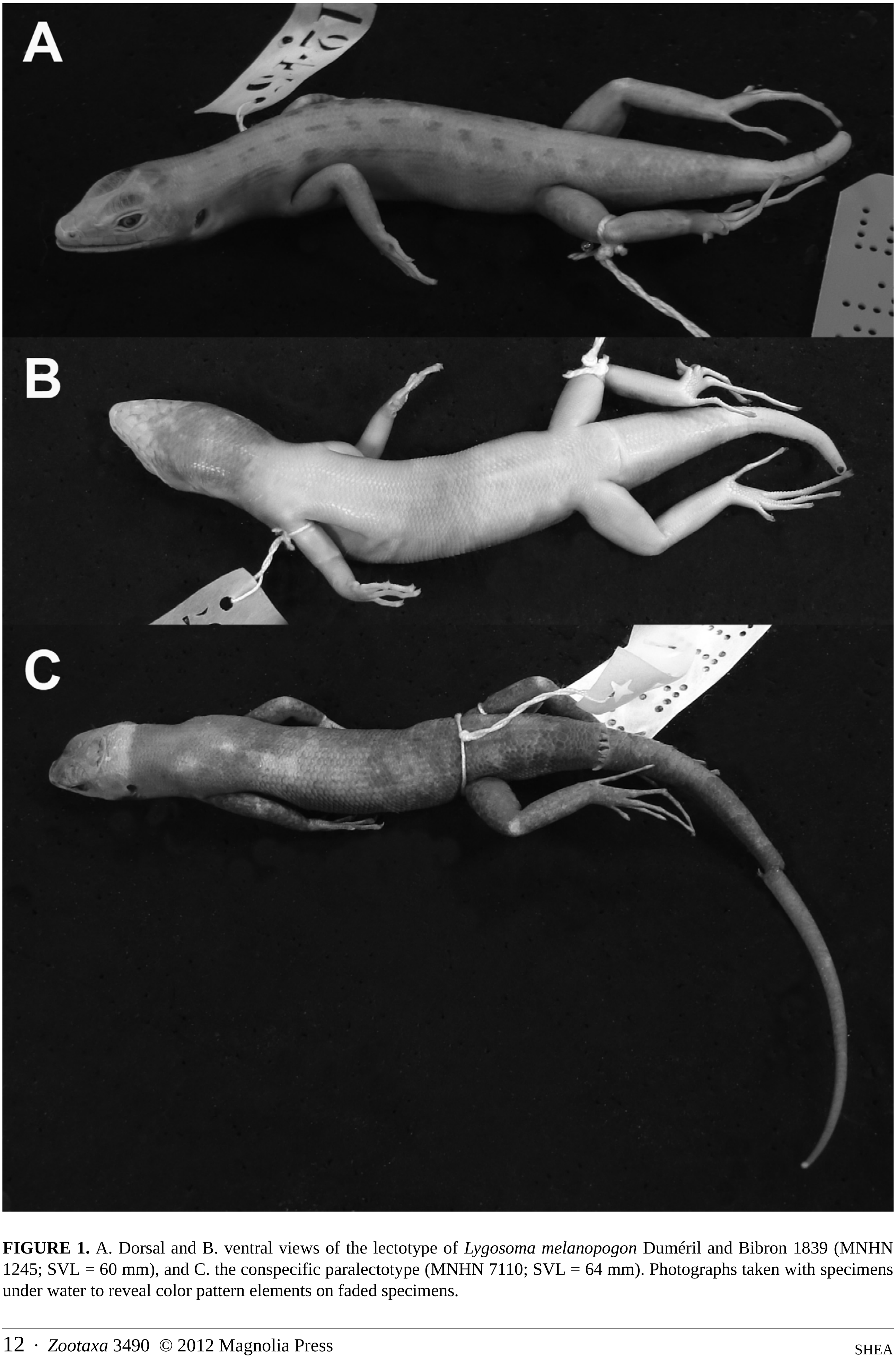

FIGURE 1. A. Dorsal and B. ventral views of the lectotype of *Lygosoma melanopogon* Duméril and Bibron 1839 (MNHN 1245; SVL = 60 mm), and C. the conspecific paralectotype (MNHN 7110; SVL = 64 mm). Photographs taken with specimens under water to reveal color pattern elements on faded specimens.

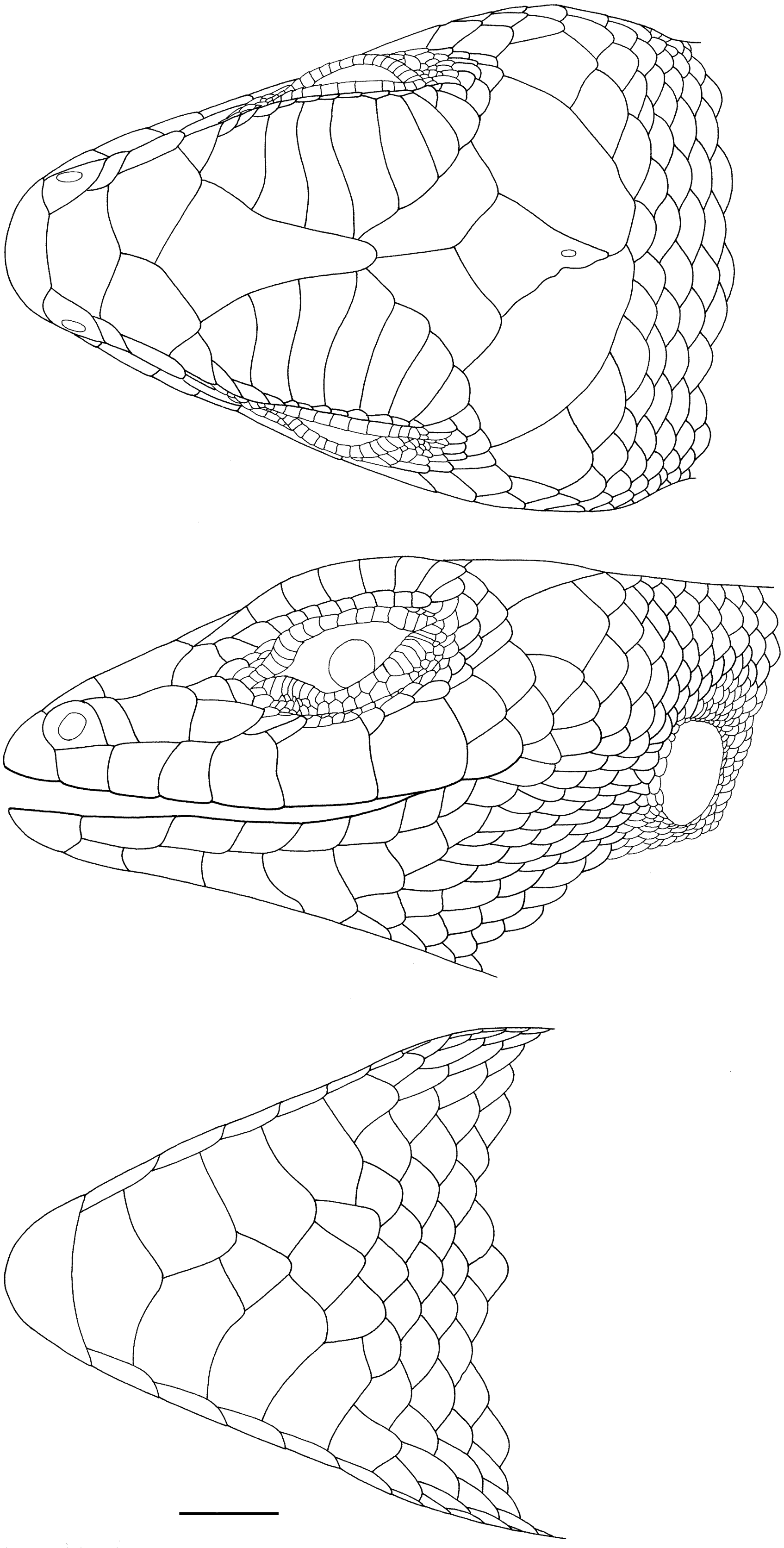

FIGURE 2. Dorsal, lateral and ventral views of head of lectotype of *Lygosoma melanopogon* (MNHN 1245). Scale bar = 2 mm.

FIGURE 3. Paralectotypes of *Lygosoma melanopogon*, representing A. the species *Sphenomorphus meyeri* (MNHN 1244; SVL = 101 mm) and B. *S. jobiensis* (MNHN 2974, SVL = 84 mm). Photographs taken with specimens under water to reveal color pattern elements on faded specimens.

supralabials seven, fifth below centre of eye, last two each divided into an anteroventral and a posterodorsal scale; primary temporals two, anterodorsal and posteroventral, the more dorsal very small; lower secondary temporal single, overlapping upper secondary temporal; scales bordering parietals between upper secondary temporals eight; ear with six low rounded lobules along anterior margin; infralabials 8/7, only first contacting postmental; first pair of chin shields in median contact; second pair medially separated by a single scale; third pair of chin shields separated by three scales; all chin shields laterally contacting infralabials.

Longitudinal scale rows at midbody 43; scales in a paravertebral row (A) 71, not broader than adjacent dorsal scales; dorsal scales finely striate, laterally and ventrally becoming smooth; median pair of precloacal scales enlarged, laterally overlapping adjacent precloacals; lamellae below fourth toe (A) 30/29; scales above fourth toe four at level of metatarsophalangeal joint, decreasing distally so that last two scales single.

SVL 60 mm; AGL 27 mm; tail regenerated; FLL 22 mm; HLL 37 mm; HL 13.1 mm; HW 9.5 mm; HL 7.6 mm.

The male lectotype of *Lygosoma florense* (ZMA 11060; Figs. 4–5) has the following differences in scalation and morphometrics from those described for the lectotype of *L. melanopogon*: posteriormost supraocular does not contact frontoparietals; supraciliaries 13/13; frontoparietals partly fused posteriorly; parietal eye spot slightly posterior to centre of interparietal; posteriormost presubocular barely interdigitating with supralabials; suboculars 5/4; postsuboculars 8/6; lower secondary temporal overlapped by upper secondary temporal (overlap pattern as for the lectotype of *L. melanopogon* in remainder of type series); ear with seven conical lobules along anterior margin; infralabials 8/9.

Longitudinal scale rows at midbody 46; paravertebral scales (A) 84; subdigital lamellae (A) 30/34.

SVL 68 mm; AGL 32 mm; tail regenerated; FLL 21.5 mm; HLL 37.5 mm; HL 15.8 mm; HW 11.4 mm; HD 9.0 mm.

FIGURE 4. A. Dorsal and B. lateral views of the lectotype of *Lygosoma florense* Weber 1891 (ZMA 11060; SVL = 68 mm).

The male lectotype of *Lygosoma Kühnei* (Figs. 6–7) has the following scalational and morphometric characteristics that differ from those described for the lectotype of *L. melanopogon*: supraciliaries 12/13; anterior loreal about same height as posterior loreal; suboculars 3/3; postsuboculars 5/6; lower secondary temporals two, the upper of the two including the upper portion of the primary temporal; ear with five low rounded lobules along anterior margin; infralabials 7 (on left — right side not counted).

Longitudinal scale rows at midbody 40; paravertebral scales (B) 77; subdigital lamellae (B) 31.

SVL 66 mm; TL 120 mm; FLL 24 mm; HLL 39 mm. AGL and head measurements not taken.

***Sphenomorphus meyeri* (Doria 1874)**

(Figs. 9–13)

Lygosoma (*Hinulia*) *Meyeri* Doria 1874: 332; plate 11, fig 13.

Syntypes: BMNH 76.7.18.2–3; MSNG 27877a–d; NHMW 16650:1–2; RMNH. RENA 4253; ZMB 7937a–b, 9739; 12 syntypes not located; type locality Wokan, Aru Islands.

Hinulia papuensis Macleay 1877: 62.

Holotype: AM R31847. Type locality Katow, [Binaturi River, Papua New Guinea].

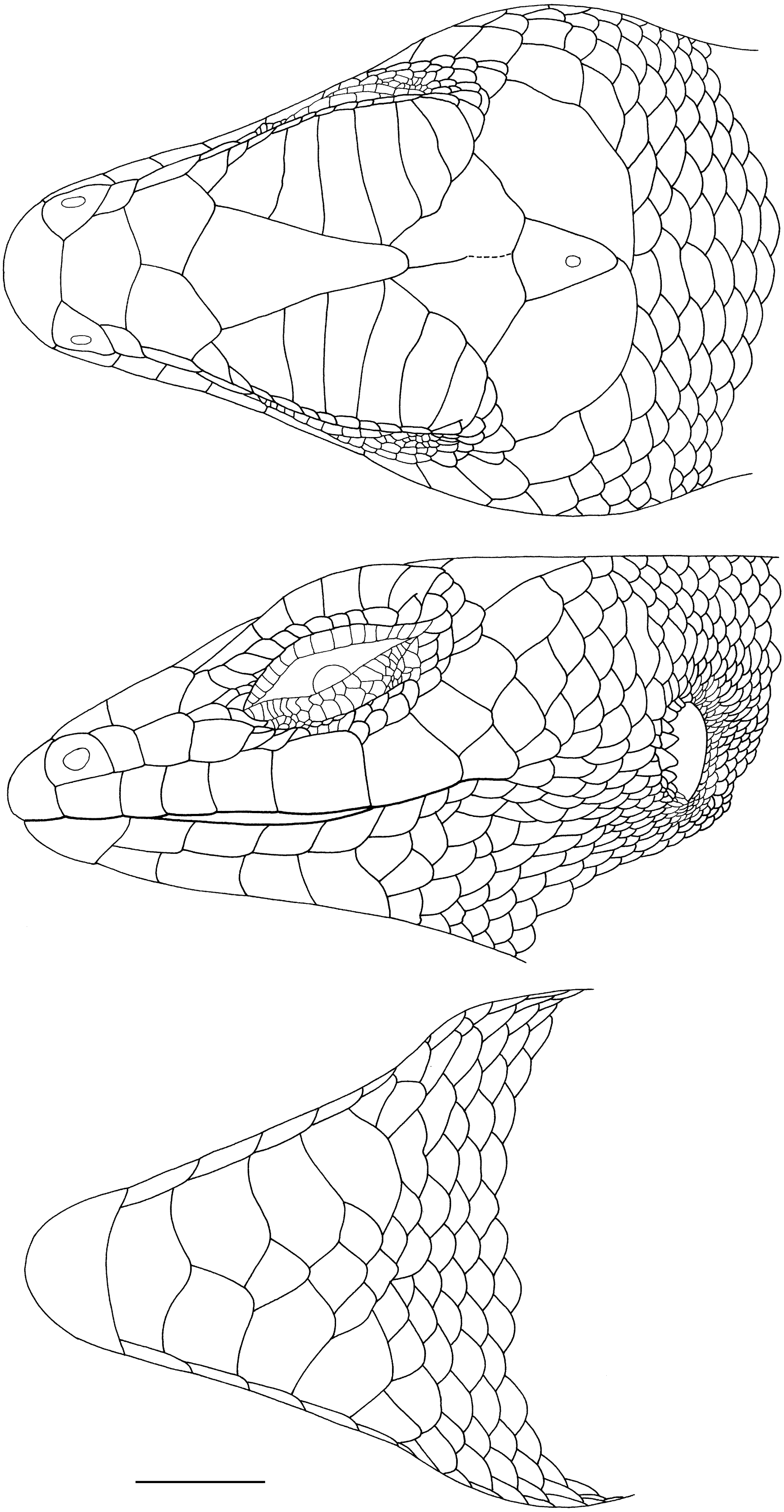

FIGURE 5. Dorsal, lateral and ventral views of head of lectotype of *Lygosoma florense* (ZMA 11060). Scale bar = 2 mm.

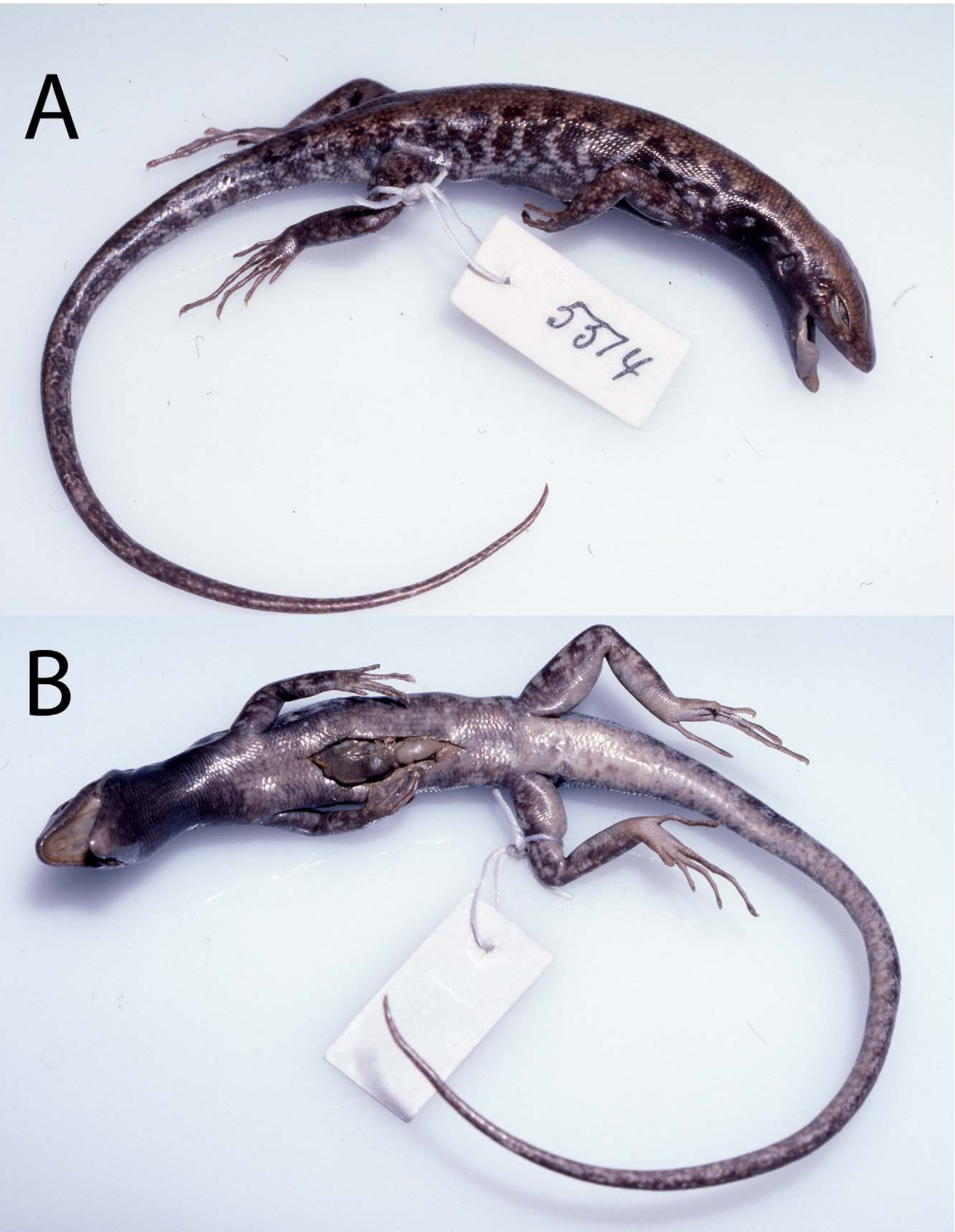

FIGURE 6. A. Dorsal and B. ventral views of the lectotype of *Lygosoma Kühnei* Roux 1910 (NMBA 5514; SVL = 66 mm).

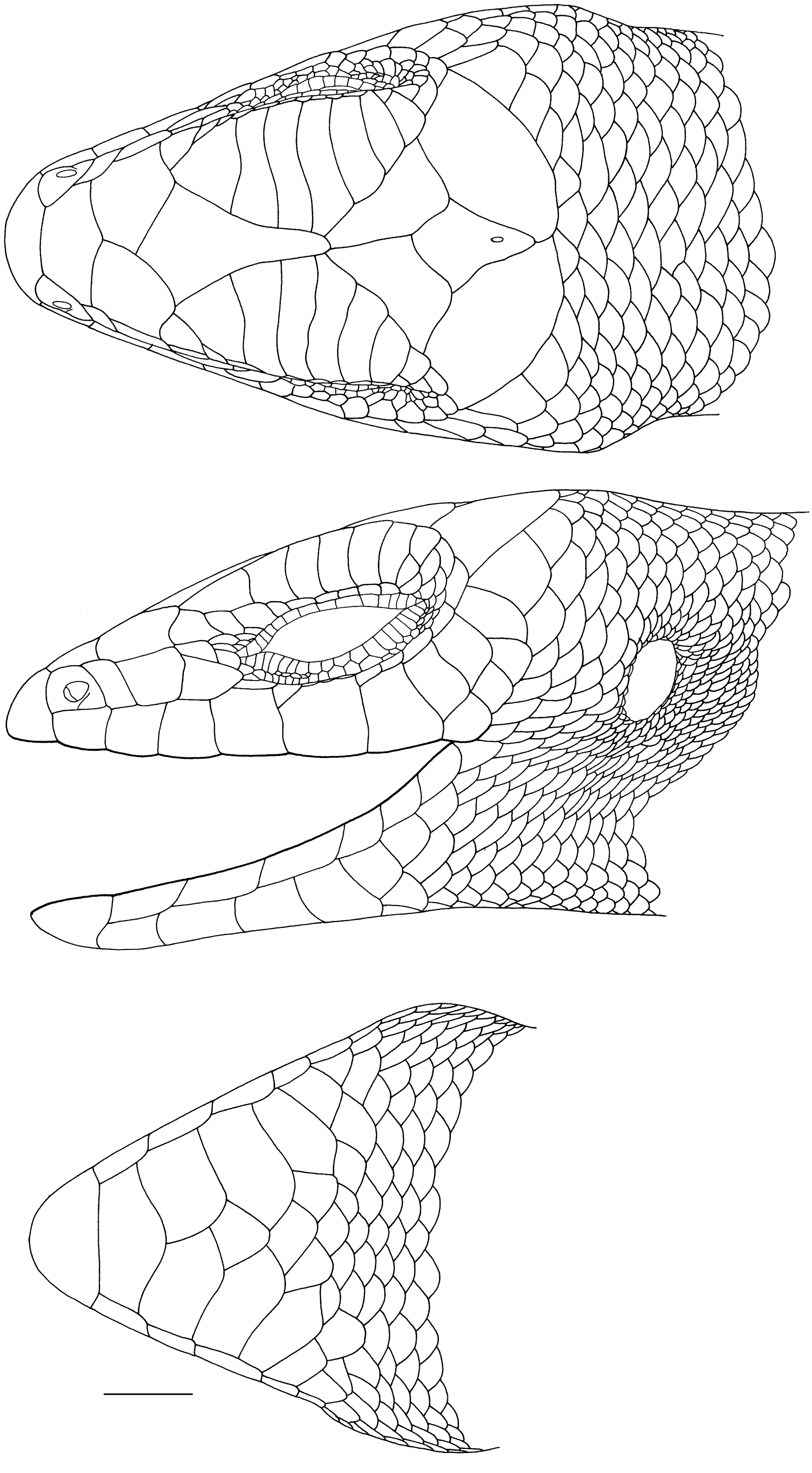

FIGURE 7. Dorsal, lateral and ventral views of head of lectotype of *Lygosoma Kühnei* (NMBA 5514). Scale bar = 2 mm.

FIGURE 8. Holotypes of A. *Sphenomorphus florensis nitidus* Dunn 1927 (AMNH 32068; SVL = 72 mm) and B. *Sphenomorphus florensis barbouri* Dunn 1927 (AMNH 32203; SVL = 63 mm).

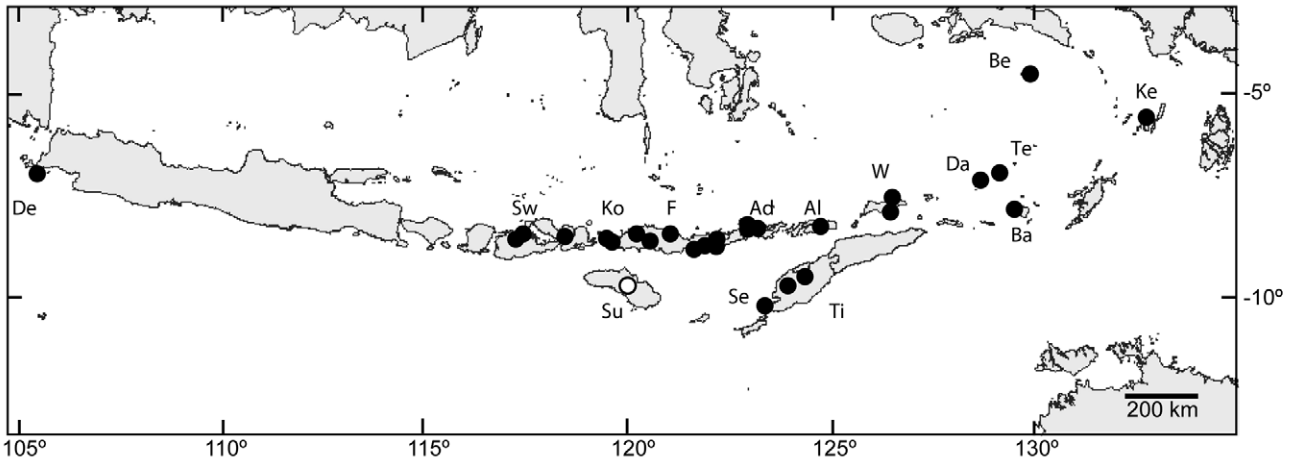

FIGURE 9. Distribution of *Sphenomorphus melanopogon*. Ad = Adonara, Al = Alor, Ba = Babar, Be = Banda Besar, Da = Damar, De = Deli and Tinjil, F = Flores, Ke = Kei, Ko = Komodo, Padar, Rinca and Besar, Se = Semau, Su = Sumba, Sw = Sumbawa, Te = Teun, Ti = Timor, W = Wetar. Open symbols represent literature records.

Diagnosis. This species can be distinguished from all other *Sphenomorphus* on the basis of the following combination of characters: size large (maximum SVL = 126 mm); prefrontals in contact or separated by an azygous scale; body scales smooth; midbody scales 40–57 (mean = 47.6, sd = 2.71, n = 198); paravertebral scales (A) 76–115 (mean = 94.2, sd = 6.83, n = 191); subdigital lamellae below the fourth toe (A) 14–22 (mean = 17.9, sd =

1.38, n = 187), divided into a larger preaxial series (from which the counts are derived) and a smaller postaxial series; frontal contacting first three (when a total of six) or four (when a total of seven) supraoculars; colour pattern consists of relatively thin, sinuous dark brown crossbars against a light brown background and some indication of a white stripe along the upper lip.

A full analysis of geographic variation in this species will be the subject of a separate paper.

Distribution. Low to mid altitudes (below 1100 m) in the western two thirds of New Guinea, including the Aru Islands and the Raja Ampat Islands (Fig. 14).

FIGURE 10. Three of the syntypes of *Lygosoma Meyeri* Doria 1874. A. BMNH 76.7.18.2–3 (SVL = 88, 93 mm respectively) and B. ZMB 9739 (SVL = 93 mm).

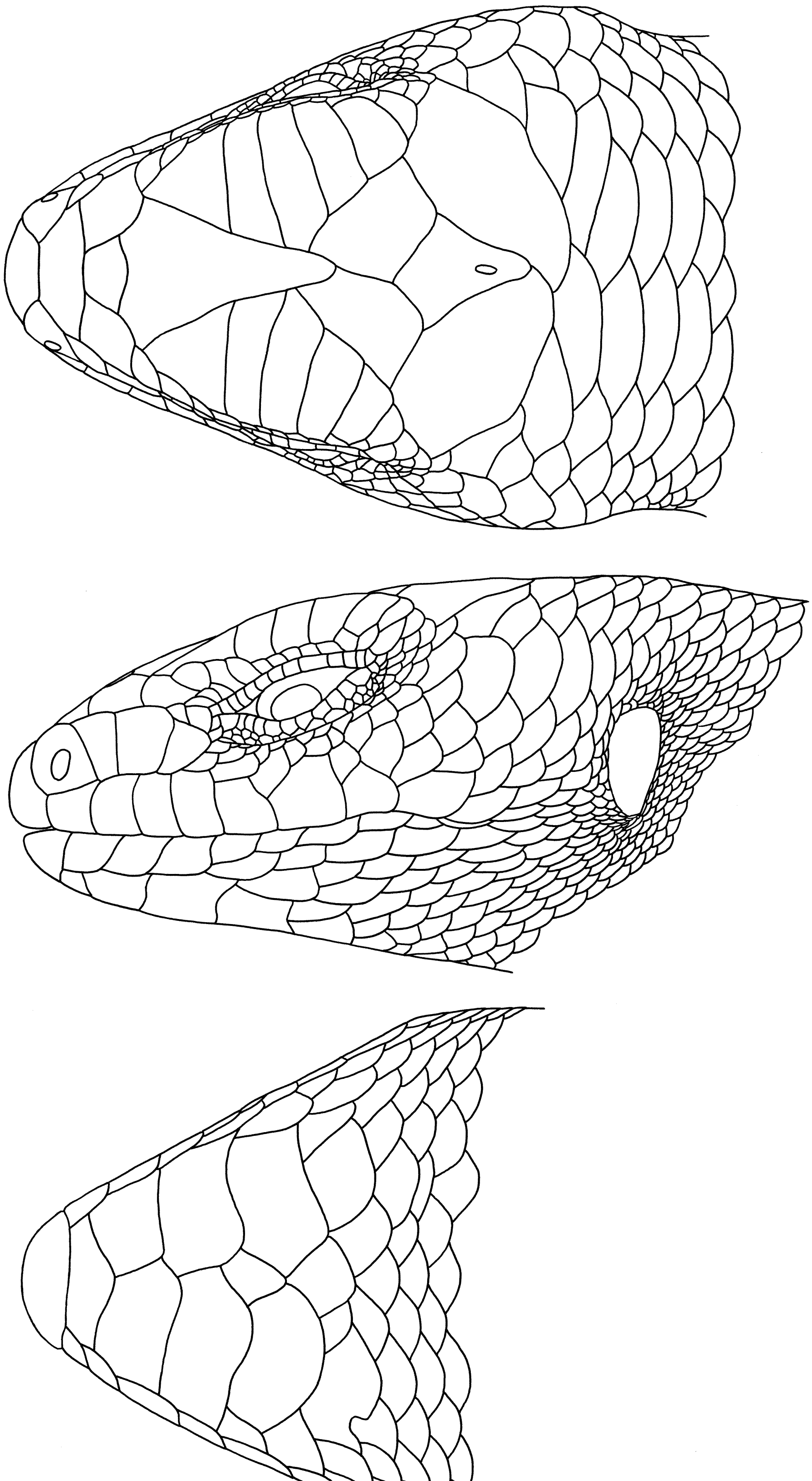

FIGURE 11. Dorsal, lateral and ventral views of the head shields of one of the syntypes of *Lygosoma Meyeri* (BMNH 76.7.18.2). Scale bar = 2 mm.

FIGURE 12. Holotype of *Hinulia papuensis* Macleay 1877 (AM R31847; SVL = 107 mm).

A new scalational character of the foot in some *Sphenomorphus* species

Within *Sphenomorphus*, there is a group that is recognisable on the basis of a character in the pes that is unique in skinks. The character concerns the squamation on the postaxial edge of the fourth metatarsal, that is, the posterior edge of the sole of the foot between the level of the free part of the fourth digit and the base of the fifth digit.

In the primitive condition, as seen in all other skinks, including the generally plesiomorphic scincine genus *Plestiodon*, there is a distinct line of demarcation between the field of flat, imbricate scales on the dorsal side of the pes and the field of more rounded or tuberculate, non-imbricate scales of the ventral side. In the derived condition, this line of demarcation has shifted onto the ventral surface and has become less distinct; in other words, it looks as if the imbricate scales of the dorsal surface have extended onto the ventral surface with a gradual merging of the morphology of the scales in the two fields (Fig. 15). The extent of this ventral extension can vary from just on the edge of the ventral surface as in *S. multisquamatus* to almost the entire ventral surface, leaving just a single arcuate line of juxtaposed scales between the bases of the first and fifth digits, as in *S. anomalopus*.

The derived character state has been obliquely mentioned by Smith (1935) and Taylor (1963) for *S. maculatus*, although both authors emphasised the restriction of the tuberculate juxtaposed scales rather than the extension of the imbricate scales. It has also been illustrated for *S. anomalopus* by Smith (1937).

Species which show the derived character state are *S. amabilis* (Müller) (MCZ 112192), *S. anomalopus* (Boulenger) (BMNH 1913.6.4.3), *S. cyanolaemus* Inger and Hosmer (MCZ 83210–11), *S. dussumieri* (Duméril & Bibron) (AMNH 107258, BMNH 1946.8.15.38–44), *S. maculatus* (Blyth) (AM R171873–74), *S. melanopogon*, *S. multisquamatus* Inger (AMNH 92893–94, 111913, MCZ 83213), *S. nigrilabris* (Günther) (BMNH 1946.8.19.69, MCZ 110309), *S. sabanus* Inger (MCZ 22951), *S. sanctus* (Duméril & Bibron) (MCZ 7663a–b), *S. sarasinorum* (Boulenger) (BMNH 1946.8.15.9–10), *S. simus* (Sauvage) (AM R120338, R120351), *S. striolatus* (ZMA 10945), *S. tersus* (Smith) (BMNH 1946.8.3.22–23, MCZ 39285), *S. tropidonotus* (Boulenger) (SMF 14472; AMNH 142999) and *S. variegatus* (MCZ 20138, 26610).

A sharp line of demarcation between imbricate dorsal scales and juxtaposed plantar tubercles (the plesiomorphic state) occurs in *S. acutus* (Peters) (AM R120570–71, R104881, R104886, MCZ 20115; USNM 497028), *S. annectens* (Boulenger) (MSNG 29115), *S. buettikoferi* (Lidth de Jeude) (RMNH 4471a–c), *S. cameronicus* Smith (BMNH 1946.8.3.27), *S. concinnatus* (Boulenger) (AM R121595, R121764), *S. consobrinus* (Peters & Doria) (SMF 14455, 14457, 14459–60), *S. courcyanus* (Annandale) (BMNH 1946.8.16.91), *S. cryptotis* Darevsky, Orlov and Ho (VNMN 1225–26, 1288), *S. darlingtoni* (Loveridge) (AM R23019–20), *S. diwata* Brown and Rabor (USNM 496805), *S. formosensis* Van Denburgh (AMNH 34878–79, 34887), *S. fragosus* Greer and Parker (MCZ 92262–65), *S. granulatus* (Boulenger) (AM R129754, R129772), *S. incognitus* (Thompson) (AMNH 33178–79, 34904, MCZ 110307, USNM 65368), *S. indicus* (Gray) (AM R96605, R171635–36, R173604, MCZ 39263–64), *S. jobiensis* (AM R24721, R24789), *S. kinabaluensis* (Bartlett) (MCZ 22952, 43496), *S. maculicollus* Bacon (FMNH 161484), *S. meyeri* (AM R118736, R118739), *S. mimicus* Taylor (MCZ 39256), *S. mimikanus*

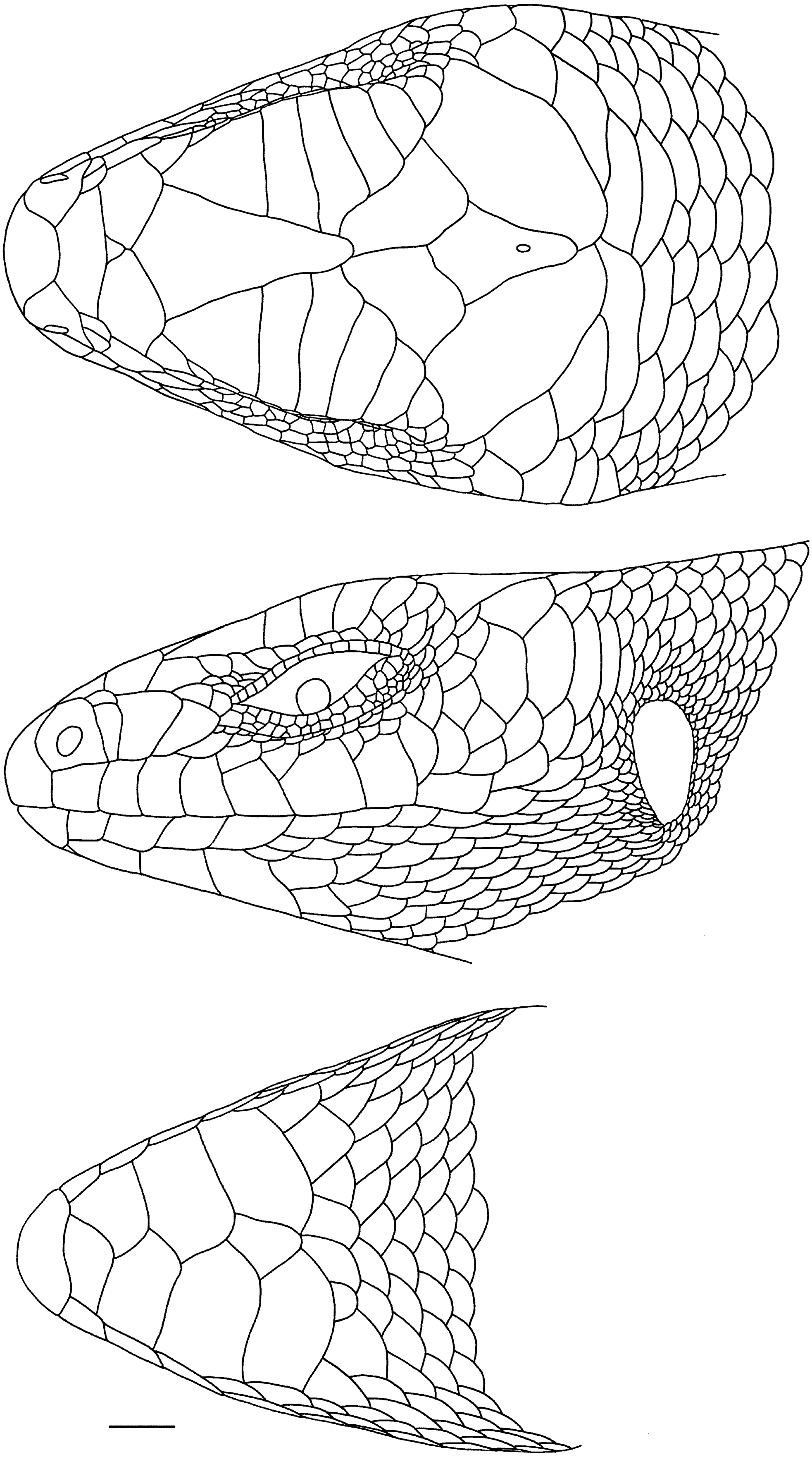

FIGURE 13. Dorsal, lateral and ventral views of head of holotype of *Hinulia papuensis* (AM R31847). Scale bar = 2 mm.

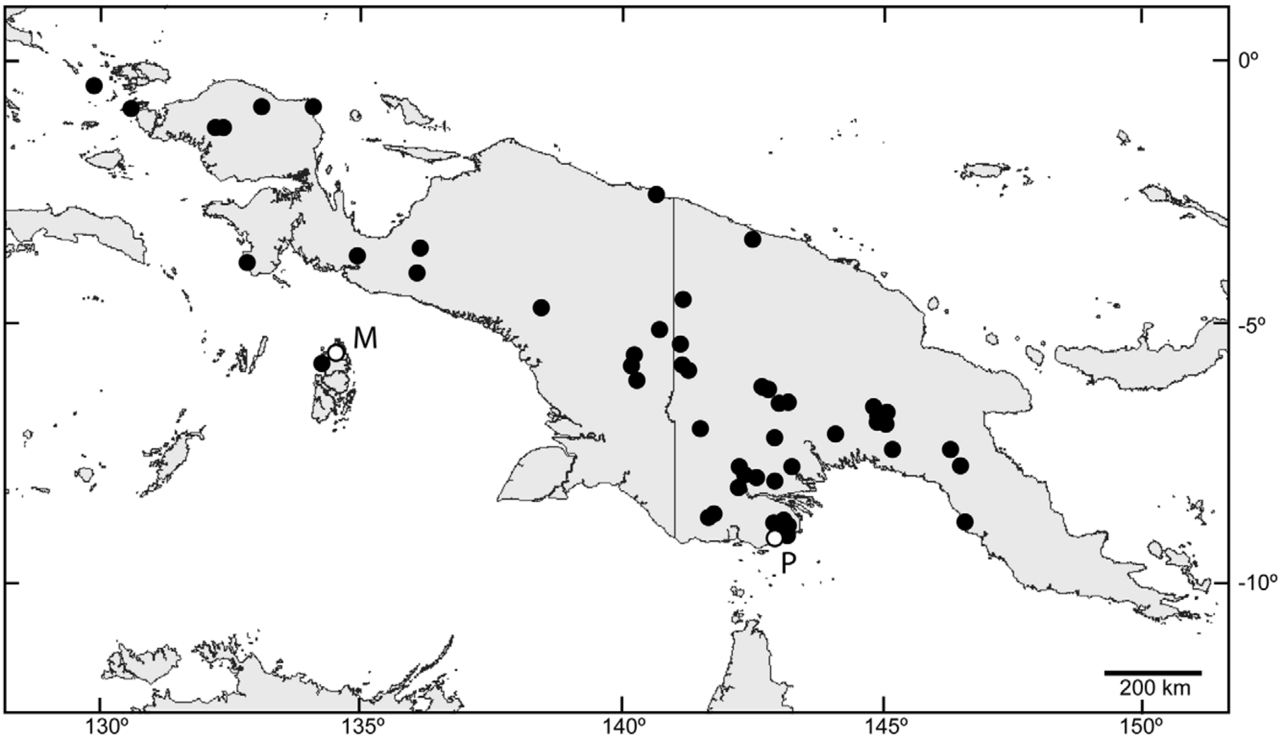

FIGURE 14. Distribution of *Sphenomorphus meyeri*. Open symbols represent type localities for *L. meyeri* (M) and *H. papuensis* (P).

(Boulenger) (BMNH 1946.8.15.11), *S. muelleri* (Schlegel) (AM R13865, R14569), *S. murudensis* Smith (BMNH 1946.8.15.6), *S. neuhaussi* (Vogt) (AM R9867–68), *S. praesignis* (Boulenger) (BMNH 1906.2.28.15, 1916.3.27.22, 1946.8.15.53, 1974.3857, 1974.4988), *S. pratti* (Boulenger) (AM R129522, R129682), *S. scotophilus* (Boulenger) (AM R153110–11, BMNH 1946.8.16.94), *S. stellatus* (Boulenger) (MCZ 39283), *S. taiwanensis* Chen and Lue (AM R161050, R161053), *S. tanneri* Greer and Parker (AM R31132–33, R121594), *S. taylori* Burt (MCZ 65857, 96223), *S. temmincki* (Duméril & Bibron) (AM R6809–10; USNM 43346), *S. textus* (Müller) (BMNH 95.2.27.2), *S. transversus* Greer and Parker (MCZ 76485), *S. wollastoni* (Boulenger) (BMNH 1946.8.3.70), *S. woodfordii* (Boulenger) (AM R91266, R93032), and all members of the *S. maindroni* (Sauvage) species-group of Greer and Shea (2004). This condition is also present in a number of Philippine species formerly in *Sphenomorphus* that were recently transferred to other genera by Linkem *et al*. (2011), including *Insulasaurus arborens* (Taylor) (MCZ 20142–43, USNM 496765), *I. victoria* Taylor (MCZ 44162), *I. wrighti* (Taylor) (MCZ 26301), *Otosaurus cumingi* Gray (MCZ 26302; USNM 229156), *Parvoscincus beyeri* (Taylor) (MCZ 26365; USNM 337768), *Pa. decipiens* (Boulenger) (MCZ 20144–45), *Pa. laterimaculatus* (Brown & Alcala) (USNM 318341, 318343–44), *Pa. lawtoni* (Brown & Alcala) (MCZ 26375; USNM 318981), *Pa. luzonensis* (Boulenger) (AMNH 67098, MCZ 163156, USMM 512761), *Pa. steerei* (Stejneger) (MCZ 26409). *Pinoyscincus coxi* (Taylor) (MCZ 26330; USNM 318437), *Pi. jagori jagori* (Peters) (MCZ 20136–37, 26303, 173396), *Pi. jagori divergens* (Taylor) (MCZ 20134), *Tytthoscincus atrigularis* (Stejneger) (MCZ 26379), *T. biparietalis* Taylor (MCZ 26385), and *T. hallieri* (Lidth de Jeude) (MCZ 22632),

I can only speculate as to the functional significance of this distinctive morphology. In general, the skinks with the derived morphology tend to be gracile with relatively long legs. This suggests that they may be able to run more rapidly or to climb more adeptly than their shorter-legged relatives. Furthermore, the partial loss of the distinct plantar scale morphology suggests that during locomotion, the posterior edge of the plantar area of the pes may make less areal or temporal contact with the ground than in other skinks. Perhaps during high-speed locomotion or in climbing, these skinks deploy the foot in a way that lessens the contact of this part of the pes with the substrate.

In a recent genetic analysis of Philippine *Sphenomorphus* (Linkem *et al*. 2011), all five of the species showing the derived condition that were included in the analysis (*S. cyanolaemus*, *S. maculatus*, *S. multisquamatus*, *S. sabanus* and *S. variegatus*), together with one species not showing this condition (*S. indicus*) formed a distinct

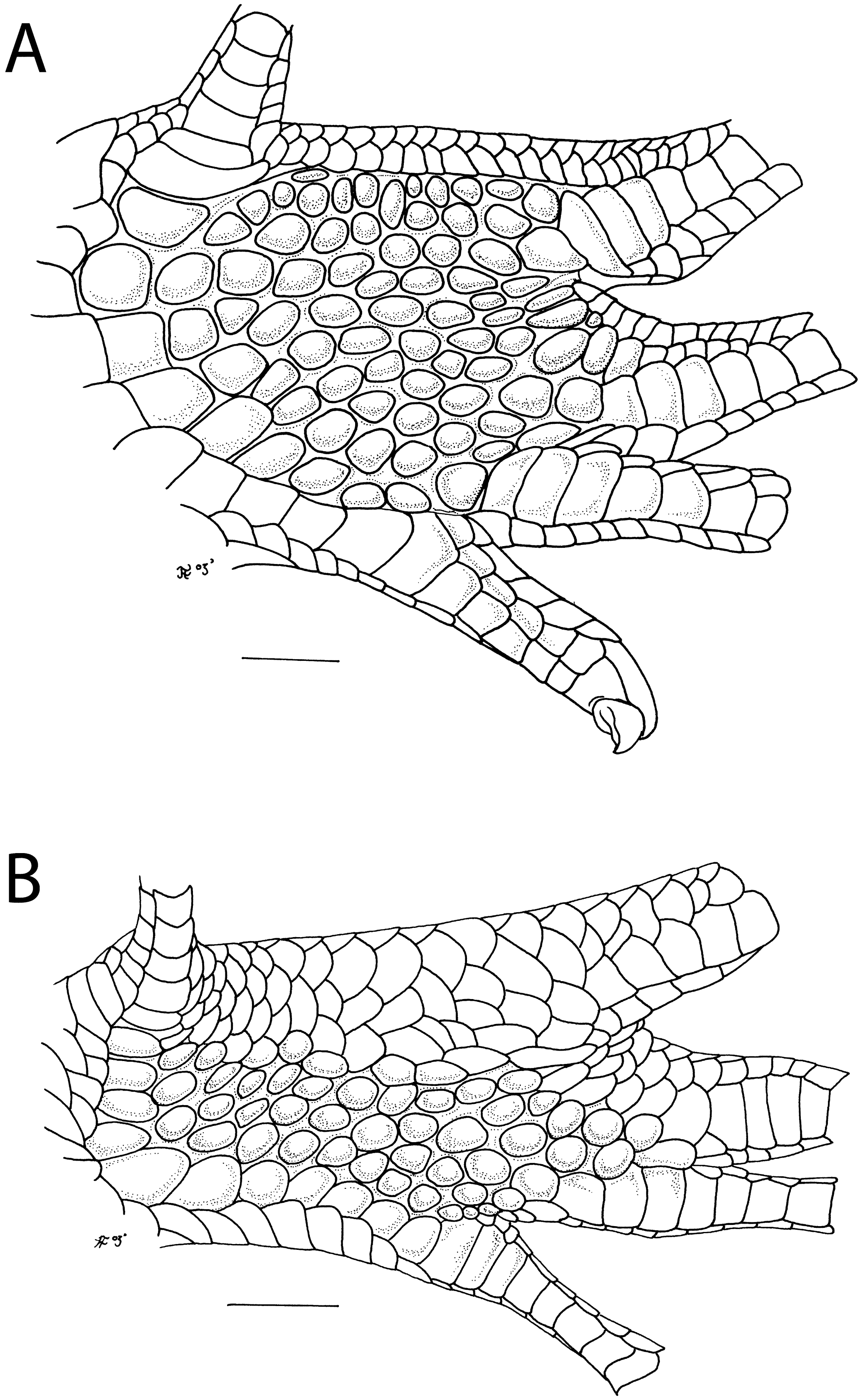

FIGURE 15. The ventral surface of the pes in two species of *Sphenomorphus*, showing a difference in squamation within the genus: A. *S. jobiensis* (AM R115431) in which the scales of the dorsal and ventral surface of the pes show a distinct line of demarcation along the posterior edge of the pes, and B. *S. melanopogon* (MNHN 1245) in which the scales of the dorsal surface extend onto the ventral surface with loss of contrast between the two scale fields. Scale bars = 1 mm.

well-supported lineage ("Clade B"). Assuming that the derived condition represents a synapomorphy of part or all of this clade, with *S. melanopogon* also a member, the name *Sphenomorphus* can be applied to this clade. However, determination of the extent of *Sphenomorphus* in this restricted sense requires assessment of the character in the many species of *Sphenomorphus* that have not yet been examined for it, as well as genetic data for *S. melanopogon* and wider genetic sampling of non-Philippine taxa.

Specimens examined

Sphenomorphus melanopogon (n = 195) (all localities are in Indonesia)

Pulau Deli (7º00'S 105º32'E): SMF 53924–35. Sumbawa: SMF 23263–64, Sumbawa Besar (8º30'S 117º26'E); 23265, Batoe-Doelang (= Batudulang 8º36'S 117º19'E); 23266, Dompoe (= Dompu 8º32'S 118º28'E). Komodo: AMNH 32068 (holotype), 32055–67, 32070 (paratypes), 2000'; 32101–04 (paratypes of *nitidus*), sea level; SMF 61005–06. Pulau Padar (8º40'S 119º35'E): AMNH 32000–01, 32003, MCZ 27015, SMF 61015–16. Flores: BMNH 1946.8.15.50 (paralectotype of *florensis*), Maumeri [= Maumere 8º37'S 122º14'E]; BMNH 97.6.21.18–20; BMNH 97.12.30.74, E. Flores; MCZ 9319, Larutuka [= Larantuka 8º21'S 122º59'E]; RMNH.RENA 5817a–b, Larutoko, E. Flores [=Larantuka]; SMF 23267–69, Rana Mese [20 km SE Ruteng *fide* Mertens, 1930:140]; SMF 23270–71, Endeh [=Ende 8º50'S 121º39'E]; SMF 23272–73, Wolo Waroe [= Wolowaru 8º46'S 121º54'E]; SMF 23283, Sita [8º29'S 120º14'E]; ZMA 11056–58 (paralectotypes of *florensis*), 11813a–c, Sikka, E. Flores [= Sika 8º45'S 122º12'E]; ZMA 11060 (lectotype), 11059, 11061–64 (paralectotypes of *florensis*), Maumeri [= Maumere]; ZMA 11814, Rieng Kemie [= Riangkamie 8º16'S 122º58'E]; ZMA 11815, Rioeng region, North coast [= Riung 8º28'S 121º03'E]; ZMA 11816a–p, Larantoeka [= Larantuka]; ZMA 11817, Flimandiri, above Tabali**,** E. Flores [= Ili Mandiri 8º19'S 122º58'E]; ZMA 11818a–b, north slope of Flimandiri, E. Flores [= Ili Mandiri]; ZMA 11819, no specific locality. Pulau Adonara (8º20'S 123º10'E): RMNH.RENA 4880a–b. Pulau Semau (10º13'S 123º22'E): RMNH.RENA 2534a–l, Samao. Timor: BMNH 1926.10.30.58–59, MCZ 25381–85, Lelogama, S. Timor [9º44'S 123º57'E]; MNHN 1245, 7110 (lectotype, paralectotype of *melanopogon*); RMNH.RENA 5817a–b, Noil Toko, Dutch Timor [=Noeltoko 9º33'S 124º22'E]; RMNH.RENA 2535a–k. Pulau Alor (8º15'S 124º45'E): BMNH 97.12.30.11–14. Wetar: AMNH 32203 (holotype), 32192–202 (paratypes), MCZ 27026–31 (paratypes of *barbouri*), nr Uhak, N coast [7º35'S 126º30'E]; NMBA 6476–77, RMNH.RENA 5532a–d; SMF 14415–21, Iliwaki [= Ilwaki 7º56'S 126º26'E]; ZSM 20/1915a–b, Fliwaki [= Ilwaki]. Pulau Damar (7º09'S 128º40'E): MCZ 20996 (holotype of *weberi*), Damma; BMNH 92.4.13.1–2, 1900.2.9.5–10, Damna Island. Pulau Teun (6º59'S 129º08'E): RMNH.RENA 5090a–c; BMNH 1932.1.1.1, Teoen, Damnar I., Banda See. Kepulauan Babar: RMNH.RENA 5089a–d, Teboe, Baber Eil. [= Tepa, Pulau Babar 7º52'S 129º31'E]; 7232a–b, Babber Is.; ZMA unregistered (n = 6), Babar Eil.; ZMA unregistered (n = 2), Tepa, Babar Eil. Pulau Banda Besar: RMNH.RENA 5091a–b, Lonkoer, Banda Is. [= Lonthoir (4º32'S 129º52'E). Kepulauan Kai: MCZ 27945 (paralectotype), NMBA 5514 (lectotype), 5513, 5515–17 (paralectotypes of *kühnei*), Kei-Inseln.

Sphenomorphus meyeri [n = 212]

Indonesia: Kepulauan Aru: BMNH 76.7.18.2–3, RMNH.RENA 4253, ZMB 7937–38, 9739 (syntypes of *meyeri*), [Wokam], Aru Islands [5°35'S 134°32'E]; WAM R109628, R109580, R109583, R109591, Karangguli (5°48'S 134°15'E).

Indonesian New Guinea: No precise locality: MNHN 1244, RMNH.RENA 3830a-c.

Papua Barat Province: AMNH 94313, Mt Besar, above Wailebet, 1500', Batanta I., Raja Ampat Is. (0°53'S 130°36'E); BPBM 3122, Kebar Valley, 550 m, Vogelkop (0.867°S 133.083°E); RMNH.RENA 7425a-b, Batanta I., Raja Ampat Is.; 7426a-b, Gagie [Pulau Gag 0°27'S 129°52'E] or Gebe [Pulau Gebe 0°05'S 129°20'E]; 30003–05, Kampong Gariau, Jamoer Meer [3°42'S 134°56'E]; 30006, Ajamaroe [Ajamaru], Vogelkop [1°14'S 132°12'E]; 30007, Manokwari [0°52'S 134°05'E]; 30008, Djitmau, Vogelkop [1°14'S 132°20'E]; 30009, Toeog, Vogelkop [coordinates unknown]; 30010, Komara, Vogelkop [?Koemana/Kumawa, Bomberoi Peninsula 3.8333°S 132.8333°E]; 30011, Pasir Poetih [=Pasir Putih, Vogelkop, 0°52'S 134°06'E].

Papua Province: AMNH 66354, Hollandia, Indonesia [2°32'S 140°41'E]; BPBM 3395, Itoda (4.036°S 136.09°E); FMNH 152333, MCZ 28681, Mimika River [*ca*. 4°43'S 138°28'E]; MCZ 68919, Kamu Valley [*ca*.

3°33'S 136°089'E]; RMNH.RENA 29982–30000, Tanah Merah [6°06'S 140°17'E]; 30001–02, Kauh, Digoel River [5°50'S 140°12'E]; 30012–13, Kawakit, Digoel River [5°39'S 140°14'E]; 30014–16, Katem [5°09'S 140°43'E].

Papua New Guinea: Western Province: AM R31847 (holotype of *papuensis*), Katow [9°08'S 142°57'E]; R64302, AMNH 111724, MCZ 141056–60, 141064, PNGNM R22359, USNM 195770, Emeti, Bamu River (7°45'S 143°15'E); AM R93236, R121161, AMNH 105862–64, 106274, MCZ 152326, 152358–59, 152364–66, SAM R11434, Wipim (8°51'S 142°54'E); AMNH 57543, Fly River; 57902, Daru (9°05'S 143°12'E); 59941, Sturt I., Fly River, (8°10'S 142°15'E); BMNH 1987.523–26, USNM 195880, Oriomo, Oriomo River (8°52'S 143°11'E); 1987.527, Runginae, Ok Mart River [Rumginae Mission, 5°54'S 141°16'E]; MCZ 119492, Balimo (8°02'S 142°57'E); 119493–94, 140748, Ningerum (5°42'S 141°07'E); 123990, Menemsore (5°53'S 141°15'E); 134749, Morehead (8°43'S 141°38'E), 135501–02, PNGNM R22360, Oriomo Stn (8°52'S 143°11'E); MCZ 137558–59, Mata (8°40'S 141°44'E); 140846, Kuru (8°55'S 143°03'E); 152351–53, Matkomrae (5°49'S 141°09'E); 152354, Old Zim, Oriomo River (8°46'S 143°05'E); 152355, Derongo (5°25'S 141°06'E); 152360–62, Boboa I., Lake Murray (7°01'S 141°30'E); UPNG 8812, 8806A, Kasua (7°11'S 142°55'E); USNM 213383–84, Makapa village, Aramia River, Balimo subprovince (7°57'S 142°34'E); 213385, Samacki River, Aramia River, Balimo subprovince (7°46'S 142°16'E); 213386, Ali village, Aramia River, Balimo subprovince (7°54'S 142°20'E). Gulf Province: AMNH 102336, FMNH 170590, MCZ 101249–69, 101273–74, 145233–47, 145249–51, PNGNM R24282, SAM R10985, WAM R67634–35, Uraru, Purari River (6°54'S 144°54'E); BMNH 1970.859–60, MCZ 101242–46, 109236–39, Oroi, Purari River [= Orloli, 7°26'S 145°11'E]; BPBM 13120, 13122, 13130, 13164–65, Lakekamu field camp, along east branch of Avi Avi River, 120 m (7.735°S 146.496°E); 13158–59, 13162, PNGNM 25036, 25038, Ivimka, Lakekamu River (7.735°S 146.496°E); MCZ 100440–41, Camp II, Pio River, 1000' (6°44'S 144°52'E), 100442, Weiana, 1500' (6°44'S 144°52'E); 100443, Ining River, Soliabeda [Soliabedo], 1200' (6°40'S 144°55'E); 100444, Camp I, Soliabeda [Soliabedo], 3500' [6°37'S 144°50'E]; 100445, Soliabeda [Soliabedo] (6°40'S 144°55'E); 101247, Koni (6°59'S 145°03'E); 101272, Camp III, Nimi River [6°48'S 144°52'E]; 101842, Koni, Purari River, 250' (6°59'S 145°03'E); 150877, 30km N, 14 km W Kikori, Kikori River [7°08'S 144°07'E]; USNM 518582, 11 km S Tekedu, Ivimka camp (7.4405°S 146.2945°E). Central Province: AM R24428, Angabanga River, Kairuku subdivision (8°49'S 146°34'E). Sandaun Province: AM R115497, Skgonga River [4°33'S 141°10'E]; BPBM 23177–80, Camp 1, Torricelli Mountains, 550 m (3.39329°S 142.52826°E). Southern Highlands Province: AM R118731–34, Fau (6°14'S 142°42'E); R118735–39, Waro (6°32'S 143°11'E); R118740, Fogamaiyu (6°31'S 143°05'E); R118741, Namosado (6°15'S 142°47'E). Chimbu Province: BPBM 19063, Wera Sera field station, 850 m, Crater Mountain (6°43.43675'S 145°05.5575'E).

Acknowledgements

I particularly thank Dr Allen Greer, who first considered this nomenclatural conundrum in the 1960s, but did not publish his conclusions. He kindly provided his notes on the topic to me, but declined authorship on this manuscript. I also thank Ross Sadlier (AM), Linda Ford (AMNH), Colin McCarthy (BMNH), Allen Allison and Carla Kishinami (BPBM), Jose Rosado (MCZ), Franz Tiedemann (NHMW), Ilaiah Bigilale (PNGNM), Marinus Hoogmoed (RMNH), Mark Hutchinson (SAM), Konrad Klemmer (SMF), Rose Singadan (UPNG), George Zug (USNM) and Rainer Günther (ZMB), for providing facilities and access to specimens in the collections under their care, and Alan Resetar (FMNH), Ivan Ineich (MNHN), Giuliano Doria and Roberto Poggi (MSNG), Eugen Kramer (NMBA), Gunther Köhler (SMF), Paul Doughty (WAM) and Leobertus van Tuijl (ZMA) for the loan of specimens. Photographs of the type series of *Lygosoma melanopogon* were kindly provided by Hinrich Kaiser, and of the lectotype of *Lygosoma florensis* by Eelco Kruidenier and Ronald de Ruiter (RMNH). Anne Fawcett photographed the type of *Hinulia papuensis*. Final versions of Figs. 2, 5 and 7, and drafts and final versions of Fig. 15 were prepared by Hannah Findlay, and final versions of Figs. 11 and 13 by Cecilie Beatson. Jodi Rowley prepared Figs. 9 and 14.

References

Allison, A., Bickford, D., Richards, S. & Torr, G. (1998) Herpetofauna. + Appendices 13-15. *In*: Mack, A.L. (ed.). *A Biological Assessment of the Lakekamu Basin, Papua New Guinea*. Rapid Assessment Program Working Papers (9). Conservation International, Washington, pp. 58–62 + 156–172.

Auffenberg, W. (1980) The herpetofauna of Komodo, with notes on adjacent areas. *Bulletin of the Florida State Museum Biological Sciences*, 25(2), 39–156.

Baudin, N.-T. (1974) *The Journal of Post Captain Nicolas Baudin Commander-in-Chief of the Corvettes* Géographe *and* Naturaliste. (Transl. C. Cornell). Libraries Board of South Australia, Adelaide, xxi + 609 pp.

Böhme, W. (1981) A new lygosomine skink from Thailand (Reptilia: Scincidae). *Bolletino del Museo Civico di Storia Naturale di Verona*, 8, 375-382.

Boulenger, G.A. (1887) *Catalogue of the Lizards in the British Museum (Natural History). Vol. III. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleontidae*. British Museum, London, xii + 575 pp + xl pl.

Boulenger, G.A. (1914) An annotated list of the batrachians and reptiles collected by the British Ornithologists' Union Expedition and the Wollaston Expedition in Dutch New Guinea. *Transactions of the Zoological Society of London*, 20(5), 247–274.

Brongersma, L.D. (1942) Notes on scincid lizards. *Zoologische Mededelingen*, 24(1–2), 125–152 + pl. VI.

Brown, A.J. (2004) *Ill-starred Captains: Flinders and Baudin*. Fremantle Arts Centre Press, Fremantle, 528 pp.

Brygoo, É.-R. (1985) Les types des Scincidés (Reptiles, Sauriens) du Muséum national d'Histoire naturelle Catalogue critique. *Bulletin du Muséum national d'Histoire naturelle (4) Section A (Zoologie, Biologie et Ecologie animales)*, 7(3)(supplement), 1–126.

Capocaccia, L. (1961) Catalogo dei Tipi di Rettili del Museo Civico di Storia Naturale di Genova. *Annali del Museo Civico di Storia Naturale di Genova*, 72, 86–111.

Cogger, H.G. (2000) *Reptiles and Amphibians of Australia*. 6th Edition. Reed New Holland, Sydney, 808 pp.

de Jong, J.K. (1930) Reptiles from Dutch New Guinea. *Nova Guinea*, 15(3), 296–318.

de Rooij, N. (1915) *The Reptiles of the Indo-Australian Archipelago. I. Lacertilia, Chelonia, Emydosauria*. E.J. Brill, Leiden, xiv + 384 pp.

Doria, G. (1874) Enumerazione dei rettili raccolti Dal Dott. O. Beccari in Amboina, alle isole Aru ed alle isole Kei durante gli anni 1872-73. *Annali del Museo Civico di Storia Naturale di Genova*, 6, 325–357 + pl. x–xi.

Duméril, A.M.C. & Bibron, G. (1839) *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles. Vol. V.* Librairie Encyclopédique de Roret, Paris, 854 pp.

Duméril, M.C. & Duméril, M.A. (1851) *Catalogue Méthodique de la Collection des Reptiles*. Roret, Paris, 224 pp.

Dunn, E.R. (1927) Results of the Douglas Burden Expedition to the Island of Komodo. III. — Lizards from the East Indies. *American Museum Novitates*, (288), 1–13.

Dunmore, J. (1969) *French Explorers in the Pacific*. 2 Vols. Oxford University Press, London, viii + 356 + vii + 428 pp.

Duyker, E. (2006) *Francois Peron — An Impetuous Life. Naturalist and Voyager.* Melbourne University Press, Melbourne, 345 pp.

Ferner, J.W., Brown, R.M. & Greer, A.E. (1997) A new genus and species of moist closed canopy forest skinks from the Philippines. *Journal of Herpetology*, 31(2), 187–192.

Fitzinger, L. (1843) *Systema Reptilium. Fasciculus Primas Amblyglossae*. Braumüller et Seidel, Vienna, 106 pp.

Forcart, L. (1953) Die Amphibien und Reptilien von Sumba, ihre zoogeographischen Beziehungen und Revision der Unterarten von *Typhlops polygrammicus*. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 64(2), 356–388.

Fransen, C.H.J.M., Holthuis, L.B. & Adema, J.P.H.M. (1997) Type-catalogue of the Decapod Crustacea in the collections of the Nationaal Natuurhistorisch Museum, with appendices of pre-1900 collectors and material. *Zoologische Verhandelingen*, 311, i–xvi + 1–344.

Gray, J.E. (1841) A Catalogue of the Species of Reptiles and Amphibia hitherto described as inhabiting Australia, with a description of some New Species from Western Australia, and some remarks on their geographical distribution. *In*: Grey, G. *Journals of two expeditions of discovery in North-West and Western Australia, during the years 1837, 38, and 39, Under the authority of Her Majesty's Government*. Vol. 2. T. and W. Boone, London, pp. 422–449.

Gray, J.E. (1845) *Catalogue of the specimens of lizards in the collection of the British Museum*. Edward Newman, London, xxviii + 289 pp.

Greer, A.E. (1979) *Eremiascincus*, a new generic name for some Australian sand-swimming skinks (Lacertilia: Scincidae). *Records of the Australian Museum*, 32(7), 321–338.

Greer, A.E. (1983) The Australian scincid lizard genus *Calyptotis* de Vis: resurrection of the name, description of four new species, and discussion of relationships. *Records of the Australian Museum*, 35(1), 29–59.

Greer, A.E. (1991) *Lankascincus*, a new genus of scincid lizards from Sri Lanka, with descriptions of three new species. *Journal of Herpetology*, 25(1), 59–64.

Greer, A.E. (1997) *Leptoseps*: a new genus of scincid lizard from southeast Asia. *Journal of Herpetology*, 31(3), 393–398.

Greer, A.E. & Parker, F. (1967) A new scincid lizard from the northern Solomon Islands. *Breviora*, (275), 1–20.

Greer, A.E. & Shea, G.M. (2004) A new character within the taxonomically difficult *Sphenomorphus* group of lygosomine skinks, with a description of a new species from New Guinea. *Journal of Herpetology*, 38(1), 79-87.

Guibé, J. (1954) *Catalogue des types de lézards du Muséum National d'Histoire Naturelle*. Colas, Bayeux, 120 pp.

Günther, A. (1873) Notes on some reptiles and batrachians obtained by Dr. Adolf Bernhard Meyer in Celebes and the Philippine Islands. *Proceedings of the Zoological Society of London*, 1873(11), 165–172 + pl. xvii–xviii.

Hartert, E. (1900a) The birds of Dammer Island in the Banda Sea. *Novitates Zoologicae*, 7(1), 12–24.

Hartert, E. (1900b) The birds of the Banda Islands. *Novitates Zoologicae*, 7(3), 551–554.

Hartert, E. (1901) On the birds of the Key and South-East Islands, and of Ceram-Laut. *Novitates Zoologicae*, 7(1), 1–5, (2), 93–101.

Hartert, E. (1904) The birds of the South-west Islands Wetter, Roma, Kisser, Letti, and Moa. *Novitates Zoologicae*, 11(1), 174–221.

Hartert, E. (1906) On the birds of the island of Babber. *Novitates Zoologicae*, 13(23), 288–302.

Hartert, E. (1907) Heinrich Kühn. *Novitates Zoologicae*, 14(1), 340–341.

Hellmayr, C.E. (1916) Weiteres zu Avifauna von Timor. *Novitates Zoologicae*, 23, 96–111.

Kaiser, H., Carvalho, V.L., Ceballos, J., Freed, P., Heacox, S., Lester, B., Richards, S.J., Trainor, C.R., Sanchez, C. & O'Shea, M. (2011) The herpetofauna of Timor-Leste: a first report. *Zookeys*, (109), 19–86.

Kopstein, F. (1926) Reptilien von den Molukken und den benachbarten inseln. *Zoologische Mededelingen*, 9(2–3), 71–112.

Kopstein, F. (1927) Über einen fall von polymorphismus bei der Scinciden-gattung *Lygosoma*. *Treubia*, 9(4), 371–375.

Kramer, E. (1979) Typenkatalog der Echsen im Naturhistorischen Museum Basel (BM), stand 1978. *Revue Suisse de Zoologie*, 86(1), 159–166.

Lidth de Jeude, T.W. (1894) Reptiles from Timor and the neighbouring islands. *Notes from the Leyden Museum*, 16(6), 119–127.

Linkem, C.W., Deismos, A.C. & Brown, R.M. (2011) Molecular systematics of the Philippine forest skinks (Squamata: Scincidae: *Sphenomorphus*): testing morphological hypotheses of interspecific relationships. *Zoological Journal of the Linnean Society*, 163(4), 1217–1243.

Loveridge, A. (1948) New Guinean reptiles and amphibians in the Museum of Comparative Zoölogy and United States National Museum. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 101(2), 305–430.

Macleay, W. (1877) The lizards of the Chevert Expedition. *Proceedings of the Linnean Society of New South Wales*, 2(1), 60–69.

Mecke, S., Doughty, P. & Donnellan, S.C. (2009) A new species of *Eremiascincus* (Reptilia: Squamata: Scincidae) from the Great Sandy Desert and Pilbara Coast, Western Australia and reassignment of eight species from *Glaphyromorphus* to *Eremiascincus*. *Zootaxa*, (2246), 1–20.

Mertens, R. (1930) Die Amphibien und Reptilien der Insel Balik Lombok, Sumbawa und Flores. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 42(3), 117–344.

Mertens, R. (1957) Amphibien und Reptilien aus dem Äussersten Westen Java und von Benachbarten Eilanden. *Treubia*, 24(1), 83–105.

Meyer, A.B. (1874) Eine mittheilung von Hrn. Dr. Adolf Meyer über die von ihm auf Neu-Guinea und den Inseln Jobi, Mysore und Mafoor im Jahre 1873 gesammelten Amphibien. *Monatsberichte der königlich preussischen Akademie der Wissenshaften zu Berlin*, 1874, 128–140.

O'Shaughnessy, A.W.E. (1877) Reptilia. *In*: Rye, E.C. (Ed), The Zoological Record for 1875. John van Voorst, London, pp. 93–104.

Peters, W. (1864) Über die Eidechsenfamilie der Scincoiden, insbesondere über die Schneider'schen, Wiegmann'schen und neue Arten des zoologischen Museums. *Monatsberichte der der königlich preussischen Akademie der Wissenshaften zu Berlin*, 1864, 44–58.

Peters, W. (1867) Herpetologische Notizen. *Monatsberichte der der königlich preussischen Akademie der Wissenshaften zu Berlin*, 1867, 13–37.

Peters, W. & Doria, G. (1878) Catalogo dei Rettili e dei Batraci raccolti da O. Beccari, L.M. d'Albertis e A.A. Bruijn nella sotto-regione Austro-Malese. *Annali del Museo Civico di Storia Naturale di Genova*, 13, 323–450 + pl. I–VII.

Reeder, T.W. & Reichert, J.D. (2011) Phylogenetic relationships within the Australian limb-reduced lizard genus *Hemiergis* (Scincidae: Squamata) as inferred from the Bayesian analysis of mitochondrial rRNA gene sequences. *Copeia*, 2011(1), 113–120.

Roux, J. (1910) Reptilien und Amphibien der Aru- und Kei-Inseln. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 33(3), 211–247 + pl. xiii–xiv.

Scott, F., Parker, F. & Menzies, J.I. (1977) A checklist of the amphibians and reptiles of Papua New Guinea. *Wildlife in New Guinea*, (77/3), 1–18.

Smith, M.A. (1935) *The Fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. Vol. II. - Sauria.* Taylor & Francis, London, xiii + 440 + [3] pp. + 1 pl.

Smith, M.A. (1937) A review of the genus *Lygosoma* (Scincidae: Reptilia) and its allies. *Records of the Indian Museum*, 39(3), 213–234.

Stresemann, E. (1951) Type localities of Australian birds collected by the 'Expedition Baudin' (1801-1803). *Emu*, 51(1), 65–70.

Taylor, E.H. (1935) A taxonomic study of the cosmopolitan scincoid lizards of the genus *Eumeces* with an account of the distribution and relationships of its species. *Kansas University Science Bulletin*, 23, 1–643.

Taylor, E.H. (1963) The lizards of Thailand.*University of Kansas Science Bulletin*, 44(14), 687–1077.

Weber, M. (1891) Reptilia from the Malay Archipelago. I. Sauria, Crocodilidae, Chelonia. *In*: Weber, M. (Ed), Zoologische Ergebnisse einer reise in Niederländisch Ost-Indien. Vol. 1. E.J. Brill, Leiden, pp. 159–177 + pl. xiv.

Welch, K.R.G., Cooke, P.S. & Wright, A.S. (1990) *Lizards of the Orient: A Checklist*. Robert E. Kreiger, Malabar, 168 pp.

Whitaker, R., Whitaker, Z. & Mills, D. (1982) Reptiles of Papua New Guinea. *Wildlife in New Guinea*, (82/2), 1–53.

Whittell, H.M. (1954) *The Literature of Australian Birds: A History and Bibliography of Australian Ornithology.* Paterson Brokensha, Perth, xi + 140 + 788 pp.

Wichmann, A. (1910) Entdeckungsgeschichte von Neu-Guinea (1828 bis 1885). *Nova Guinea*, 2(1), i–xiv + 1–369.