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Lizard Wears Shades. A Spectacled *Sphenomorphus* (Squamata: Scincidae), from the Sacred Forests of Mawphlang, Meghalaya, North-east India

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Abstract

A new species of lygosomatine scincid lizard is described from the sacred forests of Mawphlang, in Meghalaya, north-eastern India. *Sphenomorphus apalpebratus* sp. nov. possesses a spectacle or brille, an unusual feature within the Scincidae, and a first for the paraphyletic genus *Sphenomorphus*. The new species is compared with other members of the genus to which it is here assigned, as well as to members of the lygosomatine genera *Lipinia* and *Scincella* from mainland India, the Andaman and Nicobar Islands, and south-east Asia, to which it also bears resemblance. The new taxon is diagnosable in exhibiting the following combination of characters: small body size (SVL to 42.0 mm); moveable eyelids absent; auricular opening scaleless, situated in a shallow depression; dorsal scales show a line of demarcation along posterior edge of ventral pes; midbody scale rows 27–28; longitudinal scale rows between parietals and base of tail 62–64; lamellae under toe IV 8–9; supraoculars five; supralabials 5–6; infralabials 4–5; subcaudals 92; and dorsum golden brown, except at dorsal margin of lateral line, which is lighter, with four faintly spotted lines, two along each side of vertebral row of scales, that extend to tail base. The new species differs from its congeners in the lack of moveable eyelids, a character shared with several distantly related scincid genera.

Key words: Squamata, Sauria, Scincidae, *Sphenomorphus*, new species, phylogenetic relationships, Meghalaya, India

Introduction

The origin and composition of the herpetofauna of peninsular India has been the topic of recent scholarly debate with various models being put forward, including African, Madagascan, South-east Asian or indigenous origins (see Bossuyt & Milinkovitch 2001; Biju & Bossuyt 2003; Datta-Roy *et al.* 2012). However, not much has been discussed regarding the origins of the fauna of its north-eastern region, which lies in the Indo-Burman region (*sensu van Dijk et al.* 1999), comprising north-eastern India, adjacent regions of China's Sichuan and Yunnan Provinces, Myanmar, Thailand, Lao PDR, Cambodia and Vietnam (see Kamei *et al.* 2012; Tordoff *et al.* 2012), and synonymous with the Indochinese subregion of some authors (Corbet & Hill 1992). The north-eastern part of India is also especially interesting because of its unique hill ranges with different geological origins. The Himalayan range itself is relatively recent, originating from the collision of the Indian plate with the Asian continent (Krishnan 1974). South of the eastern Himalayas, the Garo, Khasi and Jaintia Hills are relatively older, dating back to the Cretaceous (see Hora 1944; Valdiya 2010). The dearth of studies in north-eastern India appears to stem from a combination of factors, such as poor infrastructure, complicated territorial claims by multiple countries, the proliferation of tribal militant groups, diseases and other health-related factors, and complicated permitting and physical access regimes.

In this communication, we describe a new species of scincid lizard, allocated to the paraphyletic genus *Sphenomorphus* from the north-east Indian region. It differs from all known congeners in showing an absence of movable eyelids and the presence of a spectacle (or ‘brille’) that permanently covers the eye. Such structures have been previously noted in at least four families of non-gekkotan saurians (Scincidae, Gymnophthalmidae, Xantusiidae and Lacertidae), and within scincid lizards, appears to have independently evolved at least eight times (Greer 1983). Further, we determine the phylogenetic position of the new species within the *Sphenomorphus* group, based on mitochondrial markers.

Materials and methods

The type series, comprising the holotype and three paratypes, was collected from Mawphlang, East Khasi Hills, Meghalaya State, north-eastern India, between approximately 1000–1300 h, photographed in life, euthanized and tissue samples removed, fixed in buffered formalin approximately 24 h after collection, and subsequently washed in water and transferred to 70% ethanol about two weeks after collection. Geographical coordinates for the type locality were taken with a Garmin Etrex H series Global Positioning System (datum: WGS 84). Comparative material was examined on visits to, or as loans from museums (see Appendix 2 and Acknowledgements).

Specimens and tissues. Muscle from tail and liver tissue samples were dissected from freshly sacrificed specimens, and stored in absolute ethanol at -20°C. Appendix 1 provides DNA sequence data from the mitochondrial 12S rRNA and 16S rRNA gene for the new species.

DNA isolation, amplification, and sequencing. The total genomic DNA from the stored tissue sample was extracted according to a standard Phenyl – Chloroform Isoamyl alcohol protocol, as described in Sambrook and Russell (2001). The extracted DNA was quantified using an Eppendorf biophotometer and was diluted accordingly for a PCR reaction. We amplified partial sequences of mitochondrial 12S (333 bp) and 16S (445 bp) genes, as these have been used earlier for various other scincids from the Indomalayan region (Honda *et al.* 2000; Mausfeld & Schmitz 2003; Datta-Roy *et al.* 2012). These genes are also known to be rapidly evolving and variable enough to help resolve relationships within squamates (Reeder & Wiens 1996, Whiting *et al.* 2003, 2006). The PCR conditions for the aforementioned mitochondrial genes are similar to that used in previous publications. The amplified PCR product was then purified using a QIAquick PCR purification kit (Quiagen) and the sequences were obtained commercially from Eurofins Biotech Pvt. Ltd. (Bangalore, India). The obtained sequences were aligned with other published sequences using the software MUSCLE (Edgar 2004), which is integrated in the software package MEGA 5.05 (Tamura *et al.* 2011). In order to find affinities of the new species of *Sphenomorphus*, we included members from across the subfamily Lygosomatinae (not shown). However, in both trees- Maximum likelihood (ML) and Bayesian Inference (BI), the new species was nested within the ‘*Sphenomorphus* group’. Based on these preliminary data as well as morphology, we added more members of the ‘*Sphenomorphus* group’ from across its distribution (see Appendix 1) and removed the most other representatives of the Lygosomatinae except for two members each from the ‘*Ablepharus* group’ (*Asymblepharus himalayanum* and *Ablepharus grayanus*) and the ‘*Lygosoma* group’ (*Lygosoma koratense* and *Lygosoma bowringii*), which serve as outgroups. The sequences were realigned and subsequently used to build phylogenies. The ML analyses was carried out using the software PAUP* version 4.0b 10 (Swofford 2002) using a heuristic search option with 10 random sequence addition and tree bisection-reconnection (TBR) branch swapping. For the ML analyses, the substitution model was chosen using the Akaike information criterion (AIC) in MODELTEST version 3.7 (Posada & Crandall 1998) in conjunction with PAUP* for the combined dataset as well as individual genes. Bootstrap support was determined in PAUP* using 1000 pseudoreplicates for ML in a simple heuristic search option. For Bayesian analyses, the dataset was partitioned into the two genes in MrBayes version 3.1 (Ronquist & Huelsenbeck 2003). The partitions were assigned their respective DNA substitution models (based on results obtained from MODELTEST v 3.7), unlinked and the model parameters for each gene were determined separately. Bayesian analysis was run using default priors for five million generations, with two simultaneous chains and trees were sampled every 100 generations. Run length was based on the standard deviation of split frequencies, and when the value of this diagnostics fell below 0.01, the run was stopped. The log file consisting of the likelihood values of the 50,000 saved trees was loaded onto Tracer version 1.5, to determine the stage at which a stable likelihood value was obtained. The first 12,500 trees (25%) were discarded as burn-in. The saved trees were then used to generate a majority rule consensus tree in MrBayes using the *sumt* command.

The following measurements were taken with Mitutoyo™ dial vernier callipers (to the nearest 0.1 mm) approximately five months after collection: snout–vent length (SVL); tibia length (TBL), distance between surface of knee to surface of heel, with the knee flexed; head length (HL), distance between angle of jaws and snout-tip; head width (HW), measured across retroarticular process of the mandible; head depth (HD), greatest transverse depth of head, taken posterior of the orbital region; eye diameter (ED), horizontal diameter of the eyes-measured across the anterior and posterior margins of the palpebral margin; internarial distance (IN), distance between nostrils; eye to snout distance (E–S), distance between anteriormost point of eyes and tip of snout; eye to nostril distance (E–N), distance between anteriormost point of eyes and posterior-edge of nostrils; nostril to snout distance (N–S), distance between anteriormost point of nostril and tip of snout; axilla to groin distance (A–G), distance between posterior edge of forelimb at its insertion to body to anterior edge of hind limb at its insertion to body and body width (BW), greatest width of body. Colour nomenclature follows a web-accessible colour list (en.wikipedia.org/wiki/List_of_colours).

Comparative materials examined are listed in Appendix 2. Sources of additional data on character states and distribution of other species of *Sphenomorphus* are Bacon (1967), Boulenger (1887, 1894, 1900, 1908, 1912), Bourret (2009), Brongersma (1942), Brown & Alcalá (1961), Darevsky *et al.* (2004), Das (2010), Das & Greer (2002), de Rooij (1915), Greer (1977, 1989), Greer & Shea (2003), Grismer (2006, 2007, 2011), Grismer *et al.* (2009), Hartmann *et al.* (2010); Inger & Hosmer (1965), Inger *et al.* (2001), Iskandar (1994), Lim (1998), Linkem *et al.* (2010), Malkmus *et al.* (2002), Manthey & Grossmann (1997), Nguyen *et al.* (2010a; 2010b; 2011, 2012), Ouboter (1986), Shea (2012), Shreve (1940), Smith (1924, 1930, 1935), Taylor (1922, 1963), Wang *et al.* (2013), Werner (1910) and Yamasaki *et al.* (2001). Institutional abbreviations, where available, follow Sabaj Pérez (2012). These include: the Brunei Museums Department, Bandar Seri Begawan, Brunei Darussalam (BM); The Natural History Museum, London, United Kingdom (BMNH); Field Museum of Natural History, Chicago, USA (FMNH); Museum of Zoology, Department of Zoology, Graduate School of Science, Kyoto University (KUZ); Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ); Sarawak Biodiversity Centre Zoological Museum, Semenggoh, Sarawak, Malaysia (SBC); Sarawak Museum, Kuching, Sarawak, Malaysia (SM); Sabah Parks Zoological Museum, Kinabalu National Park, Sabah, Malaysia (SP); Museum of the Universiti Brunei Darussalam, Gadong, Brunei Darussalam (UBD); the Borneensis Collection, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia (UMS); Universiti Malaysia Sarawak, Kota Samarahan, Malaysia (UNIMAS); Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC; the abbreviations used in Sabaj Pérez [2012] are also RMBR, USDZ and ZRCS); Zoological Institute of the Russian Academy of Sciences, Department of Herpetology, St. Petersburg, Russia (ZISP) and Zoological Survey of India, Kolkata, India (ZSI). We deposited the type series of the new species at the new Natural History Museum of the Centre for Ecological Sciences, Indian Institute of Science, Bangalore, for which we propose the institutional abbreviation, CES.

Sphenomorphus apalpebratus sp. nov.

(Figures 1–4)

Holotype. CES 10/830 (adult, female), from Mawphlang (25.44563329°N, 91.7428503°E, alt. 1,815 m asl; datum WGS 84), East Khasi Hills District, Meghalaya State, north-east India (Fig. 6). 17 October 2010 (Aniruddha Datta-Roy, Ishan Agarwal, Ronald K. Lyngdoh Tron, N. P. I. Das and Tarun Khichi, collectors).

Paratypes. CES 10/ 831–CES 10/833 (unsexed juveniles). Collection data as for holotype.

Diagnosis. We allocate the lizard specimens collected from Mawphlang to the genus *Sphenomorphus* for showing the following characters: parietals meet behind interparietals; median preanals overlap outer preanals; and iris as dark as pupil, considered apomorphies of the *Sphenomorphus* group (Greer 1979), in addition to the absence of supranasals; five digits on fore- and hindlimbs, limbs well developed, and body elongated, but non-vermiform. Further, the new species can be differentiated from congeners from India and mainland south-east Asia in showing the following characters: inner preanals overlapping the outer ones, small body size (SVL to 42.0 mm); midbody scale rows 27–28; longitudinal scale rows between parietals and base of tail 62–64; subdigital lamellae of toe IV 8–9; supraoculars five; supralabials 5–6; infralabials 4–5; subcaudals 92; and dorsum golden brown, except at dorsal margin of lateral line, which is lighter, with four faintly spotted lines, two along each side of vertebral row of scales, extending to tail base.

Etymology. Latin for lacking eyelids, a distinctive morphological character in the new species.

Nomenclatural Notes. The name of the genus *Sphenomorphus* Fitzinger 1843 (type species: *Gongylus [Lygosoma] melanopogon* Duméril & Bibron 1839) was derived from Greek (meaning wedge-shaped, an allusion to the shape of the head) and originally coined as masculine. However, a number of species, some of which were transferred from the catchall lygosomatine genus *Lygosoma* (of neuter gender), have name terminations not matching the gender of their current generic allocation, in recent lists (e.g., Uetz 2012). These include *S. crassa* Inger *et al.* 2001, *S. mimikanum* (Boulenger 1914) and *S. nigrolineata* (Boulenger 1897). Following Article 30.1.3 of the International Code of Zoological Nomenclature (International Commission of Zoological Nomenclature 1999), the termination of these species nomina requires emendation.

Description of holotype. Based on an adult female, SVL 42.0 mm, TL 65.0 mm; snout blunt (IN:IO ratio 0.35), not projecting beyond lower jaws; nostril laterally oriented; oval, situated closer to snout-tip than to orbit; eye-nostril distance 1.44 mm, eye-snout distance 2.32 mm (E-N:E-S ratio 0.62); head long, much longer than wide (HL 6 mm, HW 4.68 mm (HL:HW ratio 1.29)); head shape slightly flattened, HD 4 mm (HL:HD ratio 1.5); rostral width (1.28 mm), broad, not projecting onto snout; posterior border of rostral curved; frontonasal trapezoidal, wider than long; frontal elongated, arrow-shaped, wider anteriorly; frontoparietals separate; prefrontals small, widely separated; interparietal single, smaller than frontonasal; parietals contact posterior to interparietal, half length of interparietal; parietal eye spot absent; five supraoculars; four supraciliaries; nostrils located in midnasal; postnasal absent; supranasals absent; loreals two, trapezoidal; anterior loreal higher than posterior; two presuboculars, separating supralabial III from orbit; six supralabials (supralabial IV contacting orbit); three postsuboculars; three postoculars; two pretemporals; three temporals, the upper secondary temporal largest; upper secondary temporals overlapped by lower; temporals larger than lateral body scales; one pair of nuchals; five infralabials; one scale separates second pair of enlarged chin shields; three scales separate third pair of chin shields; enlarged chin shields contact infralabials; auricular opening scaleless, its location indicated by a shallow depression; eyes relatively small; pupil not discernable in preserved specimen; no moveable eyelids (Fig. 2); upper palpebrals 11; lower palpebrals 12; tongue short; undivided anteriorly, tip obtuse, not pointed; teeth relatively small and somewhat blunt.

Body slender, BW 6.36 mm (BW:SVL ratio 0.15); head slightly distinct from neck and body; 64 longitudinal scale rows from parietal to above level of anterior margin of hind limb; 64 scales dorsally; 60 ventrals, counted from first postgular to last scale before preanals; body scales smooth, subcycloid; median rows not enlarged, as wide as adjacent scales; 28 transverse scale rows at midbody; 92 subcaudals; abdominal scales larger than throat scales and marginally larger than pectoral scales; median ventral scales enlarged relative to scales on flanks; median and lateral preanals enlarged, larger than adjacent ventrals (Fig. 4); median pair of preanals overlap lateral preanals and are smaller than lateral ones; tail rounded, relatively long, longer than snout-vent length (TL:SVL ratio 65.42); tail tip acute; tail base wider than rest of tail; tail gradually tapering to a point; median row of subcaudals enlarged. Visceral fat bodies present in abdomen.

Limbs short and pentadactyle, digits short and clawed; lamellae smooth, enlarged; adpressed limbs fail to meet; lamellae under finger I-2; II-3; III-5; IV-5; V-4; lamellae under toes I-3; II-6; III-8; IV-9; V-5.

Coloration (in preservative). Lateral side of head with brown-black flecks; radiating broken lines from tympanic region to axilla; broken line, in the form of spots, extending from nostril to preocular region, continuing after orbit to almost two-thirds along the length of tail. On flanks, dark stripe fuses with its partner, dorsum olive brown (Medium Spring bud, colour no. C9DC87), with four faint lines, two on each side of the vertebral row of scales. Lines start at row of scales just below single pair of nuchals, and continue to tail base, where they become diffused. Dorsal surface of tail marginally darker than rest of dorsum; tail tip (regenerated) slightly lighter than rest of tail; flanks speckled with brown-black below lateral line; venter anterior to preanal scales lacking dark pigment, gulars cream coloured; pectoral to preanal region bright yellow; venter of tail grey, spotted with brown-black speckles to tip, darker apically. Tail venter with lighter pigments than dorsal side. Both fore- and hind limbs heavily spotted on dorsal side and lightly spotted ventrally. Lamellae chocolate brown in colour.



FIGURE 1. Holotype of *Sphenomorphus apalpebratus* sp. nov. (CES 10/830) in life. Top. Dorsum; Middle. Venter; and Bottom. Close-up of head and anterior body in lateral view.

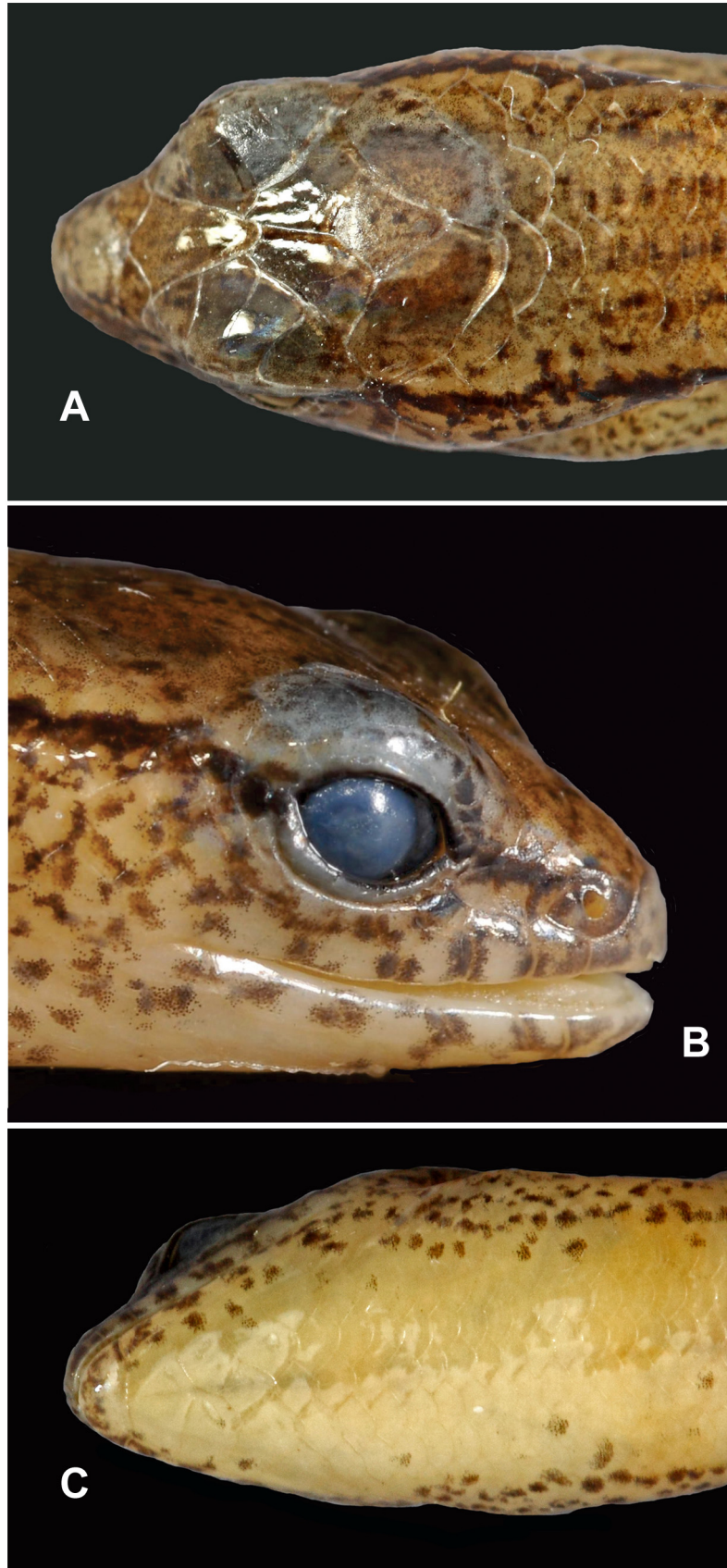


FIGURE 2. Head squamation in holotype of *Sphenomorphus apalpebratus* sp. nov. (CES 10/830). Top. Forehead; Middle. Lateral view of head; and Bottom. Throat.

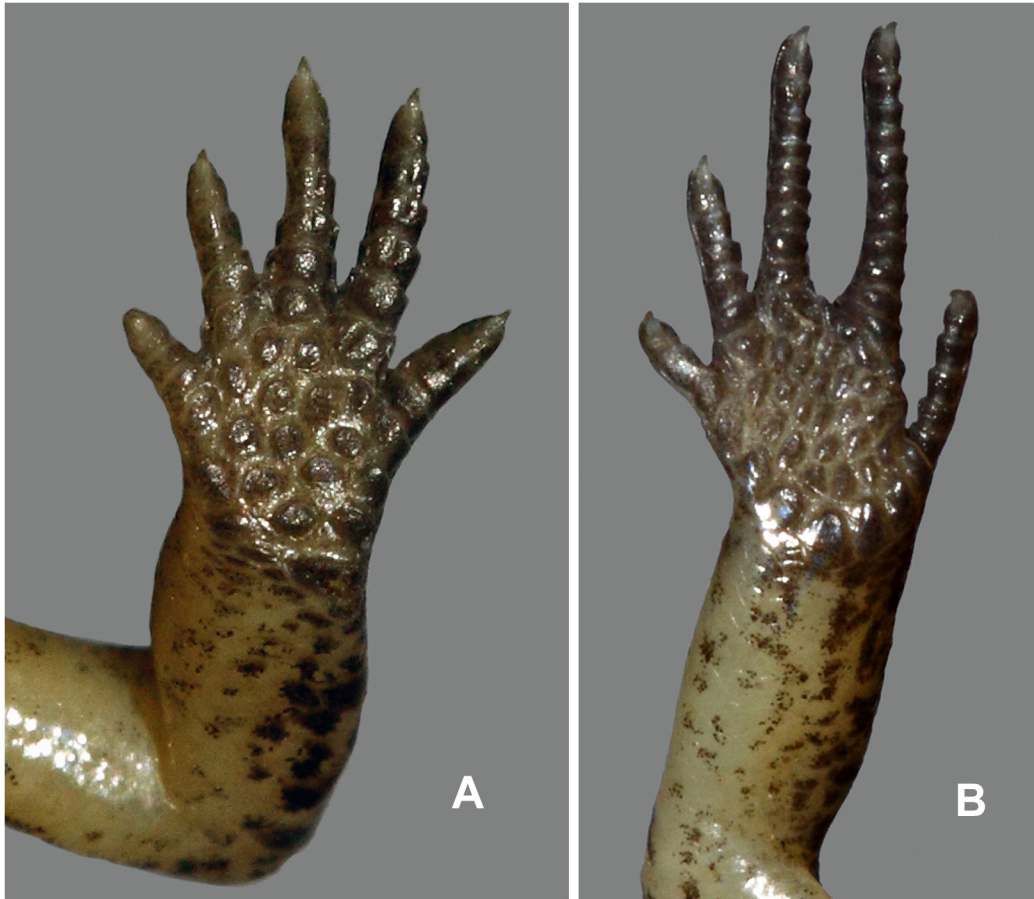


FIGURE 3. Left limb of holotype of *Sphenomorphus apalpebratus* sp. nov. (CES 10/830). A. Manus; and B. Pes.



FIGURE 4. Close-up of preanal region of holotype of *Sphenomorphus apalpebratus* sp. nov. (CES 10/830), showing preanal scales.

Coloration (in life). Lateral side of head freckled with patches of brown-black spots. A few radiating spotted lines extend from tympanic region to insertion of forelimb. A spotted line on lateral side of head from nostril to preocular, continuing beyond orbit to nearly two-thirds along the length of tail. Upper and lower palpebral series lemon yellow in colour, except at anterior and posterior corners of eye. Iris and pupil not clearly discernible. Head scales edged with black spots. Dorsum golden brown (Gamboge colour no. E49B0F), except at dorsal margin of lateral line, which is lighter. Four faintly spotted lines on dorsum, two along each side of vertebral row of scales, that continue to tail base; dorsum of tail darker than that of trunk at midbody; sides of head from snout to auricular depression, to below orbit cream coloured, gradually becoming pink around midbody between posterior margin of forelimb to anterior margin of hindlimb; yellowish near tail base. Flanks freckled with brownish-black longitudinal spots that are denser towards hindlimb than immediately behind forelimb. Dorsal surface of forelimb and hindlimb heavily spotted and appear dark. Gulars to 17th ventral scale cream-coloured and devoid of dark spots. Starting from 18th ventral row of scales, colour abruptly becomes bright lemon yellow until preanal scales or ventral margin of tail base. Yellow spots more dense in midregion of ventral scales, gradually becoming non-pigmented at scale boundary. Ventral side of forelimbs less spotted and pale pink in colour, ventral side of hindlimbs lemon yellow, with marginally more brownish-black spots. Toe lamellae of both limbs dark, unspotted. Preanal region, a light shade of pink, gradually fading to white and turning cobalt blue towards tail tip; venter of tail with brownish-black flecks, becoming denser apically.

Measurements (in millimeters; holotype with variation shown in paratype series, all juveniles, in parentheses). SVL 42.00 (range 26.76–27.50, mean 26.90); HL 10.00 (range 4.32–5.10 range, mean 4.73); HW 5.50 (range 4.10–4.94, mean 4.65); HD 4.00 (range 2.98–2.98, mean 2.98); BW 6.36 (range 4.10–4.60, mean 4.37); TBL 3.38 (range 2.24–2.46, mean 2.35); ED 1.46 (range 1.00–1.16, mean 1.05); IN 1.24 (range 1.00–1.00, mean 1.00); E–S 2.32 (range 1.42–1.80, mean 1.59); E–N 1.44 (range 1.00–1.20, mean 1.11); N–S 0.70 (range 0.40–0.48, mean 0.44); A–G 25.82 (range 14.50–15.58, mean 15.03); and TL 65.00 (tail tips of paratypes clipped for DNA extractions).

Squamation (holotype with variation shown in paratype series, all juveniles, in parentheses). Transverse scale rows at midbody 28 (range 27–28, mean 27.33); longitudinal scale rows 64 (range 62–64, mean 63); ventral scale rows 60 (range 56–58, mean 57); supralabials 6 (range 5–5, mean 5); infralabials 5 (range 4–4, mean 4); subcaudals 92 (tail of paratypes clipped for DNA extraction); and lamellae under toe IV 9 (range 8–9, mean 8.33).

Results and discussion

Morphological comparisons. Few lineages show immovable eyelids and lack a palpebral slit (i.e., “ablepharine eye” sensu Greer 1974; see also Jacobsen & Broadley 2000). These include the Australian *Lerista* (which includes both species with eyelids and with spectacles), *Morethia* and *Proablepharus*, the Eurasian *Ablepharus*, the African *Afroablepharus*, *Lacertaspis*, *Leptosiphos* and *Panaspis*, and the Indo-Pacific *Cryptoblepharus*. In the species from Meghalaya, an immovable clear spectacle permanently covers the eye, and no palpebral slit is evident.

The genus *Sphenomorphus* Fitzinger 1843, is demonstrably paraphyletic (Mittleman 1952 provided a working list of constituent species; see also Honda *et al.* 2000; Linkem *et al.* 2011; Shea 2012), showing a distribution from southern Asia, eastward through mainland south-east Asia, to the archipelagoes of the Sundas, Sulawesi, the Philippines, New Guinea, Australia and island groups of the western Pacific. Species formerly assigned to the genus from México and Central America (see Greer 1974; Myers & Donnelly 1991), have recently been allocated to *Scincella* by Linkem *et al.* (2011). A total of 122 nominal species are allocated to the genus as presently constituted (see Uetz 2012), making it one of the largest genera within the Scincidae. Several authors have attempted to partition *Sphenomorphus* into smaller subgroups (see Boulenger 1887; Brown & Alcalá 1980; Greer 1974, 1979; Inger & Hosmer 1965; Taylor 1922; Smith 1937). Reeder (2003) reported monophyly of its Australian members, while the Philippine *Sphenomorphus* have been shown to be paraphyletic (Linkem *et al.* 2011). However, global scale phylogenies have thus far been not attempted, for which reason, allocation of the north-east Indian material to a particular group is not possible at this time. Our comparisons thus must rely on squamation and colour pattern. In this section, we compare the new species with its congeners from the Asian mainland, listing opposing suite of characters that separate it from the respective species. No previously described species within the genus shows a brille or ‘spectacle.’ There is precedence for intrageneric variation in this character in Australian

scincids of the genus *Lerista*, in which about one fourth of the known species exhibit an “ablepharine” eye, whereas the rest have ‘windowed eyelids’ and one has vestigial eyes, at the time of the reviews published by Greer (1967; 1983).

Because of our retention of the new species in the genus *Sphenomorphus*, we compare it initially with the three north-east Indian species of the genus. It differs from *S. indicus* (Gray 1853) (distribution: Bhutan, Nepal, India, Myanmar, China, Vietnam and Thailand, possibly also northern Peninsular Malaysia): supralabials seven; large ear opening; midbody scale rows 30–38; lamellae under toe IV 16–22 and an uninterrupted dark flank stripe; *S. courcyanus* (Annandale 1912) (distribution: Arunachal Pradesh and Mizoram States, north-eastern India): supralabials seven; large, tympanum sunk, lacking a tympanic annulus; lamellae under toe IV 12–13 and an uninterrupted dark dorsolateral stripe, edged with a paler one, and *S. maculatus* (Blyth 1853) (including the subspecies *mitanensis* Annandale 1905, distribution: Bhutan, eastern India, the Andaman and Nicobar Islands, Myanmar, Cambodia and Thailand): supralabials seven; infralabials 7–8; midbody scale rows 36–44; lamellae under toe IV 15–23; a paired median series of dark spots and an uninterrupted dark flank stripe.

The new species differs from all species of *Sphenomorphus* (including several recently allocated to other genera, especially from the Philippines, see Linkem *et al.* 2011), from mainland and insular south-east Asia (the Greater Sundas, including Palawan): *S. helenae* Cochran 1927 (distribution: central Thailand): supralabials seven; a large ear opening; midbody scale rows 30 and an uninterrupted dark lateral stripe; *S. orientale* (Shreve 1940) (distribution: Pakokku-Chin Hills, Myanmar): supralabials seven; midbody scale rows 24–26 and longitudinal scale rows between parietals and base of tail 69–71; *S. tonkinensis* Nguyen, Schmitz, Tao, Orlov, Böhme & Ziegler 2011 (distribution: northern Vietnam and Hainan Island, China): supralabials seven; midbody scale rows 32–38; longitudinal scale rows between parietals and base of tail 65–76 and lamellae under toe IV 14–19; *S. aesculeticolus* (Inger *et al.* 2001: distribution: northern Borneo; currently assigned to the genus *Tytthoscincus* by Linkem *et al.* 2011): supraciliaries 8–10; forehead and dorsum medium to dark brown, many scales dark spotted that form a series of dark lines or checkered pattern; scales on undersurface of tail, where scales have with small, dark centres; *S. alfredi* (Boulenger 1898) (distribution: central Borneo: supraciliaries eight; preanals not enlarged; midbody scale rows 26 and lamellae under toe IV 12; *S. anomalopus* (Boulenger 1890) (distribution: Peninsular Malaysia, Pulau Nias and Sumatra): nuchal absent; supraciliaries 11–12; supralabials seven; midbody scale rows 39 and lamellae under toe IV 16–17; *S. bacboensis* (Eremchenko 2003, sometimes assigned to the monotypic *Livorimica*; see Eremchenko 2003; Das 2010, but assigned to *Sphenomorphus* by Nguyen *et al.* 2011) (distribution: northern Vietnam): prefrontals in broad contact; supraoculars four; midbody scale rows 29–32 and pad-like lamellae under manus and pes; *S. buenloicus* Darevsky & Nguyen Van Sang 1983 (distribution: southern Vietnam): supraciliaries 11; midbody scale rows 32–34; lamellae under toe IV 16 and venter reddish-brown; *S. bukitensis* Grismer 2007 (distribution: Peninsular Malaysia): prefrontals in contact; midbody scale rows 31–33; paravertebral scale rows 73–74 and lamellae under toe IV 12–13; *S. butleri* (Boulenger 1912) (distribution: Peninsular Malaysia): supraciliaries 9–10; midbody scale rows 33; lamellae under toe IV 11–12 and an uninterrupted dark flank stripe; *S. buettikoferi* (Lidth de Jeude 1905) (distribution: western Borneo): lower eyelid scaly; supraoculars four; supraciliaries nine; supralabials III–V in midorbital position; midbody scale rows 24; lamellae under toe IV 22 and dorsum reddish-brown, with four longitudinal rows of darker spots, two in the paravertebral region, one on each flank; *S. cameronicus* Smith 1924 (distribution: Peninsular Malaysia): supraciliaries 10; supralabials seven; midbody scale rows 38; lamellae under toe IV 20–21; *S. cophias* Boulenger 1908 (distribution: Peninsular Malaysia): supralabials seven; enlarged nuchals absent; midbody scale rows 22–24 and an uninterrupted dark flank stripe; *S. crassus* Inger *et al.* 2001 (new emendation of species epithet: see ‘Nomenclatural Notes’) (distribution: northern Borneo): tympanum deeply sunk, lacking a tympanic annulus; supraoculars four; supraciliaries eight; supralabials seven; lamellae under toe IV 18 and midbody scale rows 32); *S. cyanolaemus* Inger & Hosmer 1965 (distribution: Peninsular Malaysia, Sumatra and Borneo): tail long, exceeding head and body length; nuchals absent; supraoculars six; supraciliaries 12–15; midbody scale rows 37–42; lamellae under toe IV 16–19 and head, throat and pectoral regions blue); *S. florensis* (Weber 1890) (distribution: Java, Lesser Sundas, Timor, Wetar and Damma, Indonesia): auricular opening with 4–7 lobules; no enlarged nuchals; supraoculars 6–7; supralabials seven; midbody scale rows 44–50 and lamellae under toe IV 24–29); *S. grandisonae* Taylor 1962 (distribution: Thailand): midbody scale rows 34; nuchals absent; subcaudals not enlarged and dorsals bear blunt keels); *S. haasi* Inger & Hosmer 1965 (distribution: northern Borneo): supraoculars six; nuchals absent; supraciliaries 13–14; supralabials seven; midbody scale rows 41–42; lamellae under toe IV 16–18; *S. hallieri* (Lidth de Jeude 1905,

currently assigned to the genus *Tytthoscincus* by Linkem *et al.* 2011) (distribution: Borneo): parietals reduced; no enlarged nuchals; supraciliaries 9–10; midbody scale rows 36–39; lamellae under toe IV 10–15; flanks light brown or olive with numerous small yellow or greenish spots and throat of males light blue with dense black spots); *S. incognitus* (Thompson 1912) (distribution: eastern China and north-eastern Vietnam): supraciliaries 9–11; supralabials seven; midbody scale rows 38; paravertebral scale rows 67–80 and lamellae under toe IV 18–24); *S. ishaki* Grismer 2006 (distribution: Pulau Tioman, off Peninsular Malaysia): prefrontals in narrow contact; supraoculars four; midbody scale rows 30–32; lamellae under toe IV 11 and dorsal scales with a pale centre); *S. kinabaluensis* (Bartlett 1895) (distribution: northern Borneo): prefrontals in wide contact with each other; supralabials seven; nuchals absent; midbody scale rows 32–38; lamellae under toe IV 15–17; dorsum brown, with several longitudinal rows of dark brown to yellow spots and speckles); *S. langkawiensis* Grismer 2008 (distribution: Pulau Langkawi, Peninsular Malaysia): midbody scale rows 34–37; lamellae under toe IV 12; subdigital lamellae keeled; supraoculars four and a light dorsolateral and postorbital stripe present); *S. lineopunctulatus* Taylor 1962 (distribution: Thailand, Cambodia and Laos): supraoculars four; parietals in contact; nuchals absent; supraciliaries 9–10; supralabials seven; midbody scale rows 38–40 and a dark, uninterrupted flank stripe present); *S. maculicollus* Bacon 1967 (distribution: Borneo): prefrontals separated by an azygous scale; supraciliaries 15–16; supraoculars eight; nuchals absent; midbody scale rows 36; scales between mental and vent 90; head light brown, speckled with minute dark brown spots); *S. malayanus* (Doria 1888) (distribution: Peninsular Malaysia and Sumatra, Indonesia): supraoculars four; prefrontals in contact; supralabials seven; no enlarged nuchals; midbody scale rows 32–33; lamellae under toe IV 12–13 and uninterrupted dark flank stripe); *S. mimicus* Taylor 1962 (distribution: northern Thailand and northern Vietnam): prefrontals in contact; supralabials seven and midbody scale rows 30; *S. modiglianii* (Boulenger 1894) (distribution: Pulau Sipura, Indonesia): supraoculars four; prefrontals in contact; no enlarged nuchals; midbody scale rows 32 and lamellae under toe IV 15; *S. multisquamatus* Inger 1958 (distribution: northern and western Borneo): prefrontals in broad contact; nuchals absent; supraoculars 6–7; supraciliaries 14–15; midbody scale rows 40–49; lamellae under toe IV 18–23; and dorsum dark greyish-brown, with 2–4 rows of squarish black spots); *S. murudensis* Smith 1925 (distribution: north-western Borneo): prefrontals in contact; supraoculars six; supraciliaries eight; nuchals absent; midbody scale rows 30–32 and toe IV lamellae 16; *S. necopinatus* Brongersma 1942 (distribution: Java, Indonesia): supraoculars four; no enlarged nuchals; midbody scale rows 28–32; lamellae under toe IV 11–15 and dorsal scales with a dark centre, producing eight dark stripes); *S. palawanensis* (Brown & Alcalá 1961; allocated to *Parvosincus* by Linkem *et al.* 2010; 2011) (distribution: Palawan, Philippines): prefrontals absent; midbody scale rows 22–24 and lamellae under toe IV 10–12; *S. perhentianensis* Grismer, Wood & Grismer 2009 (distribution: Pulau Perhentian Besar, off Peninsular Malaysia): midbody scale rows 29; supraoculars four and lamellae under toe IV 10; *S. praesignis* (Boulenger 1900) (distribution: southern Thailand and Peninsular Malaysia): habitus robust; supraoculars four; supralabials seven and lamellae under toe IV 20–26; *S. puncticentralis* Iskandar 1994 (distribution: Java, Indonesia): supralabials seven; infralabials seven; midbody scale rows 29; lamellae under toe IV 25 and dorsum brown with 14 dark spots on paravertebral region; *S. sabanus* Inger 1958 (distribution: northern and apparently also, western Borneo): habitus relatively robust; supraoculars six; supraciliaries 14–17; supralabials seven; midbody scale rows 38–42; lamellae under toe IV 18–22; forehead orange-brown, with dark grey areas in each scale and dorsum of body olive yellow, with pale grey broken paravertebral rows of elongate marks); *S. sanctus* (Duméril & Bibron 1839) (distribution: Sumatra, Java and Maluku, Indonesia): prefrontals in contact; supralabials seven; nuchals absent; midbody scale rows 32–34 and lamellae under toe IV 26–27; *S. scotophilus* (Boulenger 1900) (distribution: southern Thailand and Peninsular Malaysia): prefrontals in contact; nuchals absent; supralabials seven; midbody scale rows 30; lamellae under toe IV 23 and a dorsolateral series of rounded, cream coloured spots present; *S. shelfordi* (Boulenger 1900) (distribution: western Borneo): supraciliaries seven; midbody scale rows 30–34 and lamellae under toe IV 27–29; *S. sibuensis* Grismer 2006 (distribution: Pulau Sibul, off Peninsular Malaysia): supraoculars four; prefrontals in contact; nuchals absent; midbody scale rows 29 and a yellow dorsolateral stripe present; *S. stellatus* (Boulenger 1900) (distribution: Peninsular Malaysia, Cambodia and southern Vietnam, also reported also from western Borneo): supraciliaries eight; nuchals six; midbody scale rows 22–24; median row of dorsal scales widened; lamellae under toe IV 18–23; dorsum greenish- or bronze-brown with small, star-like white areas and throat with 7–8 distinct longitudinal dark bands between scale rows; *S. tanahtinggi* Inger *et al.* 2001 (distribution: northern Borneo): habitus robust; three small superimposed anterior loreal scales; no enlarged nuchals; midbody scale rows 40–42; dorsum olive-brown, darker over tail, without markings or with

widely scattered small dark spots on centres of a few scales and a light line along dorsal margin of dark lateral band; *S. temengorensis* Grismer *et al.* 2009 (distribution: Peninsular Malaysia): supraoculars four; midbody scale rows 30–35; paravertebrals 68–70; lamellae under toe IV 10–11 and an uninterrupted dark dorsolateral stripe, bordered by a cream stripe, along flanks; *S. temminckii* (Duméril & Bibron 1839) (distribution: Sumatra, Java and Bali, Indonesia): supraoculars four; nuchals absent; preanal scales not enlarged; midbody scale rows 30–37 and an uninterrupted dark stripe along flanks present; *S. tenuiculus* (Mocquard 1890) (distribution: northern Borneo): limbs relatively long; parietals in contact with one another; supralabials seven; midbody scale rows 26; lamellae under toe IV 21–24; dorsum brown and spots on dorsum not fusing to form longitudinal lines; *S. tersus* (Smith 1916) (distribution: southern Thailand and Peninsular Malaysia): nuchals absent; supraoculars four; supralabials seven; midbody scale rows 34 and lamellae under toe IV 18–19; *S. tridigitus* (Bourret 1937) (distribution: Vietnam): forelimbs with three digits; midbody scales rows 18–20; lower eyelids scaly and external ear opening absent; *S. tetradactylus* (Darevsky & Orlov 2005) (distribution: central Vietnam): supraoculars four; nuchals in six pairs; forelimbs with four digits; midbody scale rows 18–20 and lamellae under toe IV 10; *S. traanorum* Linkem, Diesmos & Brown 2010 (distribution: Palawan, Philippines): prefrontals in contact; midbody scale rows 29–33; supraoculars four and lamellae under toe IV 16; *S. vanheurni* (Brongersma 1942) (distribution: Java and Bali, Indonesia): supraoculars four; midbody scale rows 31; digits short and thick; lamellae under toe IV 12–15 and dorsum with six longitudinal stripes, composed of dark brown spots; *S. victoria* Brown & Alcalá 1980 (allocated to the genus *Insulasaurus* by Linkem *et al.* 2011) (distribution: Palawan, Philippines): midbody scales 30–31; lamellae under toe IV 18–21; dorsum brown with black bars on vertebral scales and an uninterrupted black stripe on flanks) and *S. wrighti* (Taylor 1925; reallocated to *Insulasaurus* by Linkem *et al.* 2011) (distribution: Palawan, Philippines): midbody scale rows 37–41 and dorsum brown with dark bars on vertebral scales).

In lacking a distinct tympanum, the new species from Meghalaya is morphologically similar to *S. cryptotis* Darevsky *et al.* 2004, a poorly known species from northern Vietnam, and restricted to watercourses (Bain *et al.* 2007; Bauer & Jackman 2008). However, it can be set apart in showing 16–21 lamellae under toe IV; 36–39 midbody scale rows and tail compressed laterally. An auricular depression and lack of a distinct tympanum have also been reported from *S. anotus* from New Guinea (see Greer 2002), which differs from the new species in showing a head that is bluntly conical, short, widely separated limbs and midbody scale rows 26. Loss of the tympanum in lygosomatines has occurred in 33 species, representing dozens of independent derivations in the history of the clade, and may be associated with fossoriality (Greer 1973).

Preliminary molecular phylogenetic results indicated a sister relationship with another lygosomatine skink, *Lipinia*. A majority of the constituent species of this genus is distributed over the Indo-Pacific, and are characterized by a slender habitus, long, tapering tails and a dorsal pattern comprising pale stripes (exceptionally absent, as in *L. relictata* and *L. surda*). There is a history of erroneous allocation of certain *Sphenomorphus* species to this genus (see Shea & Greer 2002). Representatives on the Asian mainland are *L. surda* Boulenger 1900 (distribution: Peninsular Malaysia): supralabial V contacts eye; midbody scale rows 20; lamellae under toe IV 15 and eyelids present and *L. vittigera* (Boulenger 1894) (distribution: Myanmar, Thailand, Cambodia, Vietnam and Peninsular Malaysia, also Singapore, Borneo and the Mentawai Archipelago): lamellae under toe IV 25; dorsum bears light stripes and eyelids present. Three additional species are known from the Sundas, all from Borneo and adjacent islands. *L. inexpectata* Das & Austin 2007 (distribution: Borneo): lower eyelid with spectacle; midbody scale rows 20; lamellae under toe IV 16–17 and dorsum brown with dark grey-brown stripes); *L. miangensis* (Werner 1910) (distribution: Pulau Miang, off the east coast of Borneo): paired, enlarged vertebral scales; supraoculars four; midbody scale rows 24; three pairs of nuchals; lamellae on toe IV 21 and dorsum with two brown stripes) and *L. nitens* (Peters 1871) (western Borneo): paired, enlarged vertebral scales; midbody scale rows 20–22; lamellae under toe IV 16; dorsum metallic green, flanks spotted with black and green and a pale yellow vertebral stripe, with jagged edged black lines, present.

Finally, we compare the new species with South and South-east Asian members of another lygosomatine genus, *Scincella*, with which members of *Sphenomorphus* have occasionally been confused (see Nguyen *et al.* 2011; Linkem *et al.* 2011). Members of this lineage are diagnosed by a moveable lower eyelid and the presence of an opaque “window”, presence of a spectacle being unknown in any described member of the genus. *Scincella apraefrontalis* Nguyen, Nguyen, Böhme & Ziegler 2010 (distribution: north-east Vietnam): a single loreal; prefrontals absent; lower eyelid with an opaque window; external ear openings absent and midbody scales in 18 rows; *S. barbouri* (Stejneger 1925) (distribution: Yunnan and Sichuan, western China): body elongate; supralabial

V in suborbital position; nuchals 4–5; longitudinal scales between parietal and base of tail 70–79; midbody scale rows 24–28 and lamellae under toe IV 15–17; *S. capitanea* Ouboter 1986 (distribution: central Nepal): midbody scale rows 30–32; auricular opening slit-like; tympanum deeply sunk; lamellae under toe IV 15–17 and broad greyish dorsolateral stripes; *S. darevskii* Nguyen, Ananjeva, Orlov, Rybaltovsky & Böhme 2010 (distribution: Vietnam): external ear opening with lobules; supraciliaries seven; supralabials seven; midbody scale rows 28 and an uninterrupted dark flank stripe; *S. devorator* (Darevsky, Orlov & Cuc 2004) (distribution: north-eastern Vietnam): supralabials seven; supraciliaries eight; midbody scale rows 30; toe IV lamellae 17 or 19 and uninterrupted flank stripe; *Scincella doriae* (Boulenger 1887) (distribution: northern Myanmar): nuchals enlarged, in 4–5 pairs; longitudinal scale rows 66–76; midbody scale rows 30–32 and lamellae under toe IV 15–18; *Scincella kohtaensis* (Cochran 1927) (distribution: Surat Thani Province, Thailand): supralabials V and VI in subocular position; midbody scale rows 29–31 and lamellae under toe IV 14–17; *S. macrotis* (Steindachner 1867) (distribution: Nicobar archipelago, India): lower eyelid with transparent window; midbody scale rows 31 and an uninterrupted dark flank stripe; *S. melanosticta* (Boulenger 1887) (distribution: Myanmar, Thailand and Vietnam): supralabials V and VI in subocular position; midbody scale rows 32–38 and lamellae under toe IV 16–20; *S. monticola* (Schmidt 1925) (distribution: southern China and northern Vietnam): four pairs of nuchals; lamellae under toe IV 11; midbody scale rows 22–26 and an uninterrupted dark flank stripe; *S. ochracea* (Bourret 1937) (distribution: Vietnam): lower eyelid with clear window; 2–4 auricular lobules present; supralabials seven; lamellae under toe IV 15–20 and midbody scale rows 30–32; *S. punctatolineata* (Boulenger 1893) (distribution: south-eastern Myanmar and western Thailand): body elongate with short limbs; supraciliaries 6–7; midbody scale rows 22–28 and lamellae under toe IV 13–15; *S. rara* (Darevsky & Orlov 1997; originally described as a species of the monotypic genus, *Paralipinia*) (distribution: southern Vietnam): double rows of subdigital pads; lower eyelid with clear window; paired median vertebrae enlarged; midbody scale rows 24 and uninterrupted dark flank stripe; *Scincella reevesii* (Gray 1838) (distribution: Nepal, Bangladesh, China, Myanmar, Thailand, Vietnam and Cambodia, possibly also Korea and Peninsular Malaysia): prefrontals large, typically forming a broad suture; supralabials V and VI in suborbital position; midbody scale rows 29–33 and lamellae under toe IV 14–21; *S. rufocaudatus* (Darevsky & Nguyen Van Sang 1983; assigned by some authors to the genus *Sphenomorphus*, but here retained in *Scincella* following Nguyen et al. 2010) (distribution: southern Vietnam, Cambodia and Laos): supralabials seven; midbody scale rows 31–34; tail base and subcaudals red and uninterrupted dark flank stripe; *S. rupicola* (Smith 1916) (distribution: Thailand, Laos and southern Vietnam): lower eyelid with clear window; midbody scale rows 32–34; lamellae under toe IV 17–18 and uninterrupted dark flank stripe; and *S. victoriana* (Shreve 1940) (distribution: Pakokku-Chin Hills, Myanmar): dorsals keeled; three pairs of nuchals; supralabials seven; tympanum deeply sunk; midbody scale rows 26 and lamellae under toe IV 15–16.

Phylogenetic position. Preliminary molecular analyses unambiguously place the new species within the ‘*Sphenomorphus* group’ (Lygosomidae, or more correctly, Lygosomatidae, of Hedges & Conn 2012, and these results are supported by morphological data). To determine its position within the ‘*Sphenomorphus* group’, additional analyses were undertaken. In the preliminary phylogeny of the ‘*Sphenomorphus* group’ based on mitochondrial 12S and 16S genes, *Sphenomorphus apalpebratus* was sister to *Lipinia vittigera*. This relationship received high Bayesian posterior probability support (> 0.9), but low ML bootstrap support. However, since the *Lipinia vittigera* specimen (collected from Thailand) whose sequences were available in Genbank (see Honda *et al.* 2003 for original source) was not available for verification (A. Mori, pers. comm.), and as a revision or phylogenetic study of *Lipinia* is beyond the scope of the current study, we excluded it from the final analysis. Furthermore, in this tree, neither *Lipinia* nor *Sphenomorphus* were retrieved as monophyletic. The ML tree (Fig. 5) and the Bayesian inference tree show identical topologies wherein *Sphenomorphus apalpebratus* was sister to a clade consisting of *S. maculatus* + *S. indicus* + *S. simus*. Although allocation of the new species to the ‘*Sphenomorphus* group’ is supported by both morphological and molecular data, its generic assignment is equivocal. Given both our poor sampling of the group as a whole and the unsettled taxonomic status of many constituent taxa, we regard our generic allocation of the new species to *Sphenomorphus* to be most appropriate. It is hoped that future research will result in the dismantling of this paraphyletic group of skinks and provide a more clear basis for establishing the affinities of *S. apalpebratus*.

Ecological notes. The type series was collected from under dead and decaying wood and under leaf litter within a sacred forest (Fig. 6). The vegetation of Mawphlang has been described as subtropical wet hill forest (Champion & Seth 1968), and the tree flora is dominated by alpine elements, including *Quercus dealbata*, *Schima*

khasiana, *Manglietia insignis*, *Corylopsis himalayana*, *Phyllanthus glaucus*, *Manglietia caveana* and *Myrica esculenta*, growing on nitrogen-rich lateritic soil (Khan *et al.* 1987). Although not within India's protected areas system, Mawphlang is protected as a sacred grove by the local Khasi communities, and logging or even encroachment, without permit from the local stakeholders, especially headmen, is forbidden. Three amphibian species are endemic to this forest patch- *Odorrana mawphlangensis* (Pillai & Chanda 1977), *Leptolalax khasiorum* Das, Tron, Rangad & Hooroo 2009 and *Fejervarya sengupti* Purkayastha & Matsui 2012. The inventory of the reptiles of Mawphlang remains incomplete, although the scincid, *Sphenomorphus indicus* has been recorded from this locality by Mathew (1995).

The present study underscores the importance of both the role indigenous human communities play in biodiversity conservation, and the potential for remarkable discoveries in India's remote north-east.

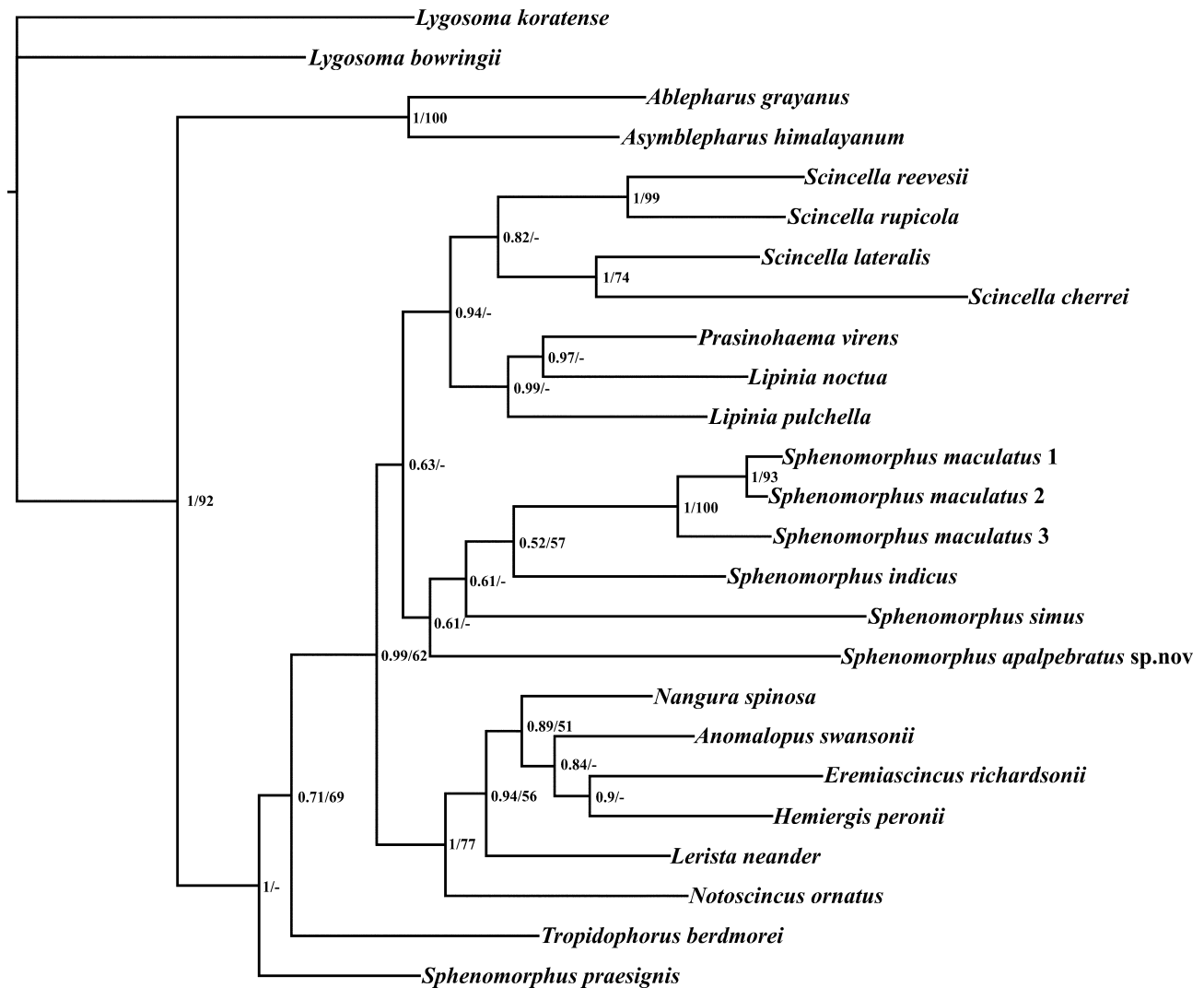


FIGURE 5. Maximum Likelihood Tree, based on the 12S and 16S mt DNA dataset of the 'Sphenomorphus group'. Node support values represent Bayesian posterior probability and ML bootstrap values (BI-pp/ ML-bs). Support values below 50 percent are denoted as '-'.
 NEW INDIAN SPHENOMORPHUS

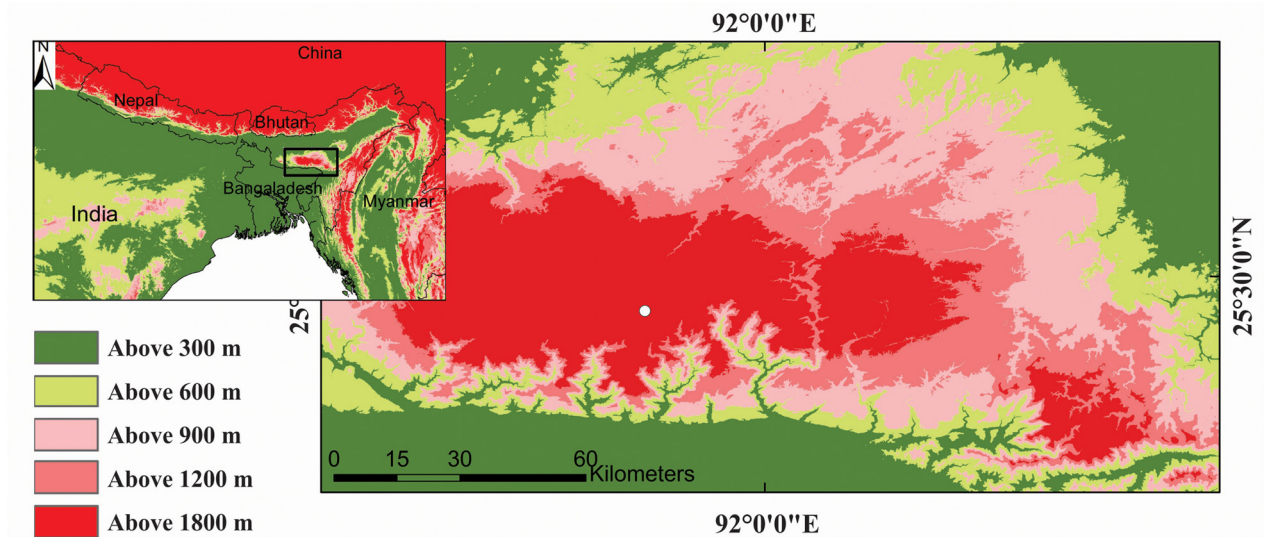


FIGURE 6. Top. Location of the type locality of *Sphenomorphus apalpebratus* **sp. nov.** at Mawphlang, Meghalaya State, north-eastern India and Bottom. Habitat of *Sphenomorphus apalpebratus* **sp. nov.** at Mawphlang, Meghalaya State, north-eastern India.

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APPENDIX 1. DNA sequence data from the mitochondrial 12S and 16S genes. '—' refers to voucher material from previously published studies.

Taxon	12S	16S	Voucher number
<i>Ablepharus grayanus</i>	KF514642	KF514647	CES 09/ 858
<i>Anomalopus swansonii</i>	AY169576	AY169613	—
<i>Asymblepharus himalayanus</i>	KF514643	KF514648	CES 09/ 868
<i>Eremiascincus richardsonii</i>	AY169582	AY169619	—
<i>Hemiergis peronii</i>	AY169590	AY169627	—
<i>Lerista neander</i>	EF672796	EF672867	—
<i>Lipinia noctua</i>	JF497868	JF497992	—
<i>Lipinia pulchella</i>	JF497869	JF497993	—
<i>Lygosoma bowringi</i>	AY308415	AY308263	—
<i>Lygosoma koratense</i>	AB028805	AB028817	—
<i>Nangura spinosa</i>	AY169593	AY169630	—
<i>Notoscincus ornatus</i>	AY169594	AY169631	—
<i>Prasinohaema virens</i>	AY169596	AY169633	—
<i>Scincella cherrei</i>	AB057377	AB057392	—
<i>Scincella lateralis</i>	AY169598	AB057402	—
<i>Scincella reevesii</i>	AY308449	AY308300	—
<i>Scincella rupicola</i>	AB057388	AB057403	—
<i>Sphenomorphus apalpebratus</i>	KF514646	KF514651	CES 10/ 831
<i>Sphenomorphus indicus</i>	AB028808	AB028820	—
<i>Sphenomorphus maculatus</i> 1	KF514644	KF514649	CES 10/ 828
<i>Sphenomorphus maculatus</i> 2	KF514645	KF514650	CES 09/ 895
<i>Sphenomorphus maculatus</i> 3	AB028809	AB028821	—
<i>Sphenomorphus praesignis</i>	AB028810	AB028822	—
<i>Sphenomorphus simus</i>	AY218017	AY217967	—
<i>Tropidophorus berdmorei</i>	AB028811	AB028823	—

APPENDIX 2. Comparative material examined.

- Lipinia inexpectata* Das & Austin 2007. ZRC 2.5728, ZRC 2.5729–5730 (holotype and paratypes). Pulau Manukan, Sabah, Malaysia; FMNH 138538 (paratype), Nanga Tekalit Camp, Sungei Mengiong, Kapit, Sarawak, Malaysia; UMS 04399–04400. Danum Valley Field Centre, Lahad Datu, Sabah, Malaysia.
- Lipinia macrotympanum* (Stoliczka 1873). ZSI 5571 (holotype). "South Andaman..on a sandy beach in Macpherson's Straits" (in the Bay of Bengal, India); MCZ R-176760. Pulo Ulan, Little Nicobar, India.
- Lipinia nitens* (Peters 1872). ZRC 2.4861. Gunung Pueh, Sarawak, Malaysia; ZRC 2.5746. base of Gunung Matang, Sarawak, Malaysia.
- Lipinia quadrivittata* (Peters 1867). ZRC 2.5606. Pulau Sipadan, Sabah, Malaysia; ZRC 2.4652. Salopa Waterfall, north-west of Poso, Sulawesi, Indonesia.
- Lipinia vittigera* (Boulenger 1894). ZRC 2.5474–5478. Bau Sau, Nam Cat Tien, Dong Nai Province, Vietnam; ZRC 2.1637. Jor, Batang Padang, Perak, Malaysia; ZRC 2.4622. The Gap, Selangor, Malaysia; ZRC 2.5151. Salang, Pulau Tioman, Pahang, Malaysia; ZRC 2.4677. Kota Samarahan, Sarawak, Malaysia; SBC R.1. Bukit Meraja, Bau, Kuching, Sarawak, Malaysia; SM uncatalogued (2 specimens). Pulau Talang Talang Besar, Sarawak, Malaysia; BMNH 97.3.4.2. Baram District, Sarawak, Malaysia; BM 74.2006. Tasek Merimbun Heritage Park, Tutong, Brunei Darussalam; SP 06775. Tawau Hills Park, Tawau District; ZRC 2.4575. Nee Soon Swamp, Singapore.
- Scincella kohtaoensis* (Cochran 1927). ZRC 2.5479. Nam Cat Tien, Bau Sau, Dong Nai Province, Vietnam.
- Scincella modesta* (Günther 1864). BMNH 1946.8.16.75–76 (*ex* BMNH 54.2.10.5–6; two syntypes). "Ningpo" (= Ningbo Shi, Zhejiang Province, China); ZSI 4270 (holotype of *Mococa exigua* Anderson 1879). 'Momien' (= Tengchong County, Yunnan Province, southern China).
- Scincella sikimensis* (Blyth 1853). ZSI 2501–05 (syntypes of *Mococa sikimensis* Blyth, 1853). 'Sikim' (= Sikkim, eastern India). ZSI 2391 (holotype of *Mococa sacra* Stoliczka 1871). 'Parisnáth; W. Bengal' (in eastern India).
- Scincella reevesii* (Gray "1838" 1839). BMNH 1946.8.16.37–38 (two syntypes). "China".
- Sphenomorphus aesculeticolus* Inger, Tan, Lakim & Yambun 2002. SP 06426–27, 06429, 06431–41. Gunung Kinabalu National Park, Ranau, Sabah, Malaysia.
- Sphenomorphus butleri* (Boulenger 1912). ZRC 2.5944. Telom Valley, Kuala Terla, Pahang, Malaysia; ZRC 2.4619, Danau Gunung Tujuh, Kerinci, Sumatra, Indonesia.

- Sphenomorphus courcyanus* (Annandale 1912). ZSI 16899 (syntype of *Lygosoma courcyanum* Annandale 1912). 'Upper Rotung (ca. 2,000 ft.)' (Arunachal Pradesh, north-eastern India); ZSI 16900 (syntype), 'Rotung (91,300 ft.)' (Arunachal Pradesh, north-eastern India).
- Sphenomorphus cryptotis* Darevsky, Orlov & Cuc 2004. ZISP 29905, ex ROM 27682 (paratype). "Khe Cam river near Chan Nga village, Quy Chan district, Nghe An province, Vietnam".
- Sphenomorphus cyanolaemus* Inger & Hosmer 1965. ZRC 2.5314–5316, ZRC 2.5767. Niah National Park, Sarawak, Malaysia; ZRC 2.5347–5348. Lambir Hills National Park, Sarawak, Malaysia; ZRC 2.1625–1629). Baram District, Sarawak, Malaysia; UBD 195, 204, 278, 538. Batu Apoi, Temburong, Brunei Darussalam; BM 1992.84; 1992.88–89. Sungei Ingei, Belait District, Brunei Darussalam; BM 1992.172–73; 1992.227. Sungei Sibut, Batang Duri, Temburong, Brunei Darussalam; BM 1992.183, 1992.225. Sungei Pendaruan, Temburong, Brunei Darussalam.
- Sphenomorphus haasi* Inger & Hosmer 1965. ZRC 2.5307. Gunung Gading National Park, Sarawak, Malaysia.
- Sphenomorphus hallieri* (Lidth de Jeude 1905). ZRC 2.5363. No data; BM 1992.105. Sungei Ingei, Belait, Brunei Darussalam; BM 1993.144. Sungei Sibut, Batang Duri, Temburong, Brunei Darussalam.
- Sphenomorphus indicus* (Gray 1853). BMNH 1946.8.15.49 and BMNH 1946.8.19.27 (syntypes). "Sikkim Himalaya" (= Sikkim State, eastern India); ZSI 12076 (holotype of *Lygosoma cacharensis* Annandale 1905). 'Nemotha, Cachar' (in Assam State, north-eastern India); ZRC 2.4813. Lam Tseun, New Territories, Hong Kong, China; ZRC 2.4796, Taitung, Lalipaxi, Taitung, Taiwan; ZRC 2.5366. Chon Buri Province, Khao Khieo Waterfall, Chon Buri Province, Thailand.
- Sphenomorphus kinabaluensis* (Bartlett 1895). BMNH 1946.8.15.8 (holotype). "Kina Balu, N. Borneo"; SP 06011. Gunung Kinabalu Park Headquarters, Sabah, Malaysia; UMS 01006. Lambah Danum, Lahad Datu, Sabah, Malaysia; ZRC 2.1581–1582. Gunung Kinabalu, Sabah, Malaysia; ZRC 2.1583. Lumu Lumu, Gunung Kinabalu, Sabah, Malaysia;
- Sphenomorphus maculatus maculatus* (Blyth 1853). ZRC 2.4691–4692. Saddle Peak, North Andaman Island, India; ZRC 2.1585. Dawei, Myanmar; ZRC 2.1586. Paiyu, Thailand; ZRC 2.4903, Khao Phanom Bencha National Park, Krabi, Thailand.
- Sphenomorphus maculatus mitanense* (Annandale 1905). ZSI 5399 (holotype). 'Meetan, Lower Burma' (= Mitan Chaung, southern Myanmar).
- Sphenomorphus maculicollis* Bacon 1967. FMNH 161484 (holotype). "near Sungei Pesu, Bintulu District, Sarawak, Malaysia"; ZRC 2.1623, Kinokok, Sabah, Malaysia.
- Sphenomorphus multisquamatus* Inger 1958. ZRC 2.5350–5351. Lambir Hills National Park, Sarawak, Malaysia; SM c.c.6.2.2.2 six specimens). Gunung Pueh, Sarawak, Malaysia; BMNH 93.3.6.42–43 (two paratypes). Sungei Sarawak, Kuching, Sarawak, Malaysia; UNIMAS 7966. Pelagus Rapids, Kapit District, Sarawak, Malaysia; BMNH 1904.7.19.50–51 (two paratypes). "Balingean", possibly Gunung Balingan, Sibul Division, Sarawak, Malaysia.
- Sphenomorphus murudensis* Smith 1925. ZRC 2.5308. Lepo Bunga at base of Gunung Murud, Sarawak, Malaysia.
- Sphenomorphus praesignis* (Boulenger 1900). ZRC 2.1841. Tanah Rata, Cameron Highlands, Pahang, Malaysia.
- Sphenomorphus sabanus* Inger 1958. ZRC 2.1620–1622. Betotan, Sabah; ZRC 2.1616–1619, ZRC 2.1624, ZRC 2.1630. Gunung Kinabalu, Sabah, Malaysia; BMNH 1957.1.9.13. East Coast Residency, Sandakan Forest Reserve, Sabah, Malaysia; UNIMAS 8752. Poring Hot Spring, Ranau, Sabah, Malaysia; UMS Re. 291; 295–96; 305. Marak Parak, Kota Marudu, Sabah, Malaysia; UMS Re. 191 and 225. Lembah Danum, Lahad Datu, Sabah, Malaysia.
- Sphenomorphus scotophilus* (Boulenger 1900). ZRC 2.4859–4860. Moon Gate at foot of Bukit Bendera, Pulau Pinang, Malaysia; ZRC 2.5928. Pulau Jarak, Perak, Malaysia; ZRC 2.3494. Pulau Tioman, Pahang, Malaysia.
- Sphenomorphus stellatus* (Boulenger 1900). ZRC 2.4620. Gunung Belumut, Johor, Malaysia.
- Sphenomorphus temminckii* (Duméril & Bibron 1839). ZRC 2.1612. Garit, Java, Indonesia.
- Sphenomorphus tersus* Smith 1916. ZRC 2.4915. Forest Research Institute Malaysia, Kepong, Selangor, Malaysia.