*Zoological Journal of the Linnean Society*, 2019, **186**, 1067–1096. With 5 figures.

# Multilocus phylogeny and a new classification for African, Asian and Indian supple and writhing skinks (Scincidae: Lygosominae)

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*Received 10 May 2018; revised 6 December 2018; accepted for publication 24 December 2018*

The genera *Lepidothyris*, *Lygosoma* and *Mochlus* comprise the writhing or supple skinks, a group of semi-fossorial, elongate-bodied skinks distributed across the Old World Tropics. Due to their generalized morphology and lack of diagnostic characters, species- and clade-level relationships have long been debated. Recent molecular phylogenetic studies of the group have provided some clarification of species-level relationships, but a number of issues regarding higher level relationships among genera still remain. Here we present a phylogenetic estimate of relationships among species in *Lygosoma*, *Mochlus* and *Lepidothyris* generated by concatenated and species tree analyses of multilocus data using the most extensive taxonomic sampling of the group to date. We also use multivariate statistics to examine species and clade distributions in morpho space. Our results reject the monophyly of *Lygosoma s.l.*, *Lygosoma s.s.* and *Mochlus*, which highlights the instability of the current taxonomic classification of the group. We, therefore, revise the taxonomy of the writhing skinks to better reflect the evolutionary history of *Lygosoma s.l.* by restricting *Lygosoma* for Southeast Asia, resurrecting the genus *Riopa* for a clade of Indian and Southeast Asian species, expanding the genus *Mochlus* to include all African species of writhing skinks and describing a new genus in Southeast Asia.

ADDITIONAL KEYWORDS: Africa – India – *Lamprolepis* – *Lepidothyris* – *Lygosoma* – *Mochlus* – *Riopa* – Southeast Asia – taxonomy.

## INTRODUCTION

The lizard family Scincidae is the most species-rich family of squamate reptiles. Skinks are ecologically and morphologically diverse, with more than 1600 taxa currently recognized (Uetz *et al.*, 2019) as occurring in tropical and temperate zones on all continents excluding Antarctica, as well as on many oceanic islands (Greer, 1970a; Vitt & Caldwell, 2013). Despite this high diversity, inter- and intrageneric phylogenetic relationships across many clades in the family remain poorly resolved (Pyron *et al.*, 2013; Skinner *et al.*, 2013; Barley *et al.*, 2015a; Lambert *et al.*, 2015; Zheng & Wiens, 2016), However, with the continued growth in available genetic data and increased taxonomic sampling in molecular systematic studies of various clades, research over the last decade has contributed greatly to an improved understanding of the diversity of scincid lizards (e.g. Linkem *et al.*, 2011; Siler *et al.*, 2011; Brandley *et al.*, 2012; Datta-Roy *et al.*, 2012; Sindaco *et al.*, 2012; Skinner *et al.*, 2013; Datta-Roy *et al.*, 2014; Barley *et al.*, 2015a; Pinto-Sánchez *et al.*, 2015; Karin *et al.*, 2016; Klein *et al.*, 2016; Erens *et al.*, 2017). Additionally, this nascent body of work has resulted in

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[Version of record, published online on 5 April 2019; http://zoobank.org urn:lsid:zoobank.org:pub:8AA92D8A-A294-4B62-9A75-5CA4534CFCBC]

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a dramatic increase in the discovery of morphologically cryptic lineages (e.g. Daniels *et al.*, 2009; Linkem *et al.*, 2010; Chapple *et al.*, 2011; Heideman *et al.*, 2011; Siler *et al.*, 2011, 2012, 2014, 2016, 2018; Kay & Keogh, 2012; Barley *et al.*, 2013; Davis *et al.*, 2014, 2016; Geheber *et al.*, 2016; Heitz *et al.*, 2016; Medina *et al.*, 2016; Busschau *et al*, 2017; Conradie *et al.*, 2018; Karin *et al.*, 2018; Pietersen *et al.*, 2018). In spite of all these efforts, there remain many lingering taxonomic and phylogenetic challenges in the family, possibly none more so than in the large and diverse subfamily Lygosominae.

One of three subfamilies recognized widely in the lizard family Scincidae (Greer, 1970a; Pyron *et al.*, 2013; Skinner *et al.*, 2013; Lambert *et al.*, 2015; Karin *et al.*, 2016; Linkem *et al.*, 2016; Zheng & Wiens, 2016; but see an alternative, less widely accepted classification in: Hedges & Conn, 2012; Hedges, 2014; Uetz *et al.*, 2018), the Lygosominae contains approximately 1354 species (estimated from: Uetz *et al.*, 2019) and represents, currently, the most species-rich radiation of scincid lizards, with a broad, global distribution (Greer, 1970a; Honda *et al.*, 2000; Skinner *et al.*, 2011). The radiation likely began diversifying 100.6–63.6 Mya, during the Late Cretaceous to Early Palaeocene (Skinner *et al.*, 2011). Extant lygosomine genera exhibit a rich biogeographical history, with evidence for historical transoceanic dispersal in some lineages (Carranza & Arnold, 2003; Honda *et al.*, 2003; Rocha *et al.*, 2006; Linkem *et al.*, 2013; Skinner *et al.*, 2013; Karin *et al.*, 2016). Many genera have been the subject of recent phylogenetic studies, including *Afroablepharus* and *Panaspis* (Medina *et al.*, 2016), *Eutropis* (Datta-Roy *et al.*, 2012; Barley *et al.*, 2013, 2015a), *Lygosoma* (Datta-Roy *et al.*, 2014), *Mabuya* (Hedges & Conn, 2012; Pinto-Sánchez *et al.*, 2015), *Sphenomorphus* (Linkem *et al.*, 2011), *Trachylepis* (Sindaco *et al.*, 2012) and *Tytthoscincus* (Grismer *et al.*, 2018a). Although these studies have increased the understanding of diversity and relationships among these focal clades, they also have highlighted a number of phylogenetic and taxonomic issues that remain unresolved. As taxonomy reflects our knowledge of organisms in the tree of life (Vences *et al.*, 2013), resolving these conflicts is important for investigating a myriad of higher level questions, including studies of ecology, diversification, morphological evolution and conservation of imperilled species.

One prime example of unresolved taxonomic issues among lygosomine skinks is the genus *Lygosoma*, which has a long and controversial history of uncertainty regarding species- and generic-level relationships. *Lygosoma* Hardwicke & Gray 1827, the type genus of the subfamily Lygosominae, comprises 31 recognized species distributed across Africa, India, Southeast Asia, the western and southern Philippines and Christmas Island (Australia) (Geissler *et al.*, 2011; Cogger, 2014; Datta-Roy *et al.*, 2014; Heitz *et al.*, 2016; Grismer *et al.*, 2018b; Siler *et al.*, 2018; Uetz *et al.*, 2019). Genera closely allied to *Lygosoma* are *Mochlus*, consisting of 15 species found in semi-arid regions across central and subtropical southern Africa, and *Lepidothyris*, consisting of three species found in forested regions of Central Africa (Greer, 1977; Wagner *et al.*, 2009; Uetz *et al.*, 2019). Historically, the taxonomic status of these three genera has been debated extensively, with species in *Mochlus* and *Lepidothyris* often included in *Lygosoma* (e.g. Boulenger, 1887; Greer, 1977; see taxonomic history of the group below), and recent phylogenetic analyses suggest that *Lygosoma* is paraphyletic with respect to both genera (Pyron *et al.*, 2013; Datta-Roy *et al.*, 2014). Therefore, from here on out, we refer to the 49 species represented by these three genera collectively as *Lygosoma s.l.*, whereas, we refer to the 31 species in the genus *Lygosoma* (as currently recognized) as *Lygosoma s.s.*

Although Greer (1977) found all members of *Lygosoma s.l.* to be united by osteological characteristics of the secondary palate, morphology has offered few clues to the phylogenetic relationships of species and clades in the group, which has resulted in considerable taxonomic confusion regarding the status of species and genera (e.g. Broadley, 1966; Greer, 1977). Known as supple or writhing skinks, species have been allocated to *Lygosoma s.l.* generally on the basis of their semi-fossorial ecology, head scale patterns well-developed eyelids, elongate bodies and short fore- and hind limbs that do not meet when appressed (Smith, 1935; Mittleman, 1952; Greer, 1977; Geissler *et al.*, 2011; Geissler, Hartmann & Neang, 2012). All species are pentadactyl with the exception of *Lygosoma lineatum* Gray, 1839, which has tetradactyl fore-limbs (Greer, 1977). Colour and pigmentation patterns vary within and between species (Wagner *et al.*, 2009). However, beyond these generalizations, species exhibit diverse body forms that range from moderately large (e.g. *Lygosoma kinabatanganense* Grismer, Quah, Duzulkafly & Yambun, 2018: snout–vent length [SVL] = 141 mm; *L. haroldyoungi* (Taylor, 1962): SVL = 148 mm; *Mochlus sundevallii* (Smith, 1894): SVL = 140 mm) to small (e.g. *L. frontoparietale* (Taylor, 1962): SVL = 41 mm; *L. veunsaiense* Geissler, Hartmann & Neang, 2012: SVL = 34 mm) and more robust with short limbs (e.g. *M. brevicaudis* Greer, Grandison & Barbault, 1985), to elongate and more gracile with small, slender limbs and shorter digits (e.g. *L. quadrupes* (Linnaeus, 1766)) (Broadley, 1966; Greer, 1977; Geissler *et al.*, 2011). As a result of this considerable diversity in body form, researchers have struggled to define morphological boundaries between groups (Boulenger, 1887; Smith, 1937a; Greer, 1977).

More recently, molecular phylogenetic techniques have been employed to examine species-level relationships in *Lygosoma s.l.*, resulting in increased taxonomic resolution (Ziegler *et al.*, 2007; Wagner *et al.*, 2009; Pyron *et al.*, 2013; Datta-Roy *et al.*, 2014). Nevertheless,

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not only have the results of these studies revealed significant genetic lineage diversity, but also they have failed to support the monophyly of several taxonomic groups, including *Lygosoma s.s.* with respect to *Mochlus* and *Lepidothyris* and *Lygosoma s.l.* with respect to the species *Lamprolepis smaragdina* (Lesson, 1830) (Honda *et al.*, 2000, 2003; Pyron *et al.*, 2013; Datta-Roy *et al.*, 2014). Unfortunately, to date, the paucity of available genetic samples for many species has limited the degree to which studies have been able to resolve the intra- and intergeneric relationships in *Lygosoma s.l.* Additionally, several new species have been described recently based on genetic and/or morphological data (*Lygosoma boehmei* Ziegler, Schmitz, Heidrich, Vu & Nguyen, 2007, *L. kinabatanganense, L. peninsulare* Grismer, Quah, Duzulkafly & Yambun, 2018, *L. samajaya* Karin, Freitas, Shonleben, Grismer, Bauer & Das, 2018, *L. siamense* Siler, Heitz, Davis, Freitas, Aowphol, Termprayoon & Grismer, *L. tabonorum* Heitz, Diesmos, Freitas, Ellsworth, Grismer, Aowphol, Brown & Siler, *L. veunsaiense* and *Lepidothyris hinkeli* Wagner, Böhme, Pauwels & Schmitz, 2009), but how these species relate to others in *Lygosoma s.l.* remains unresolved. In this manuscript, we employ phylogenetic approaches and analyses of external morphology to investigate species- and generic-level relationships and taxonomic conflicts in *Lygosoma s.l.*

## TAXONOMIC HISTORY OF *LYGOSOMA S.L.*

### *Early classifications based on morphology*

The taxonomy of *Lygosoma s.l.* has a long and complex history. In *Lygosoma s.l.*, the traditional phenotypic characters used in skink classifications are non-diagnostic and have overlapping numerical values, making it difficult to classify groups. Historically, taxonomic hypotheses for skinks employed a variety of morphological characters in genus-level classifications, such as the degree of body elongation, limb size and digit number, size of the ear opening, lower eyelid characteristics (i.e. scaly vs. with a transparent disc), head scalation patterns and pigmentation patterns (e.g. Duméril & Bibron, 1839; Gray, 1839). However, many of these characters have been shown to be convergent among skinks, calling into question the breadth of their diagnostic utility, especially in *Lygosoma s.l.*, in which species exhibit varying body sizes and degrees of elongation (Smith, 1937a; Greer, 1977). Further complicating clear morphological definitions for members of this radiation is the anomalous morphology of the type species of *Lygosoma*, *L. quadrupes*, which has a thin, snake-like body, tiny limbs, short digits and an atypical head scale pattern (single frontoparietal scale, nasals fused with supranasals; Greer, 1977). Whereas other species in the radiation also possess some of these characters (e.g. *L. lineatum* and *L. vosmaerii* (Gray, 1839) have bodies nearly as elongate as *L. quadrupes*; *L. isodactylum* (Günther, 1864b) has nasals fused anteriorly with supranasals [Greer, 1977; Geissler *et al.*, 2011, 2012]), the combination of morphological traits in *L. quadrupes* is different from other species in *Lygosoma s.l.* (although the recently described species *L. siamense* and *L. tabonorum*, both part of the *L. quadrupes* species complex, also have these morphological characters; Heitz *et al.*, 2016; Siler *et al.*, 2018). Therefore, historically it has been difficult to classify *L. quadrupes* in a broader taxonomic context, as evidenced by multiple taxonomists classifying the species not with other members of *Lygosoma s.l.*, but with superficially similar elongate-bodied species (e.g. Boulenger, 1887; Smith, 1935, 1937a; Mittleman, 1952) that have been shown subsequently not to be closely related. As a result, during the previous 150 years, species in *Lygosoma s.l.* have alternated between being placed in the same genus or being separated into multiple genera (e.g. Boulenger, 1887; Smith, 1935, 1937a; Mittleman, 1952; Broadley, 1966; Greer, 1977; Wagner *et al.*, 2009), leading to taxonomic instability in the group.

Currently, three genera are recognized in *Lygosoma s.l.*: *Lygosoma s.s.*, *Lepidothyris* and *Mochlus* (Datta-Roy *et al.*, 2014). However, a decade ago, a fourth genus, *Riopa*, also was considered valid (Wagner *et al.*, 2009). Of these four genera, the genus *Lygosoma* has undergone the most revisionary changes through the years, with species and species-group compositions (i.e. sections and subgenera) a subject of continued confusion and debate (e.g. Smith, 1935, 1937a; Mittleman, 1952; Glauert, 1960; Laurent & Gans, 1965). The genus *Lygosoma* Hardwicke & Gray was first described in 1827 for the species *Lacerta serpens* Bloch, 1776. In their description, the authors noted that *Lacerta serpens* is a distinct species from *Anguis quadrupes* Linnaeus, 1766, failing to realize that Bloch's description of *Lacerta serpens* was a redescription of Linnaeus' *Anguis quadrupes*. Bloch (1776) redescribed *Anguis quadrupes* because Linnaeus' original description of the species had classified it as a four-legged snake (reviewed in Bauer & Günther, 2006). Hardwicke & Gray's (1827) oversight, which may have resulted from the assignment of additional specimens to *Lacerta serpens* that were not truly *quadrupes* specimens (G. Shea, pers. comm.), was not resolved until Smith (1935) synonymized *Lacerta serpens* with *Anguis quadrupes*, thus making *Lygosoma quadrupes* the type species of *Lygosoma*. Over the next two centuries, in addition to *Lygosoma*, species currently in *Lygosoma s.l.* have been described as members of 12 disparate genera: *Campsodactylus* Duméril & Bibron, 1839; *Chiamela* Gray, 1839; *Eumeces* Wiegmann, 1834; *Hagria* Gray, 1839; *Lepidothyris* Cope, 1892



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(*nomen nudum* until Cope, 1900); *Mochlus* Günther, 1864a; *Podophis* Wiegmann, 1834; *Riopa* Gray, 1839; *Sphenosoma* Fitzinger, 1843; *Sepacontias* Günther, 1880; *Squamicilia* Mittleman, 1952; and *Tiliqua* Gray, 1825. These genera were revised and reorganized in major works throughout the 19th century (Schneider, 1801; Daudin, 1802; Fitzinger, 1826, 1843; Wiegmann, 1834; Cocteau, 1836; Duméril & Bibron, 1839; Gray, 1839, 1845; Günther, 1864b; Theobald, 1876), culminating in Boulenger's (1887) monograph cataloguing the lizards in the British Museum. Faced with the difficulty of classifying 2340 specimens of scincid lizards representing 369 recognized species, and having remarked on the difficulty of classifying skink genera, Boulenger (1887) synonymized most of these genera with *Lygosoma*, which resulted in the genus comprising 159 species (43% of all skink species recognized at the time). Additionally, Boulenger (1887) subdivided *Lygosoma* into 11 sections (*Emoa* [sic] Gray, 1845, *Hemiergis* Wagler, 1830, *Hinulia* Gray, 1845, *Homolepida* [sic] Gray, 1845, *Keneuxia* Gray, 1845, *Liolepisma* [sic] Duméril & Bibron, 1839, *Lygosoma*, *Otosaurus* Gray, 1845, *Rhodona* Gray, 1839, *Riopa* and *Siaphos* [sic] Gray, 1831) based on limb proportions and head scalation characters. For half a century his revision was the only large-scale treatment of skink taxonomy.

By the early 1900s, there was growing concern about taxonomic confusion resulting from piecemeal adoption of a subset of Boulenger's (1887) *Lygosoma* sections as genera. For example, his section *Emoa* [sic] was recognized as the genus *Emoia* by Barbour (1912), his section *Otosaurus* as the genus *Otosaurus* by Taylor (1923), his section *Rhodona* as the genus *Rhodona* by Loveridge (1933) and his section *Liolepisma* [sic] as the genus *Leiolopisma* by Smith (1935). Consequently, in 1937 Smith undertook a large-scale revision of *Lygosoma*, re-evaluating and reclassifying Boulenger's (1887) 11 sections. In doing so, Smith (1937a) elevated five sections to genera, believing each to be distinct enough morphologically from the rest of *Lygosoma* to warrant generic status: *Emoia*, *Keneuxia* (elevated as the genus *Dasia* Gray, 1839), *Otosaurus*, *Rhodona* and *Riopa*. Four subgenera were recognized in *Riopa*: *Eugongylus* Fitzinger, 1843, *Eumecia* Barboza du Bocage, 1870, *Panaspis* Cope, 1868 and *Riopa* (Smith 1937a). Additionally, Smith (1937a) synonymized the section *Homolepida* [sic] with the genus *Tiliqua* and considered the sections *Hemiergis* and *Siaphos* [sic] invalid due to a lack of diagnostic characters, placing their species into the section *Leiolopisma*. Despite these many changes, the genus *Lygosoma*, as defined by Smith (1937a), remained species-rich, comprising more than 166 taxa separated into three sections: *Leiolopisma*, *Lygosoma* and *Sphenomorphus* Fitzinger, 1843; and the subgenus *Ictiscincus* Smith, 1937a. In his revision, Smith (1937a: 219) lamented on the lack of diagnostic characters separating species and sections in this large genus, writing, 'I am unable to find any character by which to separate the well-developed forms of *Lygosoma*…from the degenerate ones. Between the extremes in each section, the difference is enormous, but the gap can be bridged by connecting forms showing every stage of development.'

The next major revision of *Lygosoma* was conducted by Mittleman (1952), who felt that a taxonomic system in which genera are defined narrowly was preferable to the approach of Boulenger (1887) and Smith (1937a), both of whom, in struggling to find diagnostic characters, treated *Lygosoma* as a catch-all genus. Therefore, in his revision, Mittleman (1952) avoided using subgenera and sections and instead defined multiple genera for species formerly included in Boulenger's (1887) and Smith's (1937a) definitions of *Lygosoma*. Although he worked primarily from the literature instead of examining specimens (G. Shea, pers. comm.), Mittleman described three new genera and resurrected and redefined 30 genera based on body proportions, limb size, size of the ear opening and head scalation patterns (Mittleman, 1952). Consequently, the number of species in *Lygosoma* was reduced considerably to eight elongate, small-limbed species from Southeast Asia and Australia. Of the new genera described, the genus *Squamicilia* Mittleman, 1952 contained a species of *Lygosoma s.l.* (*isodactylum*) included previously in *Riopa* subgenus *Riopa* by Smith (1937a) and was defined on the basis of a scaly lower eyelid and absence of contact between supranasals (Mittleman, 1952). Additionally, the genera *Mochlus* and *Riopa* were redefined to comprise 14 and nine species, respectively (Mittleman, 1952). Prior to this work, *Mochlus* had long been treated as a synonym of *Riopa*, regardless of whether *Riopa* was considered a genus or a section at the time (Boulenger, 1887; Schmidt, 1919; Barbour & Loveridge, 1928; Loveridge, 1933; Smith, 1937a; FitzSimons, 1943). Mittleman (1952), in an effort to define genera that more accurately reflected perceived evolutionary relationships, considered *Mochlus* as a genus distinct from *Riopa* based on its scaly (vs. transparent) lower eyelid and more robust (vs. small) limbs. However, many authors have questioned the diagnostic value of the lower eyelid state and relative limb proportions for genera, noting considerable variation in states for both characters among many genera of skinks (Smith, 1937a; Broadley, 1966; Greer, 1974, 1977; Datta-Roy *et al.*, 2015). As a result of this uncertainty, and concerns with over-splitting of genera by Mittleman (1952), many subsequent studies rejected Mittleman's (1952) separation of

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*Mochlus* and *Riopa* and continued to treat *Mochlus*, along with *Squamicilia*, as synonyms of *Riopa* (Loveridge, 1957; Broadley, 1962, 1966; Taylor, 1963; Greer, 1977).

Despite disagreements regarding the taxonomic rank and species composition of *Riopa*, *Mochlus* and *Squamicilia*, species included in these genera have been recognized as being closely allied, (Boulenger, 1887; Smith, 1937a). The genus *Lepidothyris*, mentioned by Cope (1892) (as a *nomen nudum*) and attributed formally to the species *Lepidothyris fernandi* (Burton, 1836) by Cope (1900), also has been historically allied with *Riopa* + *Mochlus* (the genus was synonymized with *Riopa* subgenus *Riopa* by Smith [1937a] and *Mochlus* by Mittleman [1952]). In contrast, since Boulenger (1887), the species composition of *Lygosoma* has changed considerably, with Smith (1937a) and Mittleman (1952) both offering different morphological definitions and species compositions for the genus – Smith treating the genus as a catch-all group comprising otherwise unclassifiable species and Mittleman treating it as a narrowly defined unit. After Mittleman (1952), authors continued to reclassify species in *Lygosoma*, placing them in different genera (e.g. Storr, 1964, 1967; Greer, 1970a; Cogger, 1975), so that by 1977, the only species that remained in the genus *Lygosoma* was the type species, *Lygosoma quadrupes*.

The taxonomy of the genus *Lygosoma* was not revisited until Greer (1977) re-examined the morphology of *Lygosoma quadrupes*, looking at internal osteological characters of the skull in addition to traditional external morphological characters. In a paper that laid the foundations of our current understanding of *Lygosoma s.l.* phylogenetic relationships, Greer (1977) proposed that *L. quadrupes* was closely related to species in the genus *Riopa* [which included Mittleman's (1952) *Mochlus* and *Squamicilia*] based on the morphology of the secondary palate. He further suggested that the characteristic elongate body plan of *L. quadrupes* was part of a gradient in body form morphology that encompassed the less elongate body morphologies of species of *Riopa,* and he concluded that the amount of overlap in characters between *Riopa* and *Lygosoma quadrupes* was insufficient to warrant the recognition of two separate genera (Greer, 1977). The genus *Riopa* was, therefore, synonymized with *Lygosoma*, resulting in a genus of 32 recognized species (Greer, 1977). Since Greer's (1977) work, more recent phylogenetic studies of the genus have corroborated the close relationship between *Lygosoma quadrupes* + *Riopa* (Ziegler *et al.*, 2007; Wagner *et al.*, 2009; Pyron *et al.*, 2013; Datta-Roy *et al.*, 2014; see below), and this work remains a major influence on our current understanding of evolutionary patterns in *Lygosoma s.l.*

### *Recent classifications based on molecular sequence data*

Over the last two decades, molecular phylogenetic studies focusing on lygosomine skinks have helped to resolve some of the long-standing taxonomic issues regarding genera in Lygosominae (Honda *et al.*, 2000, 2003; Skinner *et al.*, 2011). Although molecular studies have increased our understanding of relationships among certain taxa in *Lygosoma s.l.*, these studies exposed additional taxonomic challenges regarding the taxonomic rank and allocation to clusters of species variably ascribed to the genera *Lepidothyris*, *Lygosoma*, *Mochlus* and *Riopa*. Ziegler *et al.* (2007) conducted the first molecular phylogenetic study of *Lygosoma s.l.*, collecting *16S* mitochondrial sequence data for six Southeast Asian and Indian species. Not only did this study confirm Greer's (1977) hypothesis of a close relationship between *Lygosoma quadrupes* and *Riopa*, but it also recovered *L. quadrupes* as nested in a clade of species recognized previously by Mittleman (1952) as part of the genus *Mochlus* (Ziegler *et al.*, 2007).

Wagner *et al.* (2009) conducted a molecular study focused on African species of *Lygosoma* to infer the phylogenetic position and biogeographic history of the *Lygosoma fernandi* species group from west-central Africa. Adding a second mitochondrial gene (*12S*) and additional African, Indian and Southeast Asian taxa to the dataset of Ziegler *et al.* (2007) for a total of 11 ingroup species, analyses recovered three well-supported clades: two African clades [one comprising the *L. fernandi* species group (*L. fernandi* + *L. hinkeli* + *L. striatus* (Hallowell 1854)) and one comprising *Lygosoma afer* (Peters, 1854) + *L. sundevallii* (*L. afer* subsequently has been synonymized with *L. sundevallii* [Freitas *et al.*, 2018]), and one Southeast Asian clade comprising *L. koratense* Smith 1917 + *L. quadrupes*. However, inter-clade relationships and the placement of several Southeast Asian taxa (*L. bowringii* (Günther, 1864b), *L. lineolatum* (Stoliczka, 1870)) and Indian taxa (*L. albopunctatum* (Gray, 1846)) taxa remained poorly supported, and the monophyly of the genus *Lygosoma* was not resolved with strong support (Wagner *et al.*, 2009). Despite the lack of support at deep nodes in the phylogeny, Wagner *et al.* (2009) recommended a major revision to Greer's (1977) taxonomy by splitting *Lygosoma* into four genera: *Lygosoma* for Southeast Asian species, *Lepidothyris* for the *Lygosoma fernandi* species group, *Mochlus* for *Lygosoma sundevallii* and *Riopa* for Indian species, referencing Mittleman (1952) for the morphological

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definition of these genera. Yet, this classification contradicted Mittleman's (1952) in several ways that were not addressed. First, the species *lineolatum* and *bowringii* were placed in the genus *Lygosoma* instead of *Riopa* and *Mochlus*, respectively, as they were in Mittleman (1952) and, second, the species *albopunctatum* was moved to the genus *Riopa* instead of *Mochlus* as it was in Mittleman (1952) (Wagner *et al.*, 2009). In fact, it appears that although Wagner *et al.* (2009) refer to Mittleman (1952) for the definition of *Lygosoma*, *Mochlus* and *Riopa*, the authors did not follow Mittleman's (1952) definition of the genera and instead implicitly define them geographically (*Lygosoma* for species from Southeast Asia, *Mochlus* for species from Africa, excluding the *Lepidothyris fernandi* species group, and *Riopa* for species from India). This lack of morphological definitions and the implicit reliance on geography as a diagnostic feature for these genera resulted in an unstable taxonomy in which generic boundaries were not well-defined. Whereas *Mochlus* was widely adopted as the genus name for African species (e.g. Kennedy *et al.*, 2012; Trape *et al.*, 2012; Pyron *et al.*, 2013; Hedges, 2014; Masterson, 2014; Uetz *et al.*, 2019), most subsequent studies continued to treat *Riopa* as part of *Lygosoma* (Geissler *et al.*, 2011, 2012; Pyron *et al.*, 2013).

Poor support along the backbone of their tree meant that Wagner *et al.* (2009) could not assess the reciprocal monophyly of genera, nor were they able to estimate the relationships of the genera to each other. Additionally, a lack of tissue samples meant that most of the species in Greer's (1977) *Lygosoma* could not be ascribed to Wagner *et al.*'s (2009) genera. Pyron *et al.*'s (2013) squamate phylogeny, in which *Lygosoma s.l.* was included as part of a much larger investigation into the evolutionary relationships of squamate reptiles, had better support at deeper nodes. Although Pyron *et al.*'s (2013) study did not employ additional molecular or taxonomic sampling for *Lygosoma s.l.*, the authors' use of a supermatrix in an analysis that included thousands of other species resulted in a phylogeny that better resolved relationships among major clades in the group. *Lygosoma s.l.* was inferred to be monophyletic, but the genus *Lygosoma* was polyphyletic with respect to *Lepidothyris* and *Mochlus* (*Riopa* was treated as a synonym of *Lygosoma*), and *Mochlus* was not supported as monophyletic.

A paraphyletic *Lygosoma* was corroborated through a molecular phylogenetic analysis of *Lygosoma s.l.* by Datta-Roy *et al.* (2014), which represents the most recent study conducted to date on the genera. The 17-species dataset included additional Indian and Southeast Asian species of *Lygosoma s.l.* (Datta-Roy *et al.*, 2014). Like Pyron *et al.*'s (2013) study, the results suggested that *Lygosoma* was polyphyletic with respect to *Riopa* and to both African genera. Based on these results, Datta-Roy *et al.* (2014) synonymized *Riopa* with *Lygosoma*, but they retained *Mochlus* and *Lepidothyris* as separate genera due to low support for the placement of these two genera in the larger *Lygosoma s.l.* group. However, unlike Pyron *et al.* (2013), Datta-Roy *et al.* (2014) did not recover *Lygosoma s.l.* as monophyletic, instead observing the morphologically and ecologically distinct arboreal species *Lamprolepis smaragdina* as nested in the clade with high support, although the exact position of the species was not resolved.

Taken together, these molecular phylogenetic studies reflect the long-standing problems in arriving at a stable taxonomy for this Old World radiation of skinks. Despite considerable efforts to revise the taxonomy based on morphological characters and molecular data, the current taxonomic status of *Lepidothyris*, *Lygosoma s.s.*, *Mochlus* and *Riopa*, remain unresolved, with recent phylogenetic studies suggesting that relationships in *Lygosoma s.l.* are more complex than previously recognized (Datta-Roy *et al.*, 2014). In this study, we employ increased taxonomic and genetic sampling of *Lygosoma s.l.*, combining concatenated and coalescent-based molecular phylogenetic analyses with multivariate statistical analyses of morphological data, to address the following issues: (1) the monophyly of *Lygosoma s.l.* with respect to *Lamprolepis*; (2) the status and relationships of *Lepidothyris*, *Lygosoma s.s.*, *Mochlus* and *Riopa*; (3) the ability to determine diagnostic morphological characters for clades; and (4) the taxonomic stability of *Lygosoma s.l.*

## MATERIAL AND METHODS

### Taxon sampling

We sampled species from across the geographic distribution of *Lygosoma s.l.*, including lineages from Africa, India, Southeast Asia and the Philippines, using one to two individuals per species (when available) for phylogenetic analyses. Our ingroup sampling consisted of 34 individuals representing 22 species of *Lygosoma s.l.* 17 species of *Lygosoma s.s.*, one species of *Lepidothyris* and four species of *Mochlus* (Supporting Information, Table S1). Tissue samples for the remaining 27 species in *Lygosoma s.l.* are not available in museum collections. Outgroup sampling was chosen based on Pyron *et al.* (2013) to assess the monophyly of *Lygosoma s.l.* and comprised nine individuals of species from closely and distantly related scincid genera, the lygosomine species *Eutropis multifasciata*, *Lamprolepis smaragdina*, *Larutia* sp., *Lipinia pulchella*, *Otosaurus cumingi*, *Pinoyscincus*

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*jagori* and *Sphenomorphus fasciatus* and the scincine species *Plestiodon fasciata* (Supporting Information, Table S1).

### Genetic sampling and molecular methods

Most of the sequences used in our analyses were novel, but we were able to obtain data for several ingroup and outgroup samples from GenBank (Supporting Information, Table S1). To generate our sequence data, we extracted genomic DNA from liver or muscle tissue using a high salt precipitation method (Aljanabi & Martinez, 1997) and amplified seven nuclear loci (nuDNA; oocyte maturation factor [*CMOS*, 374 base pairs/bp], follistatin-like protein 5 [*FSTL5*, 622 bp], prolactin receptor [*PRLR*, 566 bp], prostaglandin E receptor 4 [*PTGER4*, 470 bp], RNA fingerprint protein 35 [*R35*, 665 bp], recombination activating gene 1 [*RAG1*, 828 bp], synuclein alpha interacting protein [*SNCAIP*, 484 bp]) and two mitochondrial markers (mtDNA; NADH dehydrogenase subunit 1 [*ND1*, 969 bp], 16S ribosomal RNA [*16S*, 559 bp]) using standard PCR protocols (Siler *et al.*, 2011). All loci were chosen based on their ability to resolve relationships at different tree depths, as shown in previous species-level phylogenetic studies of skinks (Whiting *et al.*, 2003; Siler *et al.*, 2011; Brandley *et al.*, 2012). Primers and annealing temperatures are listed in Table 1. PCR products were purified by ExoSAP-IT (Thermo Fisher Scientific), sequenced with BigDye Terminator v.3.1 sequencing kit (Thermo Fisher Scientific) and cleaned using ethanol precipitation. We sent sequencing products to Eurofins Genomics for visualization. All novel sequences are deposited in GenBank (Supporting Information, Table S1).

### Sequence alignment and concatenated phylogenetic analyses

Raw sequence data were examined for heterozygous sites and erroneous base calls and were trimmed in GENEIOUS v.9.0.4 (Biomatters, Ltd.). We aligned each locus with MUSCLE (Edgar, 2004) using default settings as implemented in GENEIOUS and examined the resulting alignments by eye. For protein-coding loci (all nuDNA and *ND1*), we used GENEIOUS to translate and place alignments in the correct reading frame to check for errors in the location of insertions-deletions and to detect erroneous internal stop codons. We retained ambiguous sites in the *16S* alignment after running preliminary maximum likelihood analyses on an alignment with the ambiguous sites included and an alignment with the ambiguous sites removed using RAxML v.8.0.0 (Stamatakis, 2014). The resulting topologies did not show any highly supported incongruencies, and we, therefore, used the longer alignment in our subsequent concatenated analyses to maximize the size of our dataset.

**Table 1.** The primers and annealing temperatures for the seven nuclear genes and two mitochondrial genes used in this study.

| Gene | Sequence Length (bp) | Primer | Primer Sequence (5'–3') | Annealing Temp (°C) | Reference |
|---|---|---|---|---|---|
| *CMOS* | 374 | cmosG73.1 | GGCTRTAAARCARGTGAAGAAA | 52.5 | Whiting *et al.*, 2003 |
| | | cmosG74.1 | GARCWTCCAAAGTCTCCAATC | | |
| *FSTL5* | 622 | FSTL5.F1 | TTGGRTTTATTCTTCAYAAAGA | 55 | Townsend *et al.*, 2008 |
| | | FSTL5.R2 | YTCTSAACYTCAGTGATYTCACA | | |
| *PRLR* | 566 | PRLR.F1 | GACARYGARGACCAGCAACTRATGCC | 55 | Townsend *et al.*, 2008 |
| | | PRLR.R3 | GACYTTGTGRACTTCYACRTAATCCAT | | |
| *PTGER4* | 470 | PTGER4.F1 | GACCATCCCGGCCGTMATGTTCATCTT | 55 | Townsend *et al.*, 2008 |
| | | PTGER4.R5 | AGGAAGGARCTGAAGCCCGCATACA | | |
| *R35* | 665 | R35.F | GACTGTGGAYGAYCTGATCAGTGTGG | 55 | Fry *et al.*, 2006 |
| | | R35.R | GCCAAAATGAGSGAGAARCGCTTCTG | | |
| *RAG1* | 828 | RAG-1.R13 | TCTGCTGTTAATGGAAATTCAAG | 52.5 | Groth & Barrowclough, 1999 |
| | | RAG-1.R13. rev | AAAGCAAGGATAGCGACAAGAG | | |
| *SNCAIP* | 484 | SNCAIP.F10 | CGCCAGYTGYTGGGRAARGAWAT | 55 | Townsend *et al.*, 2008 |
| | | SNCAIP.R13 | GGWGAYTTGAGDGCACTCTTRGGRC | | |
| *ND1* | 969 | 16dR | CTACGTGATCTGAGTTCAGACCGGAG | 53 | Leaché & Reeder, 2002 |
| | | tMet | ACCAACATTTTCGGGGTATGGG | | |
| *16S* | 559 | 16Sar-L | CGCCTGTTTATCAAAAACAT | 46 | Palumbi, 1991 |
| | | 16Sbr-H | CCGGTCTGAACTCAGATCACGT | | |



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Although many studies have suggested that partitioning a concatenated dataset by gene and codon position results in improved topologies (Brandley *et al.*, 2005; Brown & Lemmon, 2007; Linkem *et al.*, 2011, 2013), empirical and simulated phylogenetic data have shown that when partitions have few variable sites, over-parameterization leads to estimation of values for unidentifiable parameters, and the resulting topology can have incorrect long branch lengths due to poor estimation of substitution rate parameters (Marshall, 2010). Therefore, to determine the best partitioning strategy for each protein-coding gene, we calculated Bayes' factors to compare the unpartitioned to partitioned-by-codon topologies for each protein-coding gene. First, we selected the best substitution model for each gene and codon position using the Akaike Information Criteria (AIC; Akaike, 1974) implemented in the program JMODELTEST v.2.1.10 (Darriba *et al.*, 2012; Table 2). We then generated trees for each partitioning strategy using Bayesian Inference (BI) with MrBayes v.3.2.6 (Ronquist *et al.*, 2012). Each BI analysis consisted of two independent runs of four chains, run for 5,000,000 generations, sampling every 1000 generations. Stationarity and convergence were assessed in Tracer v.1.6 (Rambaut *et al.*, 2014). Convergence for all runs occurred in the first 3,000,000 generations and we conservatively discarded the first 10% of each run as burn-in. To estimate the marginal likelihoods of each topology, we used the stepping-stone analysis (Fan *et al.*, 2011; Xie *et al.*, 2011) implemented in MrBayes, run for 50 steps and 2,958,000 generations with the first 58,000

**Table 2.** The results of JMODELTEST v.2.1.10 showing inferred substitution models for the loci partitioned by gene and codon position. Partitions used in concatenated and coalescent-based analyses are shown in bold.

| Gene | Partition | Length (bp) | Substitution model |
|---|---|---|---|
| *CMOS* | **Gene** | **374** | **HKY + Γ** |
| | 1st Codon Position | 125 | HKY + Γ |
| | 2nd Codon Position | 125 | GTR + Γ |
| | 3rd Codon Position | 124 | HKY + Γ |
| *FSTL5* | Gene | 622 | GTR + Γ |
| | **1st Codon Position** | **207** | **GTR + Γ** |
| | **2nd Codon Position** | **207** | **F81 + Γ** |
| | **3rd Codon Position** | **208** | **HKY + Γ** |
| *PRLR* | **Gene** | **566** | **GTR + Γ** |
| | 1st Codon Position | 188 | HKY + Γ |
| | 2nd Codon Position | 189 | GTR + Γ |
| | 3rd Codon Position | 189 | GTR + Γ |
| *PTGER4* | Gene | 470 | HKY + Γ |
| | **1st Codon Position** | **157** | **GTR + Γ** |
| | **2nd Codon Position** | **156** | **F81 + Γ** |
| | **3rd Codon Position** | **157** | **GTR + Γ** |
| *R35* | Gene | 665 | GTR + Γ |
| | **1st Codon Position** | **221** | **K80 + Γ** |
| | **2nd Codon Position** | **222** | **GTR + Γ** |
| | **3rd Codon Position** | **222** | **GTR + Γ** |
| *RAG1* | **Gene** | **828** | **GTR + Γ** |
| | 1st Codon Position | 276 | GTR + Γ |
| | 2nd Codon Position | 276 | HKY + Γ |
| | 3rd Codon Position | 276 | HKY + Γ |
| *SNCAIP* | Gene | 484 | GTR + Γ |
| | **1st Codon Position** | **161** | **HKY + Γ** |
| | **2nd Codon Position** | **161** | **HKY + Γ** |
| | **3rd Codon Position** | **162** | **GTR + Γ** |
| *ND1* | Gene | 969 | GTR + Γ |
| | **1st Codon Position** | **323** | **GTR + Γ** |
| | **2nd Codon Position** | **323** | **GTR + Γ** |
| | **3rd Codon Position** | **323** | **GTR + Γ** |
| *16S* | **Gene** | **559** | **GTR + Γ** |

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generations discarded as burn-in and an additional 5000 generations removed from the beginning of each step as additional burn-in. We diagnosed the analysis every 1000 generations, resulting in 58 trees in each step. We compared the marginal likelihoods of the topologies for each gene generated by the two partitioning strategies and calculated the Bayes' factor using the equation $2\ln(BF) = 2[\ln(MarL_1)\text{-}\ln(MarL_0)]$ (Kass & Raftery, 1995; Brandley *et al.*, 2005; Brown & Lemmon, 2007), where $MarL_1$ is the marginal likelihood of the topology in which the gene was partitioned by codon position and $MarL_0$ is the marginal likelihood of the topology in which the gene was not partitioned. Results of the stepping-stone analysis supported partitioning by codon position for *FSTL5*, *PTGER4*, *R35*, *SNCAIP* and *ND1* and partitioning by gene for *CMOS*, *PRLR* and *RAG1* (Table 3). The non-protein-coding gene *16S* was partitioned by gene. We ran three additional stepping-stone analyses on the concatenated dataset, partitioning all loci by gene, codon position (except *16S*) and by the partitioning scheme determined for each gene above. The results of these additional analyses supported the partitioning scheme determined above.

Examining relationships recovered among gene trees revealed highly supported discordance for the relationship of *Lamprolepis smaragdina* and *Lygosoma s.l.* and for the relative placement of the major clades, with six of the nine genes – *CMOS*, *PTGER4*, *R35*, *RAG1* and *SNCAIP* (nuDNA) and *ND1* (mtDNA) – having discordant nodes along the backbone of their respective topologies compared with the other gene trees. However, the species composition of major clades was congruent across all loci. Therefore, we used both concatenated phylogenetic methods and coalescent-based species tree methods to analyse higher level evolutionary relationships in *Lygosoma s.l.*

We performed concatenated partitioned Bayesian phylogenetic analyses with MrBayes, partitioning the genes as determined above (Tables 2, 3). We ran two independent metropolis-coupled Monte Carlo Markov Chain runs each with four chains for 30,000,000 generations, sampling every 5000 generations. Stationarity of parameters was assessed in Tracer v.1.6 and convergence of topologies in tree space analysed using the commands topological.approx.ess and analyze.rwty in the package RWTY v.1.0.1 (Warren *et al.*, 2017) in R v.3.3.2 (R Core Team, 2016). The effective sample sizes (ESS) for all parameters were above 200 (Drummond *et al.*, 2006). The samples exhibited convergence by 2,500,000 generations and we conservatively discarded the first 10% of samples as burn-in, leaving 10,800 trees in the combined MCMC posterior distribution. Nodes with posterior probability support of at least 0.95 were considered highly supported (Huelsenbeck & Rannala, 2004) and nodes with posterior probability support of 0.75–0.94 were considered moderately supported.

### Species tree analysis

In light of our observed gene tree discordance, we conducted a coalescent-based species tree analysis in addition to concatenated phylogenetic analyses using the program *BEAST (Heled & Drummond, 2010) implemented in BEAST v.2.4.6 (Bouckaert *et al.*, 2014). When incomplete lineage sorting occurs, concatenated analyses can result in highly supported incorrect topologies (Degnan & Rosenberg, 2009; Heled & Drummond, 2010), especially if species had large ancestral population sizes and speciation was rapid (Maddison, 1997). Coalescent-based analyses use the multispecies coalescent, originally developed for population genetics (Kingman, 1982; Tajima, 1983), to assess the probability that a gene tree evolved in the framework of a particular species tree (Rosenberg, 2002; Degnan & Rosenberg, 2009). To run our species tree analysis, we pared down our concatenated dataset to include only the nuclear genes *CMOS*, *PRLR*, *R35*, *RAG1* and *SNCAIP* and the mitochondrial gene *ND1*. We excluded the nuclear genes *FSTL5* and *PTGER4*

**Table 3.** The results of the stepping-stone analysis implemented in MrBayes v.3.2.6. Positive values for 2ln(BF) were considered support for the partitioned model (partitioned by codon position) and negative values were considered support for the non-partitioned model (Brown & Lemmon, 2007).

| Gene | $\ln(MarL_0)$ | $\ln(MarL_1)$ | $2\ln(BF)$ | Supported Model |
|---|---|---|---|---|
| *CMOS* | -1393.50 | -1398.15 | -9.30 | unpartitioned |
| *FSTL5* | -1633.78 | -1570.91 | 125.74 | partitioned |
| *PRLR* | -3081.56 | -3090.07 | -17.02 | unpartitioned |
| *PTGER4* | -1577.97 | -1481.96 | 192.02 | partitioned |
| *R35* | -3369.47 | -3291.48 | 155.98 | partitioned |
| *RAG1* | -3057.01 | -3057.20 | -0.38 | unpartitioned |
| *SNCAIP* | -2095.3 | -2048.92 | 92.76 | partitioned |
| *ND1* | -14400.31 | -13853.07 | 1094.48 | partitioned |



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from our species tree analyses, because these two loci had the most missing data non-randomly distributed across ingroup taxa (i.e. these genes did not amplify across all clades), and we excluded the non-coding mtDNA gene *16S*, because while it was successful at resolving very shallow nodes, it was uncertain regarding relationships at deeper nodes in the tree where most of the problems with discordance occurred. Additionally, BEAST2 estimates the root of the tree during MCMC analyses making the inclusion of any outgroup taxa unnecessary, except to give additional information on the position of the ingroup root (Drummond & Bouckaert, 2015). Therefore, we decreased the number of outgroup species used in our analysis to the two species with the lowest amount of missing data (*Eutropis multifasciata* and *Lamprolepis smaragdina*) to reduce computation effort and errors in prior estimation that can occur during BEAST analyses when including less well-sampled taxa with long branches (Drummond & Bouckaert, 2015). The data were partitioned according to the same partitioning scheme in our concatenated analysis (Tables 2, 3) and each partition was assigned the same substitution model. Analyses were run using an estimated strict clock prior, a Yule process species tree prior and a piecewise linear and constant population size prior. We changed the default Birthrate.t:Species and popMean priors from an inverse 1/X distribution to a lognormal distribution and the default clockRate prior for all loci from a uniform [-∞,∞] distribution to an exponential distribution. These default priors are inappropriate, because they do not integrate to one (Drummond & Bouckaert, 2015). Three initial runs were conducted for 20,000,000 generations each to tune the operators to values suggested by the BEAST2 operator outputs. Following the adjustment of operators, three additional runs were conducted for 200,000,000 generations each to check the performance of priors; based on the results of these runs, several substitution rate priors were adjusted from a default gamma distribution to an exponential distribution with a mean of 1.0 to place higher probability on values closer to 0. We ran four final runs for 1,000,000,000 generations each sampling every 100,000 generations, using the CIPRES Science Gateway portal (Miller *et al.*, 2010). These runs were examined separately and together in Tracer and RWTY (see above) to assess stationarity and convergence. We combined the species tree analyses in LogCombiner v.2.4.6 (Bouckaert *et al.*, 2014), discarding the first 20% of trees in each posterior distribution as burn-in, keeping a total of 32,004 trees in the combined posterior distribution. We used TreeAnnotator v.2.4.6 (Bouckaert *et al.*, 2014) to select the maximum clade credibility tree and calculate the posterior probability of each bifurcation.

### Morphological data and multivariate analyses

Specimens were examined for 27 quantitative and qualitative characters, consisting of mensural body measurements, meristic scale counts and head scale patterns. Characters were chosen based on their utility in previous taxonomic studies of skinks (e.g. Siler *et al.*, 2010; Linkem *et al.*, 2011; Geissler *et al.*, 2012; Davis *et al.*, 2014; Grismer *et al.*, 2014) and include: snout–vent length (SVL) – distance from the tip of the snout to the anterior edge of the vent, measured on the ventral surface of the specimen; axilla–groin distance (AGD) – distance between the posterior fore-limb insertion and the anterior hind limb insertion, measured on the ventral surface of the specimen; midbody width (MBW) – width of the body approximately midway between fore-limbs and hind limbs; tail length (TL) – distance from the posterior end of the vent to the tip of the tail, measured on the ventral surface of the specimen; tail width (TW) – width of the tail at the widest part just posterior to the vent, excluding the hemipenile bulge in males; head length (HL) – distance from the tip of the snout to the widest portion of the head generally at the jaw articulation, which is anterior to the auricular opening; head width (HW) – width of the head at the widest part, generally at the jaw articulation; head depth (HD) – depth of the head from the occiput to the underside of the jaws at the widest part, generally at the jaw articulation; eye–nares distance (END) – distance from the anterior edge of the eye opening to the posterior edge of the naris along a line parallel to the mouth; snout length (SNL) – distance from the anterior edge of the eye opening to the tip of the snout along a line parallel to the mouth; internarial distance (IND) – distance between the nares; midbody scale row count (MBSRC) – number of scales around the midbody approximately midway between fore-limbs and hind limbs; axilla–groin scale row count (AGSRC) – number of dorsal scales along a line from the posterior fore-limb insertion and the anterior hind limb insertion; paravertebral scale row count (PVSRC) – number of mid-dorsal scales along a line from the parietals to the scale opposite the vent, excluding enlarged nuchals; Finger-III lamellae count (FinIIILam) – number of enlarged scales under Finger-III; Toe-IV lamellae count (ToeIVLam) – number of enlarged scales under Toe-IV; supralabial scale count (SuprL) – number of enlarged scales in a line directly dorsal and parallel to the mouth opening; infralabial scale count (InfrL) – number of enlarged scales in a line directly ventral and parallel to the mouth opening; supraocular scale count (SO) – number of enlarged scales above the eye, the ventral edges of which are in contact with the dorsal edges of the supraciliary scales and dorsal edges of which are in contact with the lateral edges of the frontal and/or frontoparietal scales; superciliary

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scale count (SC) – number of small scales directly above the eyelid and below the supraoculars, the first of which is in contact with the preoculars and the last of which begins above the eye and terminates beyond the posterior edge of the orbital opening, not including superciliary #7 of Taylor (1935: Fig. 4); supranasal scale contact (SN) – contact of supranasals along the midline; prefrontal scale contact (PF) – contact of prefrontals along the midline; frontoparietal contact (FP) – contact of frontoparietal scales along the midline; parietal contact (P) – contact of parietal scales along the midline posterior to the interparietal scale; presence of enlarged nuchals (NU); first chin shield scale contact (1stChin) – contact of first chin shields along the midline; and presence of enlarged third chin shields (3rdChin). Specimens were measured by ESF, ADR, CDS, B. Karin, E. Ellsworth and S. Pal. Because older specimens were often fixed with curved bodies, the three major body length measurements, SVL, AGD and TL, were measured with a measuring tape and rounded to the nearest mm. The remaining mensural characters were measured using digital callipers accurate to 0.01 mm. When measurements were obviously distorted due to specimen preparation (e.g. specimens flattened during preparation could lead to inaccuracies in midbody depth), the measurement was flagged and excluded from statistical analyses. When possible, characters were measured or counted on the right side of the body.

Our morphological dataset included 254 specimens representing 25 species: 20/22 ingroup species from our phylogenetic analyses were included in our morphological dataset along with five additional species (*L. kinabatanganense*, *L. koratense*, *L. pembanum* Boettger, 1913, *L. siamense* and *L. tanae* (Loveridge, 1933)) for which we were unable to obtain genetic samples (Supporting Information, Table S2). One of these species, *L. siamense* is a recently describe species from the *L. quadrupes* species complex (Siler *et al.*, 2018) and thus we consider that species as part of the same clade as *L. quadrupes*, even though we lack DNA sequence data for it. Species in our phylogeny that we did not have morphological data for are *M. guineensis* (Peters, 1879) and *Lepidothyris fernandi*. We ran principal components analysis (PCA) and discriminant analysis of principal components (DAPC) on the mensural and meristic characters, excluding the head scale patterns (SN, PF, FP, P, NU, 1stChin, 3rdChin) because of problems using discrete categorical characters in PCA when the characters do not exhibit strong taxonomic structure (Hill & Smith, 1976). We excluded juveniles (juveniles considered to be individuals whose SVL fell outside of the lower range of previously published adult SVL for the species; Broadley, 1966, 1994; Das, 2010; Geissler *et al.*, 2011, 2012; Heitz *et al.*, 2016) and outliers, which may have been individuals that were misidentified. Our final dataset comprised 199 individuals representing 25 species. Additionally, we excluded one mensural character (TL) due to missing data, as a number of species in our morphological dataset only had TL measurements from individuals with autotomized or regenerated tails. We also excluded four meristic characters (SuprL, InfrL, SO and SC) because these counts did not vary meaningfully between species and were introducing 'noise' into preliminary analyses; differences in the variance of these characters in the PCA results were artefacts of sampling, not statistically significant taxonomic differences. These excluded measurements and coded head scale patterns are used in our taxonomic descriptions below and in Supporting Information, Table S3. Therefore, we included the following 14 characters in the PCA/DAPC morphological dataset: AGD, MBW, TW, HL, HW, HD, END, SNL, IND, MBSRC, AGSRC, PVSRC, FinIIILam and ToeIVLam. Three species in our morphological dataset (*L. albopunctatum*, *L. herberti* Smith, 1916 and *L. tanae*) had a majority of individuals that were missing MBSRC data, and we filled in these missing values with average values from the literature (Tabachnick & Fidell, 2013). For the mensural characters, we converted characters to ratiometric data by dividing all measurements by SVL to lessen the disproportionate effect of body size variance on the analysis and then prior to performing multivariate analyses, we log-transformed (natural log) all mensural and meristic values to normalize the data (Tabachnick & Fidell, 2013).

We ran PCA on the data using the command prcomp in the package stats in R v.3.5.0 (R Core Team, 2018), setting scale = True so that the analysis was performed on the correlation matrix of the data. PCA analyses the variance of all measurements for all samples and determines which measurements contribute the majority of the variance to the entire dataset. Each successive principal component describes the majority of the variance that was not captured by the preceding principal component. We used the resulting principal components from the PCA as input variables for DAPC. Whereas PCA seeks to maximize the total variance captured across the dataset, DAPC compares within-group variance to between-group variance and seeks to minimize the amount of within-group variance while maximizing between-group variance (Jombart *et al.*, 2010). Therefore, PCA illustrates the distribution of the entire dataset in morpho space, whereas DAPC shows how groups differ in morpho space. We ran DAPC on the data grouping by phylogenetic clades, using the first four principal components from the PCA as the variables, which accounted for 90% of the variance. The analysis was run in R using the command dapc in the package adegenet v.2.1.1 (Jombart, 2008).



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## RESULTS

### Concatenated Bayesian phylogenetic analysis

Our concatenated alignment comprised 43 individuals (34 ingroup samples, nine outgroup samples) sequenced for seven nuclear loci and two mitochondrial markers, for up to of 5537 base pairs (bp) per individual (average = 4237 bp per individual). Ingroup taxa contained an average of 21.1% missing data for each individual (standard deviation = 18.6%) resulting from difficulty in obtaining complete sequence data for several loci for all species and species groups; for example, *PRLR* was not amplified successfully for *L. quadrupes* and *L. tabonorum* (Table S1).

Bayesian concatenated phylogenetic analyses showed strong support for four divergent clades represented by the sampled taxa (Fig. 1), with no analysis supporting the monophyly of *Lygosoma s.l.* (clade containing

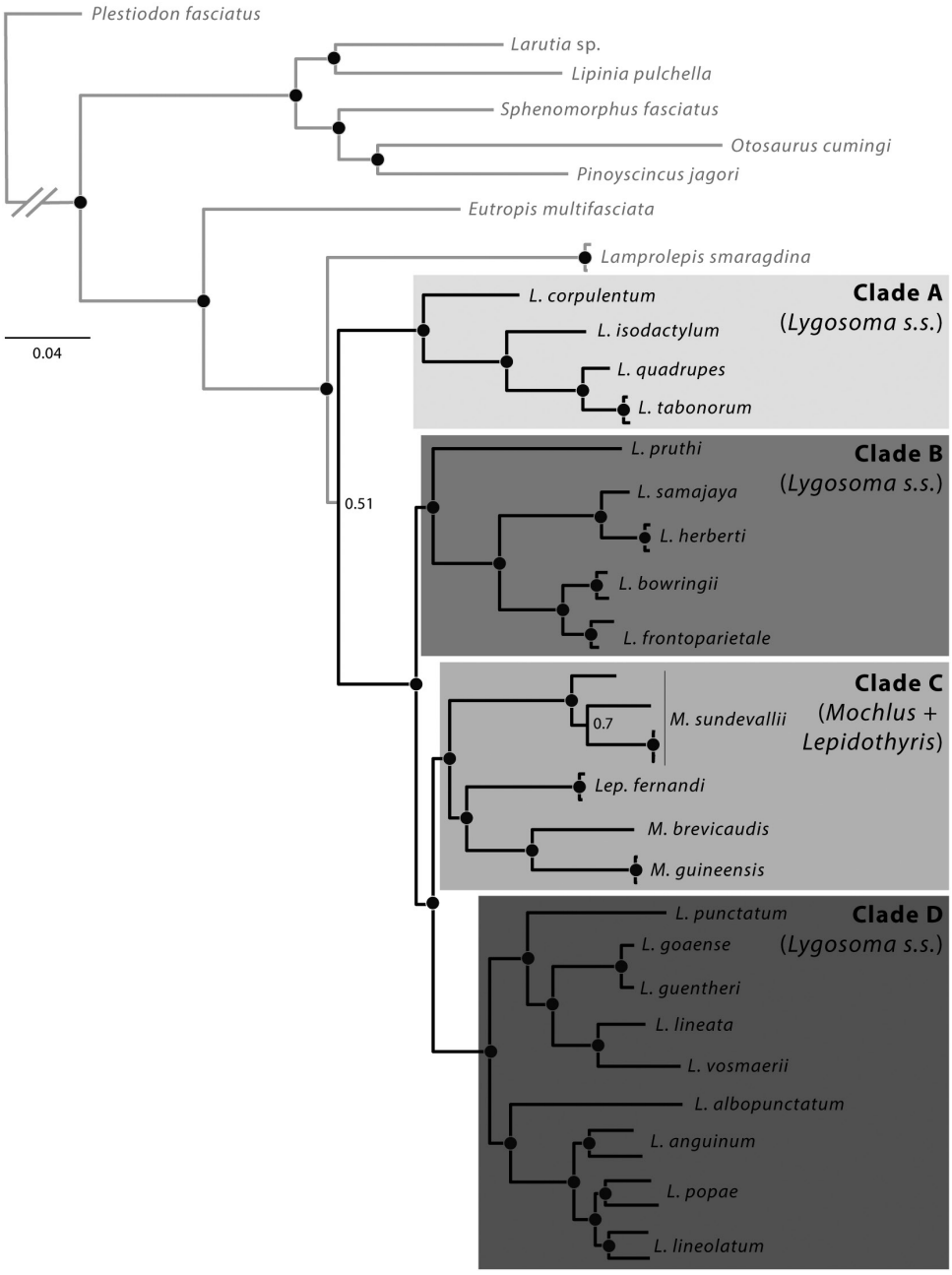


**Figure 1.** The concatenated Bayesian consensus topology. Black circles denote highly supported nodes (PP ≥ 0.95). Clades outlined in grayscale boxes refer to those listed in the results and discussion.

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*Lygosoma s.s.*, *Mochlus* and *Lepidothyris*, Bayesian posterior probability [PP] = 0.51). Instead, we recover *Lygosoma s.l.* as part of a clade also comprising *Lamprolepis smaragdina* (Fig. 1, PP = 1.0). In *Lygosoma s.l.*, we find four well-supported clades (Fig. 1, Clades A–D, PP = 1.0). The genus *Lygosoma s.s.* is not recovered as monophyletic, with the African genera *Mochlus* and *Lepidothyris* nested in *Lygosoma s.s.* (Fig. 1, PP = 1.0), breaking up *Lygosoma s.s.* into three separate clades: (1) Clade A contains the Southeast Asian species *L. corpulentum* Smith, 1921, *L. isodactylum*, *L. quadrupes* and *L. tabonorum*; (2) Clade B contains the Southeast Asian species *L. bowringii*, *L. frontoparietale*, *L. herberti* and *L. samajaya* and the Indian species *L. pruthi* (Sharma, 1977); and (3) Clade D contains the Southeast Asian species *L. anguinum* (Theobald, 1868), *L. lineolatum* and *L. popae* (Shreve, 1940) and the Indian species *L. albopunctatum*, *L. goaense* (Sharma, 1976), *L. guentheri* (Peters, 1879), *L. lineatum*, *L. punctatum* (Linnaeus, 1758) and *L. vosmaerii*. Additionally, analyses did not support the monophyly of the genus *Mochlus*, with results instead showing *Lepidothyris* as nested in *Mochlus* (Fig. 1, Clade C, PP = 1.0), sister to Clade D (PP = 1.0). The type species of *Lygosoma s.s.*, *L. quadrupes*, is recovered as part of Clade A, which is supported as sister to the remaining *Lygosoma s.l.* clades (Fig. 1, PP = 1.0).

### Species tree analysis

Similar to the results of the concatenated Bayesian phylogenetic analysis, species tree analyses recover four clades in *Lygosoma s.l.* (Fig. 2; Clades A–D, PP = 1.0, 0.85, 0.84 and 1.0, respectively), with *Lygosoma s.s.* supported as paraphyletic. The genera *Mochlus* and *Lepidothyris* are both nested in *Lygosoma s.s.*, separating the genus into three clades (Clades A, B, D; see concatenated results above for definition). Once again, *Mochlus* is found to be paraphyletic with respect to *Lepidothyris*, instead forming a *Mochlus* + *Lepidothyris* clade with moderate support (Fig. 2; Clade C, PP = 0.84). Clades B–D together are supported as a monophyletic group of taxa (PP = 1.0) to the exclusion of Clade A (Fig. 2).

The inferred species tree topology (Fig. 2) is broadly consistent with the Bayesian topology in regard to intraclade species-level relationships, with a few notable

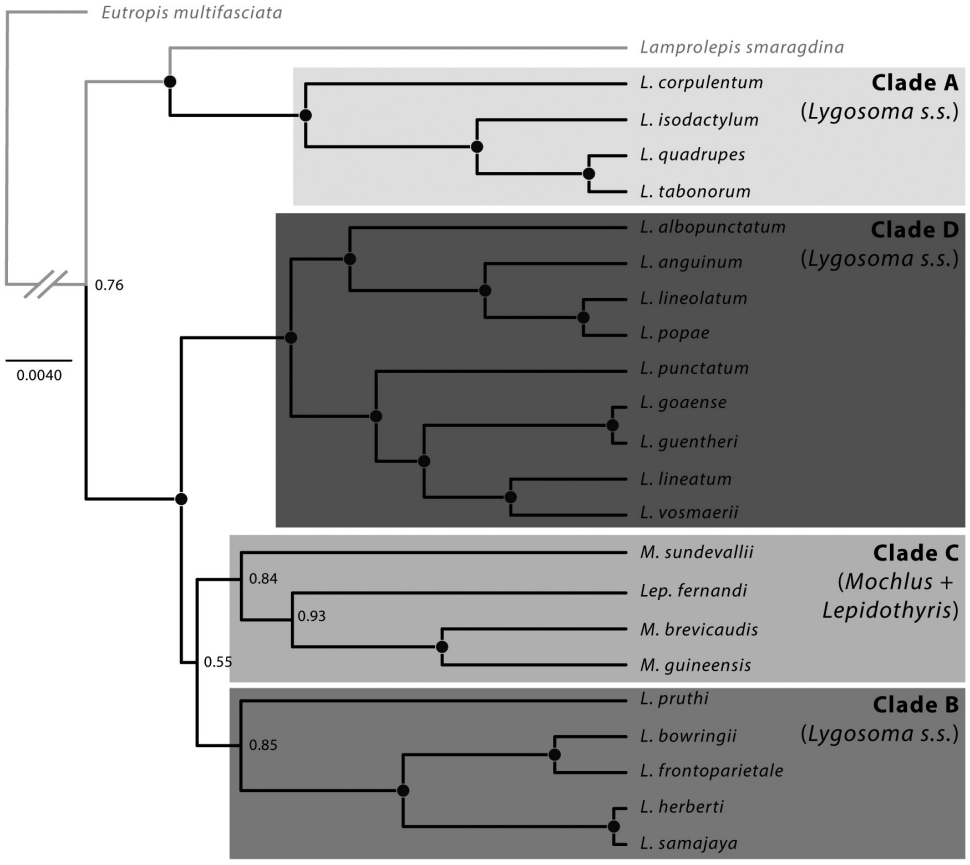


**Figure 2.** The coalescent-based maximum clade credibility species tree. Black circles denote highly supported nodes (PP ≥ 0.95). Clades outlined in grayscale boxes refer to those listed in the results and discussion.



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exceptions. First, the placement of *M. sundevallii* as part of Clade C and *L. pruthi* as part of Clade B, received moderate support (PP = 0.84 and 0.85, respectively). Second, although there is high support for a superclade comprising Clades B, C and D and excluding Clade A, there is no support for interclade sister relationships between Clades B, C and D (Fig. 2, PP = 0.55). Finally, unlike the Bayesian topology, the species tree topology supports *Lamprolepis smaragdina* as the sister taxon to Clade A (Fig. 2, PP = 0.97).

### Multivariate analyses

The principal components analysis shows that although species in *Lygosoma s.l.* vary in degree of body elongation, there is considerable overlap among species in morpho space (Fig. 3). The first two principal components (PCs) account for 82.8% of the total variance, with PC1 representing body size and accounting for 76.7% of the total variance, and PC2 representing body robustness and accounting for 6.1% of the variance (Table 4). For PC1, all characters have roughly equal loadings with the exception of MBSRC, which has a lower loading than the other characters. Three characters (AGD, AGSRC and PVSRC) are negatively correlated with the remaining characters, indicating that as body elongation increases, body width decreases. For PC2, AGD, PVSRC, MBSRC and ToeIVLam have the highest loadings, with AGD and ToeIVLam negatively correlated with PVSRC and MBSRC, suggesting that at a larger body size, relative elongation and digit lengths decrease (Table 4). The PCA reveals that clades (see Figs 1 and 2 for the phylogenetic definition of each clade) overlap highly in morpho space (Fig. 4A), with Clades B and C and Clades C and D showing the most overlap. Four species were not represented in our phylogenetic analyses and are, therefore, denoted as *incertae sedis* (*L. kinabatanganense*, *L. koratense*, *L. pembanum* and *L. tanae*; Fig. 4A), as their phylogenetic position remains unknown. As a result, we were not able to associate them definitively with any of the four *Lygosoma s.l.* clades.

Discriminant function analyses of principal components corroborates the PCA in showing that clades overlap highly in morpho space (Fig. 4B). Although the clades have, non-overlapping centroids (averages) and 95% inertia ellipses, several individual species overlap with centroids of different clades. This suggests that no clade is morphologically distinct from the other clades in *Lygosoma s.l.* Clades B and C exhibit the highest amount of overlap, whereas Clades A and B do not overlap at all. Interestingly, Clades B and C occupy smaller areas of morpho space than Clades A and D.

## DISCUSSION

### Non-monophyly of *Lygosoma s.l.* and paraphyly of *Lygosoma s.s.* and *Mochlus*

A stable taxonomy reflects evolutionary relationships of species and clades and is of paramount importance for studies in biological science. Diverse fields, from

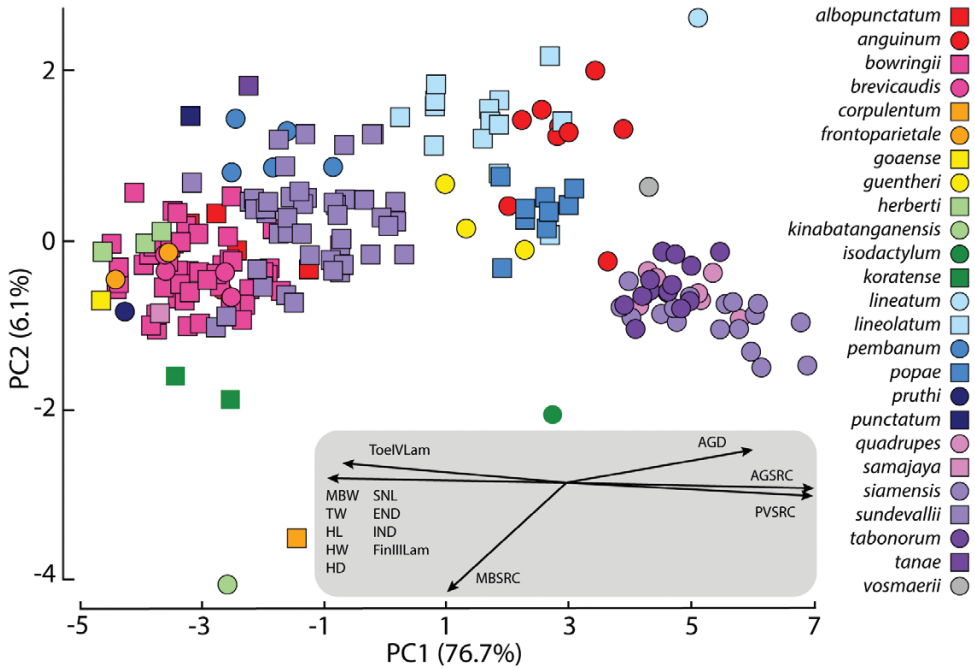


**Figure 3.** Principal components analysis of 14 characters for 25 species of *Lygosoma s.l.* Points are given a different colour and shape combination for each species. The inset arrows in the gray box shows the relative loadings for each character in the PCA.



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**Table 4.** The results of the PCA showing the variance, cumulative variance and character loadings for the first four principal components. These components were used as the input variables for the DAPC.

| | PC1 | PC2 | PC3 | PC4 |
|---|---|---|---|---|
| % variance | 76.7 | 6.1 | 3.9 | 3.1 |
| Cumulative variance | 76.7 | 82.8 | 86.7 | 89.8 |
| AGD | 0.2205 | 0.2752 | 0.7428 | -0.4484 |
| MBW | -0.2861 | -0.4484 | 0.2181 | -0.0299 |
| TW | -0.2712 | 0.0450 | 0.2999 | 0.2188 |
| HL | -0.2811 | 0.0715 | 0.0047 | -0.0911 |
| HW | -0.2920 | 0.0026 | 0.1331 | 0.0222 |
| HD | -0.2865 | -0.0056 | 0.2126 | 0.0194 |
| END | -0.2664 | 0.0782 | -0.1287 | -0.1761 |
| SNL | -0.2601 | 0.0145 | 0.2820 | 0.3981 |
| IND | -0.2829 | 0.0293 | 0.0611 | 0.2398 |
| PVSRC | 0.2918 | -0.1149 | 0.1260 | -0.0264 |
| MBSRC | -0.1440 | -0.9264 | 0.1966 | -0.2266 |
| AGSRC | 0.2933 | -0.0503 | 0.1537 | -0.0144 |
| FinIIILam | -0.2586 | 0.0596 | -0.2559 | -0.5660 |
| ToeIVLam | -0.2686 | 0.1622 | -0.0659 | -0.3483 |

ecology to development, rely on accurate species- and supra-specific-level identifications for their research (Mayr, 1976; Felsenstein, 1985; Winston, 1999; Wheeler *et al.*, 2004). Furthermore, taxonomy plays a critical role in biodiversity conservation and management, with agencies using recognized nomenclature for identification and classification of regional fauna, including rare and threatened species (e.g. CITES and IUCN; Kaiser *et al.*, 2013; Groves *et al.*, 2017; IUCN-SSC Species Conservation Planning Sub-Committee, 2017).

In supra-specific taxonomy, the genus category is included in the binomial name of a species, so although it is not based inherently on biological criteria, it is an important communication tool in the name of a species, depicting a close relationship between species in the same genus to the exclusion of other species (Cain, 1956; Winston, 1999). Therefore, the genus reflects information about the evolutionary history of the species it composes. Inger (1958) proposed a definition of genera that uses ecological criteria to determine the species that are placed in a genus, with 'mode of life' (i.e. adaptive zone; Vences *et al.*, 2013) as a major diagnostic character of the genus. However, currently this approach is problematic, especially for little-known clades, because it requires ecological knowledge of all species included in a genus and of closely related species excluded from that genus. Furthermore, congeners that live in sympatry may have undergone niche displacement (e.g. genus *Brachymeles*; Huron & Siler, unpubl. data), making the adaptive zone difficult to define empirically (Vences *et al.*, 2013). Accordingly, the only current defining characteristic of a genus is that it represents a clade in a broader family-level clade.

Among scincid lizards, studies have shown that many taxonomic groupings are not supported as monophyletic, e.g. *Amphiglossus* (Whiting, Sites & Bauer, 2004); *Sphenomorphus* (Linkem *et al.*, 2011); *Anomalopus* and *Eulamprus* (Skinner *et al.*, 2013); *Trachylepis* (Karin *et al.*, 2016); and *Afroablepharus* (Medina *et al.*, 2016). These inconsistencies between historical nomenclature and the evolutionary relationships recovered through molecular datasets necessitate the revision of genus-level classifications for taxonomic stability and for discussions of evolutionary patterns and processes within and among clades (Kaiser *et al.*, 2013; Vences *et al.*, 2013).

Our concatenated Bayesian Inference (BI) phylogenetic and coalescent-based species tree analyses reveal that *Lygosoma s.l.* is not monophyletic. Additionally, *Lygosoma s.s.* is paraphyletic, with respect to *Mochlus* and *Lepidothyris*, and the genus *Mochlus* is paraphyletic with respect to *Lepidothyris* (Figs 1–3). These results are consistent across all analyses and are in line with the findings of previous studies: Datta-Roy *et al.* (2014) observed similar relationships between *Lamprolepis* and *Lygosoma s.l.*, and *Lygosoma s.s.* and *Mochlus* in their study, albeit with low support at some of their deeper nodes. In our concatenated and coalescent-based analyses, *Lygosoma s.s.* Clade A, containing *Lygosoma quadrupes*, the type species of the genus, is supported as divergent from the other two major clades of *Lygosoma s.s.* (Figs 1–3), again corroborating the results of Datta-Roy *et al.* (2014).

Some differences between our concatenated and coalescent-based topologies are seen regarding the



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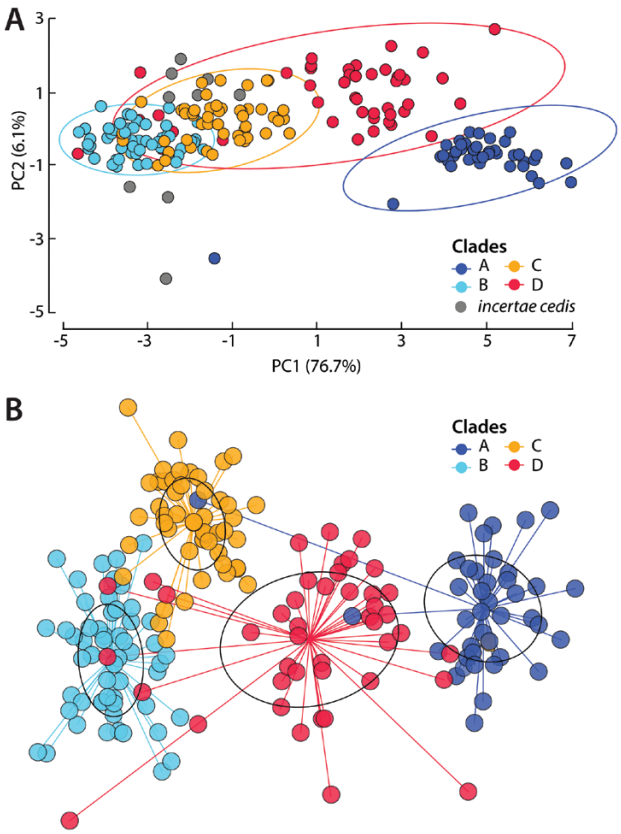


**Figure 4.** A, principal components analysis of 14 characters for 25 species of *Lygosoma s.l.* with points coloured by phylogenetic clade. Ellipses around clusters are coloured by clade and show the 95% boundary for each clade. B, discriminant analysis of principal components based on the first four principal components obtained in our PCA analysis. Points and 95% inertia ellipses are coloured by clade.

relationship between *Lamprolepis smaragdina* and *Lygosoma s.l.* In concatenated analyses, *Lamprolepis smaragdina* is recovered as part of *Lygosoma s.l.* with strong support (Fig. 1), although its position in *Lygosoma s.l.* is unresolved, suggesting that *Lygosoma s.l.* is paraphyletic with respect to *Lamprolepis smaragdina*. In contrast, the relationship between *Lamprolepis smaragdina* and *Lygosoma s.l.* is resolved fully in our coalescent-based species tree analyses, which recovered *Lamprolepis smaragdina* as the sister taxon to Clade A with strong support (Fig. 2). Although the finding of a paraphyletic *Lygosoma s.l.* with respect to *Lamprolepis smaragdina* is consistent with previous studies (Honda *et al.*, 2000, 2003; Datta-Roy *et al.*, 2014), it is surprising nevertheless given the highly divergent life histories of the species in question: *Lamprolepis smaragdina* is a larger, more robust, bright-coloured, arboreal skink, whereas most of the species in the genus *Lygosoma* are small, inconspicuously coloured and semi-fossorial (Greer, 1977; Das, 2010). In fact, Greer (1977) cited this ecological difference as evidence that the genera *Lygosoma* and *Lamprolepis* were not each other's closest relatives. The differences between our concatenated and coalescent-based analyses may be attributed gene tree discordance (Degnan & Rosenberg, 2009; Linkem *et al.*, 2016). Given the presence of discordance between loci in our nuDNA dataset, concatenation of our sequences may have resulted in a misleading BI topology.

The relationships of Clades B, C and D are fully resolved in our concatenated analyses, but not in our coalescent-based analyses (Figs. 1, 2). In our concatenated analyses, Clades C and D are supported highly as sister taxa and together are recovered as sister to Clade B. However, in coalescent-based analyses, the relationships between the three clades are not resolved, although they are still recovered as a clade distinct from Clade A with high support (Fig. 2). We suspect that incomplete taxonomic sampling across the radiation and low sample sizes for some rare or secretive species contributed to this lack of resolution. To estimate the multispecies coalescent process for each gene, sequences from at least two individuals per lineage need to be included in the dataset (Heled & Drummond, 2010), which suggests that increasing the taxonomic sampling per lineage will increase resolution of the species tree. Additionally, studies have shown that increased taxonomic sampling across the group being investigated improves species tree accuracy (Hovmöller *et al.*, 2013; Lambert *et al.*, 2015). Unfortunately, these two issues could not be addressed fully at this time given the rarity or absence of tissues in collections for some focal taxa. However, as next-generation sequencing techniques are revolutionizing approaches to phylogenetic studies by providing datasets of thousands of loci at increasingly lower costs (Ekblom & Galindo, 2011), these datasets are becoming more common in skink population and phylogenetic research (Barley *et al.*, 2015b; Brandley *et al.*, 2015; Rittmeyer & Austin, 2015; Linkem *et al.*, 2016; Bryson *et al.*, 2017). These techniques have the power to resolve difficult intra- and interclade relationships (e.g. Crawford *et al.*, 2012; McCormack *et al.*, 2012; Streicher & Wiens, 2017) and may be a promising tool for resolving the relationships among Clades B, C and D.

### Clades are not differentiated by morphology

Researchers have struggled to find diagnostic characters for *Lygosoma s.l.*, which has resulted in challenges to understanding the systematics of the group (Boulenger, 1887; Smith, 1937a; Mittleman, 1952). As a result, species relationships have been in flux for almost two centuries, with species sometimes

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placed together in a single genus (Boulenger, 1887) or separated into multiple genera (Smith, 1937a; Mittleman, 1952). In performing multivariate analyses, we investigated whether combinations of characters commonly used in delimitating species and genera could differentiate *Lygosoma s.l.* species and clades in morpho space. However, our principal components analysis (PCA) and discriminant analysis of principal components (DAPC) showed that species and clades were not separated in morpho space. This result underscores the historical difficulties of using morphology to classify *Lygosoma s.l.* skinks (Fig. 4), illustrating how traditional morphological approaches have largely failed in diagnosing clades with *Lygosoma s.l.*, because of the large amount of morphological overlap between species. Among the species examined, our PCA results show transitions in *Lygosoma s.l.* between robust and elongated body forms, with species overlapping along a morphological gradient (Fig. 3). As a result, among the major clades, we find that none form distinct clusters in morpho space (Fig. 4A), although it appears that Clade A contains the most elongated species, followed by Clade D and then by Clades B and C, with the highest amount of morphological overlap between Clades B, C and D. Given our phylogenetic results, which indicate that Clades B, C and D together form a clade to the exclusion of Clade A, our observations of these clades having the highest amount of morphological overlap makes sense.

Our DAPC, which used the principal components from the PCA as descriptor variables, was conducted to compare within-clade variance to between-clade variance and revealed Clades B and C to have the highest amount of overlap and occupy more restricted areas of morpho space when compared with Clades A and D (Fig. 4B). Interestingly, Clade A appears the most morphologically distinct clade with only two samples falling in the inertia ellipses of other clades and only a single individual from another clade (Clade D) recovered in its inertia ellipse (Fig. 4B). However, this pattern may be driven by the large number of individuals from the *Lygosoma quadrupes* species complex in our morphological dataset, which have a highly derived body form in comparison to other species in Clade A and in *Lygosoma s.l.* (Greer, 1977). It is likely that the inclusion of additional samples of other species in Clade A (e.g. *L. corpulentum* and *L. isodactylum*) and from other clades would temper this pattern.

Four species are labelled *incertae sedis* in our PCA analysis because they were not represented in our phylogenetic analyses. Among these, *Lygosoma koratense* from Southeast Asia appears morphologically most similar to species in Clade B, and *L. pembanum* and *L. tanae* from Africa appear morphologically most similar to Clade C (Figs 4, 5A). The remaining species, *L. kinabatanganense*, a large and robust species from Malaysia (Sabah, Borneo), does not fall within the morphological boundaries of any of the clades in our PCA. (Figs 4, 5A). Interestingly, a previous phylogenetic study of *Lygosoma s.l.* suggested a close relationship between *Lygosoma quadrupes* and *L. koratense* (Honda *et al.*, 2000), which was corroborated in subsequent studies using the same sequence data (Ziegler *et al.*, 2007; Wagner *et al.*, 2009; Skinner *et al.*, 2011 Pyron *et al.*, 2013; Datta-Roy *et al.*, 2014). Unfortunately, vouchered tissue samples of *L. koratense* were not available for this study. If the relationship of *L. quadrupes* and *L. koratense* holds true in future phylogenetic analyses, it would expand the extent of the occupied morpho space of Clade A and would have interesting implications for the evolution of body form in the clade.

The results of our PCA and DAPC analyses show that, like traditional morphological approaches, multivariate approaches have largely failed to differentiate clades in *Lygosoma s.l.* While there exists variation in body form among species in the group, this appears to change along a morphological gradient that only partially conforms to phylogeny (Fig. 4A). However, there are two characters not included in our PCA and DAPC analyses that have been employed historically in *Lygosoma s.l.* systematics, which are worth discussing further because they may be of use to differentiating phylogenetic clades in *Lygosoma s.l.* These characters are the morphology of the secondary palate and the character state of the lower eyelid. Of these characters, the morphology of the secondary palate is the least controversial. Greer (1977) used this character to unite *L. quadrupes* with *Riopa*, and he described all species of *Riopa* recognized at the time (31 species) as having processes that project from the posteromedial edge of the palatine bones, which separate the two pterygoid bones. Interestingly, Greer (1977) noted two character states of the secondary palate in *Lygosoma*: an open state (pterygoids emarginated along their posterior edge) and a closed state (pterygoids not emarginated along their posterior edge), each of which corresponds consistently with clades in our phylogenetic analyses (Figs. 1, 2). Greer (1977) listed all species found in our Clade B (with the exception of the recently described *L. samajaya*, which he did not examine) and our Clade C as having a closed palate, and he listed all species found in our Clade A (with the exception of *L. corpulentum*, which he did not examine) and our Clade D (with the exception of *L. vosmaerii*, which he did not examine and *L. punctatum* which was variable) as having an open palate. The palate of *L. koratense* was listed as closed, again morphologically linking this species more

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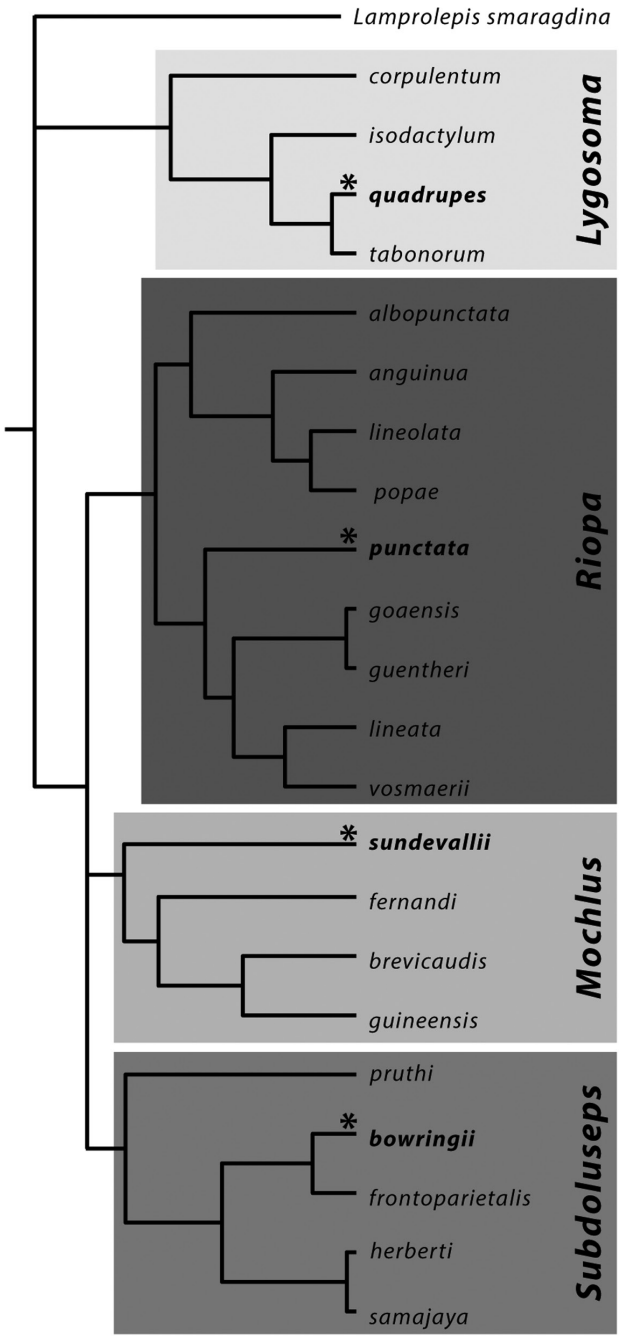


**Figure 5.** Phylogenetic tree showing the revised taxonomy of *Lygosoma s.l.* The topology is based on the species-tree topology (see Fig. 2). Support values are not shown. Species' names shown in bold with asterisks above branches represent the type species for that genus.

closely with Clade B than Clade A. Furthermore, Greer (1977) used the morphology of the secondary palate to diagnose the genus *Lamprolepis* from *Lygosoma s.l.* However, examination of written descriptions and drawings of the palate of *Lamprolepis* indicates that *Lamprolepis smaragdina* has posteromedial projecting processes separating the pterygoid bones (Greer, 1970b: Fig. 1; 1977: Fig. 5), similar to, but not as pronounced as, the processes in *Lygosoma s.l.* Therefore, the morphology of the secondary palate is useful in diagnosing the larger *Lygosoma s.l.* group of clades and may also be a useful descriptor variable for clades within *Lyogosoma s.l.*

In contrast to the morphology of the secondary palate, the taxonomic utility of the lower eyelid character state has been more controversial. Mittleman (1952) proposed the state of the lower eyelid, which has been defined broadly as either scaly or with a transparent window, as a diagnostic character separating groups, and he relied on eyelid state to split *Mochlus* from *Riopa*. Subsequent authors have disagreed with the taxonomic value of this character (Broadley, 1966; Greer, 1974, 1977), arguing that the character is highly variable within clades. Nevertheless, several recent skink taxonomic studies have mentioned the state of the lower eyelid as part of the combinations of diagnostic characters for some skink genera descriptions (*Euprepis* and *Eutropis* [Mausfeld & Schmitz, 2003]; *Brachymeles* [Siler *et al.*, 2011]; *Heremites* and *Toenayar* [Karin *et al.*, 2016]), although the presence of both states in the genus *Scincella* was noted by Linkem *et al.* (2011). In our study, the state of the lower eyelid does not appear consistent with our clades, with the exception of Clade A in which all our sampled members have a scaly lower eyelid. Instead, the lower eyelid character state appears highly variable between species and may also exhibit intraspecific variation. In Clade B, four of the five sampled species have a scaly lower eyelid; the exception being *L. pruthi*, which has a transparent disc on its lower eyelid (Sharma, 1977). In Clade C, all sampled species have a scaly lower eyelid, with the possible exception of *M. guineensis*. In its original description, *M. guineensis* was recorded as having a lower eyelid with a transparent disc (Peters, 1879), but the eyelid state was revised subsequently as scaly by Greer (1977). Additionally, four species from Africa that we lack genetic data for, but include provisionally in Clade C (*M. laeviceps* (Peters, 1874), *M. mabuiiformis* (Loveridge, 1935), *M. simonettai* (Lanza, 1979) and *M. tanae*; see justification in our taxonomic revision section), also were described originally as having a lower eyelid with a transparent disc (Peters, 1874; Loveridge, 1935; Lanza 1979). One of these lineages, *M. laeviceps*, later was reclassified as having a scaly lower eyelid (Greer, 1977). In Clade D, all of our sampled species have a transparent disc on their lower eyelid, but there is a record of one specimen of *L. albopunctatum* from Sarbhog, Assam, India in the Indian Museum, Kolkata that possesses a lower eyelid with a transparent disc on its right side and a scaly lower eyelid on its left side (Hora, 1927). Additionally,

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*L. lineolatum* was described originally as having a scaly lower eyelid (Stoliczka, 1870), but Smith (1935) reclassified the species as having a transparent disc in its lower eyelid. Nevertheless, several *Lygosoma* sp. individuals from Myanmar appear to have a scaly lower eyelid (ESF, unpubl. data), suggesting that the lower eyelid state is variable in Clade D. Therefore, unlike the morphology of the secondary palate, the lower eyelid character state seems to be inconsistent across most clades of *Lygosoma s.l.* and not useful for clade-level diagnosis.

## A REVISED CLASSIFICATION OF *LYGOSOMA S.L.*: OVERVIEW

Currently, *Lygosoma s.l.* comprises 49 nominal species: 31 species in the genus *Lygosoma s.s.*, 15 species in the genus *Mochlus* and three species in the genus *Lepidothyris*. Of these 49 species, we were able to include 22 in our phylogenetic analyses, representing all three genera, for the most complete assessment of the radiation to date. The results of our phylogenetic analyses suggest that *Lygosoma s.s.* does not form a monophyletic group with respect to the other genera in *Lygosoma s.l.* (*Lepidothyris* Cope, 1892 and *Mochlus* Günther, 1864a) and the genus *Lamprolepis* Fitzinger, 1842. Instead, *Lygosoma s.s.* is separated into three clades: one comprising elongate-bodied species from Southeast Asia, Indonesia and the Philippines (Clade A), one comprising the widespread species *L. bowringii* and other small, stouter-bodied species from India, Southeast Asia and Christmas Island (Clade B) and one comprising species from India and Southeast Asia (Clade D). Additionally, we do not recover *Mochlus* as monophyletic, with our results suggesting it is paraphyletic with respect to *Lepidothyris*. Given these results, we propose several taxonomic changes to this group (Fig. 5). First, we redefine the genus *Lygosoma* to include only Clade A, comprising the type species *Lygosoma quadrupes* and other elongate-bodied taxa. Second, we resurrect the genus *Riopa* for Clade D, comprising the type species *Riopa punctata* and other species from India and Southeast Asia. Third, we synonymize the genus *Lepidothyris* with *Mochlus*. Last, we describe a new genus, *Subdoluseps* gen. nov. for Clade B, comprising the type species *S. bowringii* and additional species distributed across India, Southeast Asia and Christmas Island. We recognize that our taxonomic sampling is incomplete considering the large diversity of species that are recognized currently in *Lygosoma s.l.* and we, therefore, advocate for continued efforts to voucher and include additional species in future studies to better understand the diversity, distribution and boundaries of this unique radiation of Old World scincid lizards.

## GENUS *LYGOSOMA* HARDWICKE & GRAY, 1827: 228

*Type species: Lacerta serpens* Bloch, 1776 = *Anguis quadrupes* Linnaeus, 1766 (Smith (1935)) by monotypy.

*Podophis* Wiegmann, 1834: 11. Type species *Anguis quadrupes* Linnaeus, 1766 by monotypy.
*Eumeces* Günther, 1864b: 84. Part, not Eumeces Wiegmann, 1834.
*Riopa* Smith, 1935: 312. Part, not Riopa Gray, 1839.
*Mochlus* Mittleman, 1952: 9. Part, not *Mochlus* Günther, 1864a.
*Squamicilia* Mittleman, 1952: 9. Type species *Eumeces isodactylus* Günther, 1864b by original designation.

### *Diagnosis*

*Lygosoma* can be identified by the following combination of characters: (1) body size small to large (SVL 49–168 mm); (2) trunk moderately elongate to elongate (AGD 58–93% SVL); (3) digits short (FinIIILam 4–9, ToeIVLam 5–13); (4) MBSRC 25–38; (5) PVSRC 84–123; (6) lower eyelid scaly; (7) supranasal scales in contact medially or not in contact medially, usually fully or partially fused with nasals; (8) prefrontals not in contact medially; (9) frontoparietal single or paired; (10) parietals in contact medially posterior to interparietal; (11) enlarged nuchal scales present or absent; and (12) palatine bones with posteriomedially projecting processes, pterygoids emarginated along posterior edge.

### *Phylogenetic definition*

This genus comprises species that share a more recent common ancestor with *L. quadrupes* than with *Subdoluseps bowringii*, *Lamprolepis smaragdina*, *Mochlus sundevallii* or *Riopa punctata*.

### *Content*

*Lygosoma quadrupes*, *L. corpulentum* Smith, 1921, *L. isodactylum* (Günther, 1864b), *L. siamense* Siler, Heitz, Davis, Freitas, Aowphol, Termprrayoon & Grismer 2018 and *L. tabonorum* Heitz, Diesmos, Freitas, Ellsworth, Grismer, Aowphol, Brown & Siler 2016.

### *Comments*

The suggested common name for this genus is Southeast Asian Writhing Skinks. *Lygosoma* means 'writhing body' in Greek (*lygos* = writhe, *soma* = body). Linnaeus (1766) provided the earliest description of the type species of the genus, *Anguis quadrupes*, and, due to its extremely elongate body and diminutive legs, mistook it for a member of Serpentes (snakes). Ten years later,

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Bloch (1776) re-described the species as the lizard *Lacerta serpens* from two specimens, one of which (ZMB 1276) is a syntype of the species and the oldest herpetological specimen in the Zoological Museum of Berlin (Bauer & Günther, 2006). Later, Hardwicke & Gray (1827) described the genus *Lygosoma* for *Lacerta serpens*, mistakenly mentioning that the species was different from *Anguis quadrupes* and, consequently, the epithet *quadrupes* was not associated with the genus until *serpens* was synonymized with *quadrupes* by Smith (1935).

Species included in *Lygosoma* display considerable variation in gross body size and shape. The smallest species included currently in the genus is *L. siamense*, which has an adult SVL of 49–79 mm, compared to the largest species, *L. corpulentum*, with an adult SVL of up to 168 mm (although this measurement is only based on a single specimen). Additionally, species differ in the degree of trunk elongation, with species in the *L. quadrupes* species complex (*L quadrupes*, *L. siamense* and *L. tabonorum*) being more elongate (AGD/SVL = 62.0–93.3%) when compared with other species such as *L. corpulentum* (AGD/SVL = 57.7%). Additional phylogenetic studies of morphological diversity and body form evolution are needed for this group.

Due to the lack of tissue samples in museum collections, we were not able to sample a large number of species from Southeast Asia from the genus *Lygosoma*, including: *L. angeli* (Smith, 1937b), *L. bampfyldei* Bartlett, 1894, *L. boehmei* Ziegler, Schmitz, Heidrich, Vu & Nguyen, 2007, *L. haroldyoungi* (Taylor, 1962), *L. kinabatanganense* Grismer, Quah, Duzulkafly & Yambun, 2018, *L. koratense* Smith, 1917, *L. opisthorhodum* Werner, 1910, *L. peninsulare* Grismer, Quah, Duzulkafly & Yambun, 2018, *L. schneideri* Werner, 1900, *L. singha* (Taylor, 1950) and *L. veunsaiense* Geissler, Hartmann & Neang, 2012. To avoid introducing additional taxonomic instability from speculating on their phylogenetic affinities, we treat these species as *incertae sedis* and hope that future studies on the phylogenetics of this group will include samples of these taxa to elucidate their relationships to other species in *Lygosoma s.l.* We also did not include the species *L. siamense* in our phylogeny, because the only available sequence was a portion of the *16S* gene on GenBank, but this species was shown to be the sister taxon to the clade comprising *L. quadrupes* + *L. tabonorum* (Siler *et al.*, 2018) and so we consider it a member of *Lygosoma*.

## GENUS *MOCHLUS* GÜNTHER, 1864A: 308

*Type species: Mochlus punctulatus* Günther, 1864a = *Eumeces afer* Peters, 1854 (Barboza du Bocage, 1867) = *Eumeces sundevallii* (*Eumices* [sic] *sunderallii* [sic]) Smith, 1849 (Freitas *et al.*, 2018) by monotypy.

*Tiliqua* Burton, 1836: 62. Not *Tiliqua* Gray, 1825.
*Sepacontias* Günther, 1880: 235. Type species *Sepacontias modestus* Günther, 1880 = *Mochlus sundevallii* (Freitas *et al.*, 2018) by monotypy.
*Euprepes* [sic]: Vaillant, 1884: 169. Part, not *Euprepis* Wagler, 1830.
*Lygosoma* Boulenger, 1887: 209. Part, not *Lygosoma* Hardwick & Gray, 1827.
*Lepidothyris* Cope, 1892: 233. Type species *Tiliqua fernandi* Burton, 1836 by subsequent designation (Cope, 1900).
*Riopa* Smith, 1935: 312. Part, not *Riopa* Gray, 1839.

### *Diagnosis*

*Mochlus* can be identified by the following combination of characters: (1) body size medium to large (SVL 55–166 mm); (2) trunk moderately elongate to elongate (AGD 44–83% SVL); (3) digits short to long (FinIIILam 6–10, ToeIVLam 9–17); (4) MBSRC 24–38; (5) PVSRC 60–78; (6) lower eyelid scaly or with a transparent disc; (7) supranasal scales in contact medially, occasionally fused or partially fused with nasals; (8) prefrontals not in contact medially, occasionally fused with frontonasal; (9) frontoparietal paired; (10) parietals in contact medially posterior to interparietal; (11) enlarged nuchal scales present or absent; and (12) palatine bones with posteriomedially projecting processes, pterygoids rounded along posterior edge.

### *Phylogenetic definition*

This genus comprises species that share a more recent common ancestor with *M. sundevallii* than with *Riopa punctata*, *Subdoluseps bowringii*, *Lygosoma quadrupes* and *Lamprolepis smaragdina*.

### *Content*

*Mochlus sundevallii*, *M. brevicaudis* (Greer, Grandison & Barbault, 1985), *M. fernandi* (Burton, 1836), *M. guineensis* (Peters, 1879), *M. hinkeli* (Wagner, Böhme, Pauwels & Schmitz, 2009) and *M. striatus* (Hallowell, 1854).

### *Comments*

The suggested common name for this genus is African Supple Skinks. Studies of other African–Southeast Asian radiations have suggested that African species comprise a single radiation on the continent (Mausfeld *et al.*, 2000; Fabre *et al.*, 2012; Oliver *et al.*, 2015; Karin *et al.*, 2016). However, without greater taxonomic sampling of African species, we cannot

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corroborate this hypothesis for African species in *Lygosoma s.l.* The majority of *Lygosoma s.l.* species in Africa lack tissue samples in museum collections and have never been included in phylogenetic studies. Therefore, we are unable to include them definitively in the genus *Mochlus* at this time. These species are: *M. grandisonianus* Lanza & Carfi, 1966, *M. laeviceps* (Peters, 1874), *M. lanceolatus* (Broadley, 1994), *M. mabuiiformis* (Loveridge, 1935), *M. mafianus* (Broadley, 1994), *M. mocquardi* (Chabanaud, 1917), *M. paedocarinatus* Lanza & Carfi, 1968, *M. pembanus* (Boettger, 1913), *M. productus* (Boulenger, 1909), *M. simonettai* (Lanza, 1979), *M. somalicus* (Parker, 1942), *M. tanae* (Loveridge, 1935) and *M. vinciguerrae* (Parker, 1932). Two of these species, *M. pembanus* and *M. tanae*, were included in our morphological dataset and appeared to occupy a similar area of morpho space as other species in *Mochlus*, but given the large amount of overlap of clades in morpho space, their morphological affinities are not strong evidence alone for their placement in *Mochlus*. Alternatively, Greer (1977: 527) suggested that *M. tanae* and another African species, *M. mabuiiformis*, were more closely related to Southeast Asian species than to other African species based on a combination of discrete character traits: open secondary palate, lower eyelid with a transparent disc, presence of pterygoid teeth, paired frontoparietal scales, distinct supranasal scales and pentadactly digits. However, combinations of these states are shared across all *Lygosoma s.l.* and are not unique to a single clade. Some of these characters may represent convergence instead of phylogenetic relatedness. Additionally, Perret & Wuest (1983) examined the scale microstructure of *M. guineensis*, *M. mabuiiformis* and *M. fernandi* and found that they were all very similar, which may suggest that *M. mabuiiformis* is more closely related to African species than Asian species in *Lygosoma s.l.* Therefore, biogeography and morphology do not help us resolve the placement of these 13 African species and so we treat them as *incertae sedis* and hope that future studies will elucidate their phylogenetic position. Two African species, *M. hinkeli* and *M. striatus*, have been included in a recent phylogenetic study (Wagner *et al.*, 2009) and were shown to form a clade with *M. fernandi*. Therefore, we treat these species as members of *Mochlus*.

## GENUS *RIOPA* GRAY, 1839: 332

*Type species: Riopa punctata* = *Lacerta punctata* Linnaeus, 1758 (Gray, 1845) by subsequent designation (Smith, 1935).

*Chiamela* Gray, 1839: 332. Type species *Chiamela lineata* Gray, 1839 by subsequent designation (Gray, 1845).

*Hagria* Gray, 1839: 333. Type species *Hagria vosmaerii* Gray, 1839 by monotypy.

*Campsodactylus* Dumeríl & Bibron, 1839: 761. Type species *Campsodactylus lamarrei* Dumeríl & Bibron, 1839 = *Hagria vosmaerii* Gray, 1839 by monotypy.

*Sphenosoma* Fitzinger, 1843: 23. Type species *Eumeces punctatus* Weigmann, 1834 = *Lacerta punctata* Linnaeus, 1758 by original designation.

*Eumeces* Günther, 1864b: 84. Part, not *Eumeces* Wiegmann, 1834.

*Lygosoma* Boulenger, 1887: 209. Part, not *Lygosoma* Hardwicke & Gray, 1827.

### *Diagnosis*

*Riopa* can be identified by the following combination of characters: (1) body size small to medium (SVL 35–96 mm); (2) trunk moderately elongate (AGD 55–75% SVL); (3) digits short to long (FinIIILam 5–11, ToeIVLam 6–16); (4) MBSRC 19–30; (5) PVSRC 70–115; (6) lower eyelid scaly or with a transparent disc; (7) supranasal scales in contact medially, occasionally barely touching; (8) prefrontals not in contact medially; (9) frontoparietal single or paired; (10) parietals in contact behind interparietal; (11) enlarged nuchal scales usually present, occasionally absent; and (12) palatine bones with posteriomedially projecting processes, pterygoids emarginated along posterior edge or occasionally rounded.

### *Phylogenetic definition*

This genus comprises the species that share a more recent common ancestor with *Riopa punctata* than with *Mochlus sundevallii*, *Subdoluseps bowringii*, *Lygosoma quadrupes* and *Lamprolepis smaragdina*.

### *Content*

*Riopa punctata*, *R. albopunctata* Gray, 1846, *R. anguina* Theobald, 1867, *R. goaensis* Sharma, 1976, *R. guentheri* (Peters, 1879), *R. lineata* (Gray, 1839), *R. lineolata* Stoliczka, 1870, *R. popae* Shreve, 1940 and *R. vosmaerii* (Gray, 1839).

### *Comments*

The suggested common name for this clade is Asian Gracile Skinks. The species *Lacerta punctata*, described by Linnaeus (1758), referred to an illustration by Seba (1735: pl. II, fig. IX) and two specimens housed in the Swedish Museum of Natural History (NRM 135). However, it was later discovered that the illustration and the specimens represented two different species. Although the majority of publications used *Lacerta punctata* to refer to the elongate Indian species now



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recognized as *Riopa punctata*, several publications used it to refer to the species now recognized as *Trachylepis homalocephala*. This led to confusion with the identity of *Lacerta punctata*, as the name was applied to the type species of two separate genera – *Riopa* and *Euprepis* Wagler, 1830 (reviewed in Bauer, 2003). Bauer (2003) fixed the name *Lacerta punctata* to Seba's drawings, choosing the illustration of the male as the lectotype.

### GENUS *SUBDOLUSEPS* FREITAS, DATTA-ROY, KARANTH, GRISMER & SILER, GEN. NOV.

*Type species: Eumeces bowringii* Günther, 1864b.

*Eumeces* Günther, 1864b: 84. Part, not *Eumeces* Wiegmann, 1834.
*Lygosoma* Boulenger, 1887: 209. Part, not *Lygosoma* Hardwicke & Gray, 1827.
*Riopa* Smith, 1935: 312. Part, not *Riopa* Gray, 1839.
*Mochlus* Mittleman, 1952: 9. Part, not *Mochlus* Günther, 1864a.

*LSID: urn:lsid:zoobank.org:act:A5D46B92-9213-4CCA-84A2-BCC025B87865*

#### *Diagnosis*

*Subdoluseps* can be identified by the following combination of characters: (1) body size small (SVL 35–70 mm); (2) trunk moderately elongate (AGD 42–69% SVL); (3) digits medium to long (FinIIILam 7–12, ToeIVLam 11–16); (4) MBSRC 26–34; (5) PVSRC 50–69; (6) lower eyelid scaly or with a transparent disc; (7) supranasal scales in contact medially or not in contact medially; (8) prefrontals not in contact medially; (9) frontoparietal single or paired; (10) parietals in contact behind interparietal; (11) enlarged nuchal scales present or absent; and (12) palatine bones with posteriomedially projecting processes, pterygoids rounded along posterior edge.

#### *Phylogenetic definition*

This genus comprises the species that share a more recent common ancestor with *S. bowringii* than with *Riopa punctata*, *Mochlus sundevallii*, *Lygosoma quadrupes* and *Lamprolepis smaragdina*.

#### *Content*

*Subdoluseps bowringii, comb. nov.*, *S. frontoparietalis* (Taylor, 1962), comb. nov., *S. herberti* (Smith, 1916), comb. nov., *S. pruthi* (Sharma, 1977), comb. nov. and *S. samajaya* (Karin, Freitas, Shonleben, Bauer & Das, 2018), comb. nov.

#### *Etymology*

From the Latin word '*subdolus*', meaning 'crafty or slippery' and the Greek word '*seps*', a snake-like animal and has been used previously in genus names for skinks. This name describes the agility of these skinks in the wild. The name is masculine. The suggested common name for this genus is Asian Agile Skinks.

## CONCLUSIONS

Having a stable taxonomy to communicate about biodiversity is crucial for both scientific study and conservation management (Mayr, 1976; Felsenstein, 1985; Winston, 1999; Wheeler *et al.*, 2004; Kaiser *et al.*, 2013; Groves *et al.*, 2017; IUCN-SSC Species Conservation Planning Sub-Committee, 2017). As molecular methods and phylogenetic analyses have improved, phylogenetic studies have contributed greatly to our growing understanding of global skink biodiversity. Over the last decade alone, five new scincid genera have been described (*Pinoyscincus* and *Tythoscincus* [Linkem *et al.*, 2011], *Toenayar* [Karin *et al.*, 2016], *Brachyseps* and *Flexiseps* [Erens *et al.*, 2017]) to better reflect the evolutionary history of the family. Given that species in *Lygosoma s.l.* are distributed across six of the 25 global biodiversity hotspots (Myers *et al.*, 2000), classifying the biodiversity in this group is critical to discussions of skink diversity in these imperilled regions. Here, using the most comprehensive taxonomic sampling available, we have employed concatenated and coalescent-based phylogenetic analyses and multivariate morphological analyses to illustrate the need for a revised classification of *Lygosoma s.l.* Therefore, we modify the taxonomy of *Lygosoma s.l.* to reflect our phylogenetic results, splitting the group into four genera: *Lygosoma*, *Mochlus*, *Riopa* and *Subdoluseps* gen. nov. Our revised classification can be used to more accurately investigate lygosomine skink biodiversity including diversification rates and biogeographic and trait evolution patterns within and between clades in *Lygosoma s.l.*

## ACKNOWLEDGEMENTS

For tissue and specimen loans (Tables S1 and S2), we thank the following people and institutions: A. Aowphol (ZMKU), A. Bauer and B. Karin (Villanova University), R. Brown and L. Welton (KU), D. Cannatella and T. Laduc (TNHC), A. Diesmos (PNM), E. Greenbaum (UTEP), A. Resetar (FMNH) and L. Scheinberg and J. Vindem (CAS). We are grateful to T. Yuri, M. Labonte and M. Penrod at SNOMNH for help



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with molecular data collection and B. Karin at MVZ, E. Ellsworth at SNOMNH and S. Pal at BNHS for help with specimen measurements. We thank J. Oaks for discussion of methods and help with *BEAST analyses and A. Bauer for reviewing our taxonomic history section and genus synonymies. This research was supported by a National Science Foundation (NSF) grant (DEB 074391) to Rafe M. Brown, travel awards from the Department of Biology and the Graduate Student Senate at the University of Oklahoma, the California Academy of Sciences Charles Stearns Memorial travel grant and a Fulbright Fellowship to ESF, the a Science and Engineering Research Board (SERB) National Postdoctoral fellowship (PDF/2017/000476 entry number 15225; http://dx.doi.org/10.13039/501100001843) to ADR and NSF grants (IOS 1353683 and DEB 1657648) to CDS.

## REFERENCES

**Akaike H. 1974.** A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19:** 716–723.

**Aljanabi SM**, **Martinez I. 1997.** Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Research* **25:** 4692–4693.

**Barbour T. 1912.** A contribution to the zoogeography of the East Indian islands. *Memoirs of the Museum of Comparative Zoology at Harvard College* **44:** 5–203, pl. 1–8.

**Barbour T**, **Loveridge A. 1928.** A comparative study of the herpetological faunae of the Uluguru and Usambara Mountains, Tanganyika Territory with descriptions of new species. *Memoirs of the Museum of Comparative Zoology at Harvard College* **50:** 87–265, pl. 1–4.

**Barley AJ**, **White J**, **Diesmos AC**, **Brown RM. 2013.** The challenge of species delimitation at the extremes: diversification without morphological change in Philippine sun skinks. *Evolution* **67:** 3556–3572.

**Barley AJ**, **Datta-Roy A**, **Karanth KP**, **Brown RM. 2015a.** Sun skink diversification across the Indian–Southeast Asian biogeographical interface. *Journal of Biogeography* **42:** 292–304.

**Barley AJ**, **Monnahan PJ**, **Thomson RC**, **Grismer LL**, **Brown RM. 2015b.** Sun skink landscape genomics: assessing the roles of micro-evolutionary processes in shaping genetic and phenotypic diversity across a heterogenous and fragmented landscape. *Molecular Ecology* **24:** 1696–1712.

**Bartlett E. 1894.** The crocodiles and lizards of Borneo in the Sarawak Museum with descriptions of supposed new species, and the variation of colours in the several species during life. *Journal of the Straits Branch of the Royal Asiatic Society* **28:** 73–97.

**Bauer AM. 2003.** On the identity of *Lacerta punctata* Linnaeus 1758, the type species of the genus *Euprepis* Wagler 1830, and the generic assignment of Afro-Malagasy skinks. *African Journal of Herpetology* **52:** 1–7.

**Bauer AM**, **Günther R. 2006.** A syntype of *Lacerta serpens* Bloch 1776 (Reptilia: Squamata: Scincidae): the oldest type specimen in the founding collection of the Zoological Museum of Berlin. *Bibliotheca Herpetologica* **6:** 17–25.

**Barboza du Bocage JV. 1867.** Segunda lista dos reptis das possesões Portuguezas d'Africa Occidental que existem no Museu de Lisboa. *Jornal de Sciencias Mathematicas Physicas e Naturaes* **1:** 217–228.

**Barboza du Bocage JV. 1870.** Description d'un saurien nouveau de l'Afrique occidentale. *Jornal de Sciencias Mathematicas Physicas e Naturaes* **3:** 66–68.

**Bloch ME. 1776.** Beschreibung der Schleicheidexe, *Lacerta serpens*. *Beschäftigungen der Berlinischen Gesellschaft Naturforschender Freunde* **2:** 28–34, pl. II.

**Boettger O. 1913.** Reptilien und Amphibien von Madagascar, den Inseln und dem Festland Ostafrikas. (Sammlung Voeltzkow 1889–1885 und 1903–1905). In: Voeltzkow A, ed. *Reise in Ostafrika in den Jahren 1903–1905 mit Mitteln der Hermann und Elise geb. Heckmann Wentzel-Stiftung Ausgeführt*. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung Nägele & Dr. Sproesser, 269–375, pl. 23–30.

**Bouckaert R**, **Heled J**, **Kühnert D**, **Vaughan T**, **Wu CH**, **Xie D**, **Suchard MA**, **Rambaut A**, **Drummond AJ. 2014.** BEAST 2: a software platform for Bayesian evolutionary analysis. *PLOS Computational Biology* **10:** e1003537.

**Boulenger GA. 1887.** *Catalogue of the lizards in the British Museum (Natural History). Volume III: Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae. Chamaelontidae, 2nd edn*. London: Taylor and Francis.

**Boulenger GA. 1909.** List of reptiles collected by Capt. G. Ferrari at Jumbo, Lower Juba. *Annali del Museo Civico di Storia Naturale di Genova* **4:** 308–315.

**Brandley MC**, **Schmitz A**, **Reeder TW. 2005.** Partitioned Bayesian analyses, partition choice, and the phylogenetic relationships of scincid lizards. *Systematic Biology* **54:** 373–390.

**Brandley MC**, **Ota H**, **Hikida T**, **Montes de Oca AN**, **Fería-Ortíz M**, **Guo X**, **Wang Y. 2012.** The phylogenetic systematics of blue-tailed skinks (*Plestiodon*) and the family Scincidae. *Zoological Journal of the Linnean Society* **165:** 163–189.

**Brandley MC**, **Bragg JC**, **Singhal S**, **Chaple DG**, **Jennings CK**, **Lemmon AR**, **Lemmon EM**, **Thompson MB**, **Moritz C. 2015.** Evaluating the performance of anchored hybrid enrichment at the tips of the tree of life: a phylogenetic analysis of Australian *Eugongylus* group scincid lizards. *BMC Evolutionary Biology* **15:** 1–14.

**Broadley DG. 1962.** A tangled group of writhing-skinks (*Riopa*). *Journal of the Herpetological Association of Rhodesia* **17:** 3–4.

**Broadley DG. 1966.** A review of the *Riopa sundevalli* group (Sauria: Scincidae) in southern Africa. *Arnoldia (Rhodesia) Series of Miscellaneous Publications National Museums of Southern Rhodesia* **2:** 1–7.

**Broadley DG. 1994.** A review of *Lygosoma* Hardwicke & Gray 1827 (Reptilia, Scincidae) on the East African coast, with the description of a new species. *Tropical Zoology* **7:** 217–222.

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**Brown JM**, **Lemmon AR. 2007.** The importance of data partitioning and the utility of Bayes factors in Bayesian phylogenetics. *Systematic Biology* **56:** 643–655.

**Bryson Jr RW**, **Linkem CW**, **Pavón-Vásquez CJ**, **Nieto-Montes de Oca A**, **Klicka J**, **McCormack JE. 2017.** A phylogenomic perspective on the biogeography of skinks in the *Plestiodon brevistrostris* group inferred from target enrichment of ultraconserved elements. *Journal of Biogeography* **44:** 2033–2044.

**Burton E. 1836.** A saurian reptile of the family Scincidae and the genus *Tiliqua* Gray. *Proceedings of the Zoological Society of London* **4:** 62.

**Busschau T**, **Conradie W**, **Jordaan A**, **Daniels SR. 2017.** Unmasking evolutionary diversity among two closely related South African legless skink species (Acontinae: *Acontias*) using molecular data. *Zoology* **121:** 72–82.

**Cain AJ. 1956.** The genus in evolutionary taxonomy. *Systematic Zoology* **5:** 97–109.

**Carranza S**, **Arnold EN. 2003.** Investigating the origins of transoceanic distributions: mtDNA shows *Mabuya* lizards (Reptilia, Scincidae) crossed the Atlantic twice. *Systematics and Biodiversity* **2:** 275–282.

**Chabanaud MP. 1917.** Revision de quelques reptiles d'Afrique et description de trois espéces nouvelles. *Bulletin du Muséum National d'Histoire Naturelle* **23:** 442–453.

**Chapple DG**, **Bell TB**, **Chapple SNJ**, **Miller KA**, **Daugherty CH**, **Patterson GB. 2011.** Phylogeography and taxonomic revision of the New Zealand cryptic skink (*Oligosoma insconspicuum*; Reptilia: Scincidae) species complex. *Zootaxa* **2782:** 1–33.

**Cocteau JT. 1836.** *Études sur les scincoïdes*. Paris: Terzuolo.

**Cogger HG. 1975.** *Reptiles and amphibians of Australia*. Sydney: Reed.

**Cogger HG. 2014.** *Reptiles and amphibians of Australia, 7th edn*. Collingwood: CSIRO.

**Conradie W**, **Busschau T**, **Edwards S. 2018.** Two new species of *Acontias* (Acontinae, Scincidae) from the Mpumalanga Highveld escarpment of South Africa. *Zootaxa* **4429:** 89–106.

**Cope ED. 1868.** Observations on reptiles of the Old World. Art. II. *Proceedings of the Academy of Natural Scienes of Philadelphia* **20:** 316–323.

**Cope ED. 1892.** On degenerate types of scapular and pelvic arches in the Lacertilia. *Journal of Morphology* **7:** 223–244, pl. XIII.

**Cope ED. 1900.** The crocodilians, lizards, and snakes of North America. *Annual Report of the United States National Museum* **1898:** 155–1270.

**Crawford NG**, **Faircloth BC**, **McCormack JE**, **Brumfield RT**, **Winker K**, **Glenn TC. 2012.** More than 1000 ultraconserved elements provide evidence that turtles are the sister group of archosaurs. *Biology Letters* **8:** 783–786.

**Daniels SR**, **Heideman NJL**, **Hendricks MGJ. 2009.** Examination of evolutionary relationships in the Cape fossorial skink species complex (Acontinae: *Acontias meleagris meleagris*) reveals the presence of five cryptic lineages. *Zoologica Scripta* **38:** 449–463.

**Das I. 2010.** *A fieldguide to the reptiles of Southeast Asia*. London: New Holland.

**Darriba D**, **Taboada GL**, **Doallo R**, **Posada D. 2012.** JModelTest2: more models, new heuristics and parallel computing. *Nature Methods* **9:** 772.

**Datta-Roy A**, **Singh M**, **Srinivasulu C**, **Karanth KP. 2012.** Phylogeny of the Asian *Eutropis* (Squamata: Scincidae) reveals an into India endemic Indian radiation. *Molecular Phylogenetics and Evolution* **63:** 817–824.

**Datta-Roy A**, **Singh M**, **Karanth KP. 2014.** Phylogeny of endemic skinks of the genus *Lygosoma* (Squamata: Scincidae) from India suggests an *in situ* radiation. *Journal of Genetics* **93:** 163–167.

**Datta-Roy A**, **Deepak V**, **Sidharthan C**, **Barley AJ**, **Karanth KP. 2015.** An addition to the endemic Indian radiation of *Eustropis dissimilis* Halowell (Squamata: Scincidae). *Zootaxa* **4027:** 145–150.

**Daudin FM. 1802.** *Histoire naturelle, générale et particulière, des reptiles: ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs sociétés savantes. Tome quatriéme.* Paris: F. Dufart.

**Davis DR**, **Feller KD**, **Brown RM**, **Siler CD. 2014.** Evaluating the diversity of Philippine slender skinks of the *Brachymeles bonitae* complex (Reptilia: Squamata: Scincidae): redescription of *B. tridactylus* and description of two new species. *Journal of Herpetology* **48:** 480–494.

**Davis DR**, **Geheber AD**, **Watters JL**, **Penrod ML**, **Feller KD**, **Ashford A**, **Kouri J**, **Nguyen D**, **Shauberger K**, **Sheatsley K**, **Winfrey C**, **Wong R**, **Sanguila MB**, **Brown RM**, **Siler CD. 2016.** Additions to Philippine slender skinks of the *Brachymeles bonitae* complex (Reptilia: Squamata: Scincidae) III: a new species from Tablas Island. *Zootaxa* **4132:** 30–43.

**Degnan JH**, **Rosenberg NA. 2009.** Gene tree discordance, phylogenetic inference and the multispecies coalescent. *Trends in Ecology and Evolution* **24:** 332–340.

**Drummond AJ**, **Bouckaert RR. 2015.** *Bayesian evolutionary analysis with BEAST*. Cambridge: Cambridge University Press.

**Drummond AJ**, **Ho SYW**, **Phillips MJ**, **Rambaut A. 2006.** Relaxed phylogenetics and dating with confidence. *PLoS Biology* **4:** e88.

**Duméril AMC**, **Bibron G. 1839.** *Erpétologie générale ou histoire naturelle compléte des reptiles. Tome cinquiéme*. Paris: Roret.

**Edgar RC. 2004.** MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32:** 1792–1797.

**Ekblom R**, **Galindo J. 2011.** Applications of next generation sequencing in molecular ecology of non-model organisms. *Heredity* **107:** 1–15.

**Erens J**, **Miralles A**, **Glaw F**, **Chatrou LW**, **Vences M. 2017.** Extended molecular phylogenetics and revised systematics of Malagassy scincine lizards. *Molecular Phylogenetics and Evolution* **107:** 466–472.

**Fabre PH**, **Irestedt M**, **Fjeldså J**, **Bristol R**, **Groombridge JJ**, **Irham M**, **Jønsson KA. 2012.** Dynamic colonization exchanges between continents and islands drive diversification in paradise-flycatchers (*Terpsiphone*, Monarchidae). *Journal of Biogeography* **39:** 1900–1918.



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**Fan W**, **Wu R**, **Chen MH**, **Lewis PO. 2011.** Choosing among partition models in Bayesian phylogenetics. *Molecular Biology and Evolution* **28:** 523–532.

**Felsenstein J. 1985.** Phylogenies and the comparative method. *American Naturalist* **125:** 1–15.

**FitzSimons VF. 1943.** *The lizards of South Africa*. Johannesburg: Voortrekerpers.

**Fitzinger LJ. 1826.** *Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften. Nebst einer Verwantschafts-Tafel und einem Verzeichnisse der Reptilien – Sammlung des K.K. Zoologischen Museum's zu Wien*. Vienna: J. G. Heubner.

**Fitzinger LJ. 1842.** Der smaragdgrüne Glanzscink. In: Trietschke F, ed. *Naturhistorischer Bildersaal des Thierreiches Dritter Band.* Pesth [Budapest]: C. A. Hartleben, 139, pl. ccxlvii.

**Fitzinger LJ. 1843.** *Systema reptilium. Fasciculus primus Amblyglossae*. Vienna: Braumüller & Seidel.

**Freitas ES**, **Bauer AM**, **Siler CD**, **Broadley DG**, **Jackman TR. 2018.** Phylogenetic and morphological investigation of the *Mochlus afer-sundevallii* species complex (Squamata: Scincidae) across the arid corridor of sub-Saharan Africa. *Molecular Phylogenetics and Evolution* **127:** 280–287.

**Fry BG**, **Vidal N**, **Norman JA**, **Vonk FJ**, **Scheib H**, **Ramjan SFR**, **Kuruppu S**, **Fung K**, **Hedges SB**, **Richardson MK**, **Hodgson WC**, **Ignjatovic V**, **Summerhayes R**, **Kochva E. 2006.** Early evolution of the venom system in lizards and snakes. *Nature (London)* **439:** 584–588.

**Geheber AD**, **Davis DR**, **Watters JL**, **Penrod ML**, **Feller KD**, **Davey CS**, **Ellsworth ED**, **Flanagan RL**, **Heitz BB**, **Moore T**, **Nguyen MDC**, **Roberts A**, **Sutton J**, **Sanguila MB**, **Linkem CW**, **Brown RM**, **Siler CD. 2016.** Additions to Philippine slender skinks of the *Brachymeles bonitae* complex (Reptilia: Squamata: Scincidae) I: a new species from Lubang Island. *Zootaxa* **4132:** 1–14.

**Geissler P**, **Nguyen TQ**, **Phung TM**, **van Devender RW**, **Hartmann T**, **Farkas B**, **Ziegler T**, **Böhme W. 2011.** A review of Indochinese skinks of the genus *Lygosoma* Hardwicke & Gray, 1827 (Squamata: Scincidae), with natural history notes and an identification key. *Biologia* **66:** 1159–1176.

**Geissler P**, **Hartmann T**, **Neang T. 2012.** A new species of the genus *Lygosoma* Hardwicke & Gray, 1827 (Squamata: Scincidae) from northeastern Cambodia, with an updated identification key to the genus *Lygosoma* in mainland Southeast Asia. *Zootaxa* **3190:** 56–68.

**Glauert L. 1960.** The family Scincidae in Western Australia. Part 2: the genus *Lygosoma*. *Western Australian Naturalist* **7:** 81–99.

**Gray JE. 1825.** A synopsis of the genera of reptiles and amphibia, with a description of some new species. *Annals of Philosophy* **10:** 193–217.

**Gray JE. 1831.** A synopsis of the species of the class Reptilia. In: Cuvier G, Griffith E, eds. *The animal kingdom arranged in conformity with its organization with additional descriptions of all the species hitherto named, and of many not before noticed*, *Vol.* **9**. London: Whittaker, Treacher and Co.

**Gray JE. 1839.** Catalogue of the slender-tongued saurians with descriptions of many new genera and species. *Annals of Natural History or, Magazine of Zoology, Botany and Geology* **2:** 331–337.

**Gray JE. 1845.** *Catalogue of the specimens of lizards in the collection of the British Museum.* London: Edward Newman.

**Gray JE. 1846.** Descriptions of some new species of Indian lizards. *Annals and Magazine of Natural History including Zoology, Botany, and Geology* **18:** 429–430.

**Greer AE. 1970a.** A subfamilial classification of scincid lizards. *Bulletin of the Museum of Comparative Zoology at Harvard College* **139:** 151–183.

**Greer AE. 1970b.** The relationships of the skinks referred to the genus *Dasia*. *Breviora* **348:** 1–30.

**Greer AE. 1974.** The generic relationships of the scincid lizard genus *Leiolopisma* and its relatives. *Australian Journal of Zoology, Supplementary Series* **31:** 1–67.

**Greer AE. 1977.** The systematics and evolutionary relationships of the scincid lizard genus *Lygosoma*. *Journal of Natural History* **11:** 515–540.

**Greer AE**, **Grandison AGC**, **Barbault R. 1985.** A new species of *Lygosoma* (Lacertilia: Scincidae) from West Africa, with comments on its biology. *Journal of Herpetology* **19:** 365–372.

**Grismer LL**, **Ismail LB**, **Awang MT**, **Rizal SA**, **Ahmad AB. 2014.** A new species of lowland skink (genus *Lipinia* Gray, 1845) from northeastern peninsular Malaysia. *Zootaxa* **3821:** 457–464.

**Grismer LL**, **Wood Jr PL**, **Quah ESH**, **Anuar S**, **Ngadi EB**, **Izam NAM**, **Ahmad N. 2018a.** Systematics, ecomorphology, cryptic speciation and biogeography of the lizard genus *Tytthoscincus* Linkem, Diesmos & Brown (Squamata: Scincindae) from the sky-island archipelago of Peninsular Malaysia. *Zoological Journal of the Linnean Society* **183:** 635–671.

**Grismer LL**, **Quah ESH**, **Duzulkafly Z**, **Yambun P. 2018b.** On the taxonomy of *Lygosoma bampfyldei* Bartlett, 1895 (Squamata: Scincidae) with descriptions of new species from Borneo and Peninsular Malaysia and the resurrection of *Lygosoma schneideri* Werner 1900. *Zootaxa* **4438:** 528–550.

**Groth JG**, **Barrowclough GF. 1999.** Basal divergences in birds and the utility of the nuclear RAG-1 gene. *Molecular Phylogenetics and Evolution* **12:** 115–123.

**Groves CP**, **Cotterill FPD**, **Gippoliti S**, **Rabovsky J**, **Roos C**, **Taylor PJ**, **Zinner D. 2017.** Species definitions and conservation: a review and case studies from African mammals. *Conservation Genetics* **18:** 1247–1256.

**Günther AG. 1864a.** Report on a collection of reptiles and fishes made by Dr Kirk in the Zambesi and Nyassa regions. *Proceedings of the Zoological Society of London* **1864:** 305–314.

**Günther AG. 1864b.** *The reptiles of British India*. London: Robert Hardwicke for the Ray Society.

**Günther AG. 1880.** Description of new species of reptiles from Eastern Africa. *Annals and Magazine of Natural History including Zoology, Botany, and Geology, ser. 5* **6:** 234–238.

**Hallowell E. 1854.** Remarks on the geographical distribution of reptiles, with descriptions of several species supposed to

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be new, and corrections of former papers. *Proceedings of the Academy of Natural Sciences of Philadelphia* **7:** 98–105.

**Hardwicke T**, **Gray JE. 1827.** A synopsis of the species of saurian reptiles, collected in India by Major-General Hardwicke. *Zoological Journal* **3:** 213–229.

**Hedges SB. 2014.** The high-level classification of skinks (Reptilia, Squamata, Scincomorpha). *Zootaxa* **3765:** 317–338.

**Hedges SB**, **Conn CE. 2012.** A new skink fauna from Caribbean islands (Squamata, Mabuyidae, Mabuyinae). *Zootaxa* **3288:** 1–244.

**Heideman NJL**, **Maulcahy DG**, **Sites Jr JW**, **Hendricks MGJ**, **Daniels SR. 2011.** Cryptic diversity and morphological convergence in threatened species of fossorial skinks in the genus *Scelotes* (Squamata: Scincidae) from the Western Cape Coast of South Africa: implications for species boundaries, digit reduction and conservation. *Molecular Phylogenetics and Evolution* **61:** 823–833.

**Heitz BB**, **Diesmos AC**, **Freitas ES**, **Ellsworth ED**, **Grismer LL**, **Aowphol A**, **Brown RM**, **Siler CD. 2016.** A new supple skink, genus *Lygosoma* (Reptilia: Squamata: Scincidae), from the western Philippines. *Herpetologica* **72:** 352–361.

**Heled J**, **Drummond AJ. 2010.** Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution* **27:** 570–580.

**Hill MO**, **Smith AJE. 1976.** Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon* **25:** 249–255.

**Hora SL. 1927.** Notes on lizards in the Indian museum. III. On the unnamed collection of lizards of the family Scincidae. *Records of the Indian Museum* **29:** 1–6.

**Honda M**, **Ota H**, **Kobayashi M**, **Nabhitabhata J**, **Yong HS**, **Hikida T. 2000.** Phylogenetic relationships, character evolution and biogeography of the subfamily Lygosominae (Reptilia: Scincidae) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **15:** 452–461.

**Honda M**, **Ota H**, **Köhler G**, **Ineich I**, **Chirio L**, **Chen SL**, **Hikida T. 2003.** Phylogeny of the lizard subfamily Lygosominae (Reptilia: Scincidae), with special reference to the origin of New World taxa. *Genes and Genetic Systems* **78:** 71–80.

**Hovmöller R**, **Knowles LL**, **Kubatko LS. 2013.** Effects of missing data on species tree estimation under the coalescent. *Molecular Phylogenetics and Evolution* **69:** 1057–1062.

**Huelsenbeck JP**, **Rannala B. 2004.** Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Systematic Biology* **53:** 904–913.

**Inger RF. 1958.** Comments on the definition of genera. *Evolution* **12:** 370–384.

**IUCN-SSC Species Conservation Planning Sub-Committee**. **2017.** *Guidelines for species conservation planning, v.1.0*. Gland: International Union for Conservation of Nature.

**Jombart T. 2008.** Adegenet: an R package for the multivariate analysis of genetic markers. *Bioinformatics* **24:** 1403–1405.

**Jombart T**, **Devillard S**, **Balloux F. 2010.** Discriminant analysis of principal components. *BMC Genetics* **11:** 1–15.

**Kaiser H**, **Crother BI**, **Kelly CMR**, **Luiselli L**, **O'Shea M**, **Ota H**, **Passos P**, **Schleip WD**, **Wüster W. 2013.** Best practices: in the 21st century, taxonomic decisions in herpetology are acceptable only when supported by a body of evidence and published via peer-review. *Herpetological Review* **44:** 8–23.

**Karin BR**, **Metallinou M**, **Weinell JL**, **Jackman TR**, **Bauer AM. 2016.** Resolving the higher order phylogenetic relationships of the circumtropical *Mabuya* group (Squamata: Scincidae): an out-of-Asia diversification. *Molecular Phylogenetics and Evolution* **102:** 220–232.

**Karin BR**, **Freitas ES**, **Shonlebin S**, **Grismer LL**, **Bauer AM**, **Das I. 2018.** Unrealized diversity in an urban rainforest: a new species of *Lygosoma* (Squamata: Scincidae) from western Sarawak, Malaysia (Borneo). *Zootaxa* **4370:** 345–362.

**Kass RE**, **Raftery AE. 1995.** Bayes factors. *Journal of the American Statistical Association* **90:** 773–795.

**Kay GM**, **Keogh JS. 2012.** Molecular phylogeny and morphological revision of the *Ctenotus labillardieri* (Reptilia: Squamata: Scincidae) species group and a new species of immediate conservation concern in the southwestern Australian biodiversity hotspot. *Zootaxa* **3390:** 1–18.

**Kennedy AM**, **Marias J**, **Bauer AM**, **Lewis PJ**, **Thies ML. 2012.** Effect of fire on the herpetofauna of the Koanaka Hills, Ngamiland, Botswana. *Check List* **8:** 666–674.

**Kingman JFC. 1982.** On the genealogy of large populations. *Journal of Applied Probability* **19:** 27–43.

**Klein ER**, **Harris RB**, **Fisher RN**, **Reeder TW. 2016.** Biogeographical history and coalescent species delimitation of Pacific Island skinks (Squamata: Scincidae: *Emoia cyanura* species group). *Journal of Biogeography* **43:** 1917–1929.

**Lambert SM**, **Reeder TW**, **Wiens JJ. 2015.** When do species-tree and concatenated estimates disagree? An empirical analysis with higher-level scincid lizard phylogeny. *Molecular Phylogenetics and Evolution* **82:** 146–155.

**Lanza B. 1979.** *Lygosoma simonettai*, a new black-headed skink from Somalia (Reptilia Scincidae). *Monitore Zoologico Italiano* Supplemento **12:** 25–32.

**Lanza B**, **Carfí S. 1966.** Note su alcuni Scincidae della Somalia e descrizione di una nuova specie di *Mochlus* (Reptilia Squamata). *Monitore Zoologico Italiano* Supplemento **1:** 34–43.

**Lanza B**, **Carfí S. 1968.** Gli scincidi della Somalia (Reptilia, Squamata). *Monitore Zoologico Italiano* Supplemento **2:** 207–260.

**Laurent RF**, **Gans C. 1965.** Lizards. In: Gans C, Laurent RF, Pandit H, eds. Notes on a herpetological collection from the Somali Republic. *Musée Royal de l'Afrique Centrale, Tervuren, Belgique: Annales – Serie in 8° – Sciences Zoologiques, Vol.* **134**: 1–93, 10 pl.

**Leaché AD**, **Reeder TW. 2002.** Molecular systematics of the Eastern Fence Lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. *Systematic Biology* **51:** 44–68.

**Linkem CW**, **Hesed KM**, **Diesmos AC**, **Brown RM. 2010.** Species boundaries and cryptic lineage diversity in a

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Philippine forest skink complex (Reptilia; Squamata; Scincidae: Lygosominae). *Molecular Phylogenetics and Evolution* **56:** 572–585.

**Linkem CW**, **Diesmos AC**, **Brown RM. 2011.** Molecular systematics of the Philippine forest skinks: testing morphological hypotheses of interspecific relationships. *Zoological Journal of the Linnean Society* **163:** 1217–1243.

**Linkem CW**, **Brown RM**, **Siler CD**, **Evans BJ**, **Austin CC**, **Iskandar DT**, **Diesmos AC**, **Supriatna J**, **Andayani N**, **McGuire JA. 2013.** Stochastic faunal exchanges drive diversification in widespread Wallacean and Pacific Island lizards (Squamata: Scincidae: *Lamprolepis smaragdina*). *Journal of Biogeography* **40:** 507–520.

**Linkem CW**, **Minin VN**, **Leaché AD. 2016.** Detecting the anomaly zone in species trees and evidence for a misleading signal in higher-level skink phylogeny (Squamata: Scincidae). *Systematic Biology* **65:** 465–477.

**Linnaeus C. 1758.** *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Edito decima, reformata*. Stockholm: L. Salvius.

**Linnaeus C. 1766.** *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Edito duodecima, reformata*. Stockholm: L. Salvius.

**Loveridge A. 1933.** New scincid lizards of the genera *Sphenomorphus*, *Rhodona*, and *Lygosoma* from Australia. *Occasional Papers of the Boston Society of Natural History* **8:** 95–100.

**Loveridge A. 1935.** Scientific results of an expedition to rain forest regions in eastern Africa. I. New reptiles and amphibians from East Africa. *Bulletin of the Museum of Comparative Zoology at Harvard College* **79:** 3–19.

**Loveridge A. 1957.** Checklist of the reptiles and amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar). *Bulletin of the Museum of Comparative Zoology at Harvard College* **117:** 153–360.

**Maddison WP. 1997.** Gene trees in species trees. *Systematic Biology* **46:** 523–536.

**Marshall DC. 2010.** Cryptic failure of partitioned Bayesian phylogenetic analyses: lost in the land of long trees. *Systematic Biology* **59:** 108–117.

**Masterson G. 2014.** *Mochlus sundevallii sundevallii* (A. Smith, 1849): Sundevall's writhing skink. In: Bates MF, Branch WR, Bauer AM, Burger M, Marias J, Alexander GJ, de Villiers MS, eds. *Atlas and Red List of the reptiles of South Africa, Lesotho and Swaziland*. Pretoria: South African National Biodiversity Institute.

**Mausfeld P**, **Schmitz A. 2003.** Molecular phylogeography, intraspecific variation and speciation of the Asian scincid lizard genus *Eutropis* Fitzinger, 1843 (Squamata: Reptilia: Scincidae): taxonomic and biogeographic implications. *Organisms, Diversity and Evolution* **3:** 161–171.

**Mausfeld P**, **Vences M**, **Schmitz A**, **Veith M. 2000.** First data on the molecular phylogeography of scincid lizards of the genus *Mabuya*. *Molecular Phylogenetics and Evolution* **17:** 11–14.

**Mayr E. 1976.** The role of systematics in biology. In: Mayr E, ed. *Evolution and the diversity of life: selected essays*. Cambridge: Belknap Press, 416–424.

**McCormack JE**, **Faircloth BC**, **Crawford NG**, **Gowaty PA**, **Brumfield RT**, **Glenn TC. 2012.** Ultraconserved elements are novel phylogenomic markers that resolve placental mammal phylogeny when combined with species-tree analysis. *Genome Research* **22:** 746–754.

**Medina MF**, **Bauer AM**, **Branch WR**, **Schmitz A**, **Conradie W**, **Nagy ZT**, **Hibbits TJ**, **Ernst R**, **Portik DM**, **Nielsen SV**, **Colston TJ**, **Kusamba C**, **Behandana M**, **Rödel MO**, **Greenbaum E. 2016.** Molecular phylogeny of *Panaspis* and *Afroablepharus* skinks (Squamata: Scincidae) in the savannas of sub-Saharan Africa. *Molecular Phylogenetics and Evolution* **100:** 409–423.

**Miller MA**, **Pfeiffer W**, **Schwartz T. 2010.** Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Gateway Computing Environments Workshop 2010. New Orleans: IEEE.

**Mittleman MB. 1952.** Generic synopsis of the lizards of the subfamily Lygosominae. *Smithsonian Miscellaneous Collections* **117:** 1–35.

**Myers N**, **Mittermeier RA**, **Mittermeier CG**, **da Fonseca GAB**, **Kent J. 2000.** Biodiversity hotspots for conservation priorities. *Nature (London)* **403:** 853–848.

**Oliver LA**, **Prendini E**, **Kraus F**, **Raxworthy CJ. 2015.** Systematics and biogeography of the *Hylarana* frog (Anura: Ranidae) radiation across tropical Australasia, Southeast Asia, and Africa. *Molecular Phylogenetics and Evolution* **90:** 176–192.

**Palumbi S. 1991.** *The simple fool's guide to PCR*. Honolulu: Department of Zoology and Kewalo Marine Laboratory.

**Parker HW. 1932.** Two collections of reptiles and amphibians from British Somaliland. *Proceedings of the Zoological Society of London* **102:** 335–367.

**Parker HW. 1942.** The lizards of British Somaliland. *Bulletin of the Museum of Comparative Zoology at Harvard College* **91:** 3–101.

**Perret JL**, **Wuest J. 1983.** La microstructure des écailles de quelques scincidés Africains et paléarctiques (Lacerilia), observée au microscope électronique á balayage, II. *Revue Suisse de Zoologie* **90:** 913–928.

**Peters W. 1854.** Diagnosen neuer Batrachier, welche zusammen mit der Früher (24. Juli und 17. August) gegebenen Übersicht der Schlangen und Eidechsen mitgetheilt werden. *Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin* **1854:** 614–628.

**Peters W. 1874.** Über einige neue Reptilien (*Lacerta*, *Eremias*, *Diploglossus*, *Euprepes*, *Lygosoma*, *Sepsina*, *Ablepharus*, *Simotes*, *Onychocephalus*). *Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin* **1874:** 368–377.

**Peters W. 1879.** Über neue Amphibien des Kgl. Zoologischen Museums (*Euprepes*, *Acontias*, *Typhlops*, *Zamenensis*, *Spilotes*, *Oedipus*). *Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin* **1879:** 773–779.

**Pietersen DW**, **Scholtz CH**, **Bastos ADS. 2018.** Multi-locus phylogeny of southern African *Acontias aurantiacus* (Peters)



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subspecies (Scincidae: Acontinae) confirms the presence of three genetically, geographically and morphologically discrete taxa. *Zootaxa* **4442:** 427–440.

**Pinto-Sánchez NR**, **Calderón-Espinosa ML**, **Miralles A**, **Crawford AJ**, **Ramírez-Pinilla MP. 2015.** Molecular phylogenetics and biogeography of the Neotropical skink genus *Mabuya* Fitzinger (Squamata: Scincidae) with emphasis on Columbian populations. *Molecular Phylogenetics and Evolution* **93:** 188–211.

**Pyron RA**, **Burbrink FT**, **Wiens JJ. 2013.** A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* **93:** 1–53.

**R Core Team**. **2016.** *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. Available at: https://www.R-project.org/.

**R Core Team**. **2018.** *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. Available at: https://www.R-project.org/.

**Rambaut A**, **Suchard MA**, **Xie D**, **Drummond AJ. 2014.** *Tracer v1.6*. Available at: http://tree.bio.ed.ac.uk/software/tracer/.

**Rittmeyer EN**, **Austin CC. 2015.** Combined next-generation sequencing and morphology reveal fine-scale speciation in Crocodile Skinks (Squamata: Scincidae: *Tribolonotus*). *Molecular Ecology* **24:** 466–483.

**Rocha S**, **Carretero MA**, **Vences M**, **Glaw F**, **Harris DJ. 2006.** Deciphering patterns of transoceanic dispersal: the evolutionary origin and biogeography of coastal lizards (*Cryptoblepharus*) in the western Indian Ocean region. *Journal of Biogeography* **33:** 13–22.

**Ronquist F**, **Telsenko M**, **van der Mark P**, **Ayres DL**, **Darling A**, **Höhna S**, **Larget B**, **Liu L**, **Suchard MA**, **Huelsenbeck JP. 2012.** MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61:** 539–542.

**Rosenberg NA. 2002.** The probability of topological concordance of gene trees and species trees. *Theoretical Population Biology* **61:** 225–247.

**Schmidt KP. 1919.** Contributions to the herpetology of the Belgian Congo based on the collections of the American Museum Congo Expedition, 1909–1915. Part I. Turtles, crocodiles, lizards, and chameleons. With field notes by Herbert Land and James P. Chapin. *Bulletin of the American Museum of Natural History* **39:** 385–624.

**Schneider JG. 1801.** *Historiae amphibiorum naturalis et literariae. Fasciculus secundus.* Jena: F. Frommann.

**Sharma RC. 1976.** Records of the reptiles of Goa. *Records of the Zoological Survey of India* **71:** 149–167.

**Sharma RC. 1977.** A new lizard of the genus *Riopa* Gray (Scincidae) from Tamil Nadu, India. *Records of the Zoological Survey of India* **73:** 41–42.

**Shreve B. 1940.** Reptiles and amphibians from Burma with descriptions of three new skincs [sic]. *Proceedings of the New England Zoological Club* **18:** 17–26.

**Siler CD**, **Diesmos AC**, **Brown RM. 2010.** New loam-swimming skink, genus *Brachymeles* (Reptilia: Squamata: Scincidae) from Luzon and Catanduanes Islands, Philippines. *Journal of Herpetology* **44:** 49–60.

**Siler CD**, **Diesmos AC**, **Alcala AC**, **Brown RM. 2011.** Phylogeny of the Philippine slender skinks (Scincidae: *Brachymeles*) reveals underestimated species diversity, complex biogeographical relationships, and cryptic patterns of lineage diversification. *Molecular Phylogenetics and Evolution* **59:** 53–65.

**Siler CD**, **Jones RM**, **Diesmos AC**, **Diesmos ML**, **Brown RM. 2012.** Phylogeny-based species delimitation in Philippine slender skinks (Reptilia: Squamata: Scincidae) III: taxonomic revision of the *Brachymeles gracilis* complex, with descriptions of three new species. *Herpetological Monographs* **26:** 135–172.

**Siler CD**, **Linkem CW**, **Cobb K**, **Watters JL**, **Cummings ST**, **Diesmos AC**, **Brown RM. 2014.** Taxonomic revision of the semi-aquatic skink *Parvoscincus leucospilos* (Reptilia: Squamata: Scincidae), with description of three new species. *Zootaxa* **3847:** 388–412.

**Siler CD**, **Davis DR**, **Freitas ES**, **Huron NA**, **Geheber AD**, **Watters JL**, **Penrod ML**, **Papes M**, **Amrein A**, **Anwar A**, **Cooper D**, **Hein T**, **Manning A**, **Patel N**, **Pinaroc L**, **Diesmos AC**, **Diesmos ML**, **Oliveros CH**, **Brown RM. 2016.** Additions to Philippine slender skinks of the *Brachymeles bonitae* complex (Reptilia: Squamata: Scincidae) II: a new species from the northern Philippines. *Zootaxa* **4132:** 15–29.

**Siler CD**, **Heitz BB**, **Davis DR**, **Freitas ES**, **Aowphol A**, **Termprayoon K**, **Grismer LL. 2018.** New supple skink genus *Lygosoma* (Reptilia: Squamata: Scincidae) from Thailand and redescription of *Lygosoma quadrupes* (Linnaeus, 1766). *Journal of Herpetology* **52:** 332–347.

**Sindaco R**, **Metallinou M**, **Pupin F**, **Fasola M**, **Carranza S. 2012.** Forgotten in the ocean: systematics, biogeography and evolution of the *Trachylepis* skinks of the Socotra Archipelago. *Zoologica Scripta* **41:** 346–362.

**Skinner A**, **Hugall AF**, **Hutchinson MN. 2011.** Lygosomine phylogeny and the origins of Australian scincid lizards. *Journal of Biogeography* **38:** 1044–1058.

**Skinner A**, **Hutchinson MN**, **Lee MSY. 2013.** Phylogeny and divergence times of Australian *Sphenomorphus* group skinks (Scincidae, Squamata). *Molecular Phylogenetics and Evolution* **69:** 906–918.

**Smith A. 1849.** *Illustrations of the zoology of South Africa consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa in the years 1834, 1835, and 1836; Fitted out by 'The Cape of Good Hope Association for Exploring Central Africa.' Reptilia.* London: Smith, Elder and Co.

**Smith MA. 1916.** Descriptions of three new lizards and a new snake from Siam. *Journal of the Natural History of Siam* **2:** 44–47.

**Smith MA. 1917.** Descriptions of new reptiles and a new batrachian from Siam. *Journal of the Natural History Society of Siam* **2:** 221–225.

**Smith MA. 1921.** New or little-known reptiles and batrachians from southern Annam (Indo-China). *Proceedings of the Zoological Society of London* **1921:** 423–440.

**Smith MA. 1935.** *The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. Volume II – Sauria*. London: Taylor and Francis.

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

**Smith MA. 1937b.** Un nouveau lézard de Cochinchine. *Bulletin du Muséum National d'Histoire Naturelle* **9:** 366.

**Stamatakis A. 2014.** RAxML v.8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30:** 1312–1313.

**Stoliczka F. 1870.** Observations on some Indian and Malayan amphibia and reptilia. *Journal of the Asiatic Society of Bengal* **39:** 134–228, pl. x–xii.

**Storr GM. 1964.** *Ctenotus*, a new generic name for a group of Australian skinks. *Western Australian Naturalist* **9:** 84–85.

**Storr GM. 1967.** The genus *Sphenomorphus* (Lacertilia, Scincidae) in Western Australia and the Northern Territory. *Journal of the Royal Society of Western Australia* **50:** 10–20.

**Streicher JW**, **Wiens JJ. 2017.** Phylogenomic analyses of more than 4000 nuclear loci resolve the origin of snakes among lizard families. *Biology Letters* **13:** 20170393.

**Tabachnick BG**, **Fidell LS. 2013.** *Using multivariate statistics*, *6th edn*. Essex: Pearson.

**Tajima F. 1983.** Evolutionary relationship of DNA sequences in finite populations. *Genetics* **105:** 437–460.

**Taylor EH. 1923.** Additions to the herpetological fauna of the Philippine Islands, III. *Philippine Journal of Science* **22:** 515–557, pl. 1–3.

**Taylor EH. 1935.** A taxonomic study of the cosmopolitan scincoid lizards of the genus *Eumeces* with an account of the distribution and relationships of its species. *University of Kansas Science Bulletin* **23:** 19–643.

**Taylor EH. 1950.** Ceylonese lizards of the family Scincidae. *University of Kansas Science Bulletin* **33:** 481–518.

**Taylor EH. 1962.** New Oriental reptiles. *University of Kansas Science Bulletin* **43:** 209–263.

**Taylor EH. 1963.** The lizards of Thailand. *University of Kansas Science Bulletin* **44:** 687–1077.

**Theobald W. 1867.** Catalogue of the reptiles of British Burma, embracing the provinces of Pegu, Martaban, and Tenasserim; with descriptions of new or little-known species. *Journal of the Linnean Society Zoology* **10:** 4–67.

**Theobald W. 1876.** *Descriptive catalogue of the reptiles of British India*. Calcutta: Thacker, Spink and Co.

**Townsend TM**, **Alagre RE**, **Kelley ST**, **Wiens JJ**, **Reeder TW. 2008.** Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: an example from squamate reptiles. *Molecular Phylogenetics and Evolution* **47:** 129–142.

**Trape JF**, **Trape S**, **Chirio L. 2012.** *Lézards, crocodiles et tortues d'Afrique occidentale et du Sahara*. Marseille: Institut de Recherché pour le Dévelopement.

**Uetz P, Freed P, Hošek J, eds. 2019.** *The reptile database*. Available at: http://www.reptile-database.org. Accessed January 2019.

**Vaillant ML. 1884.** Note sur une collection de reptiles rapportée d'Assinie par M. Chaper. *Bulletin de la Société Philomathique de Paris* **70:** 168–171.

**Vences M**, **Guayasamin JM**, **Miralles A**, **de la Riva I. 2013.** To name or not to name: criteria to promote economy of change in Linnaean classification schemes. *Zootaxa* **3636:** 201–244.

**Vitt L**, **Caldwell J. 2013.** *Herpetology: an introductory biology of amphibians and reptiles.* London: Academic Press.

**Wagler JG. 1830.** *Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vögel*. Munich: J. G. Cotta.

**Wagner P**, **Böhme W**, **Pauwels OS**, **Schmitz A. 2009.** A review of the African red-flanked skinks of the *Lygosoma fernandi* (Burton, 1836) species group (Squamata: Scincidae) and the role of climate change in their speciation. *Zootaxa* **2050:** 1–30.

**Warren D**, **Geneva A**, **Lanfear R. 2017.** RWTY (R We There Yet): an R package for examining convergence of Bayesian phylogenetic analyses. *Molecular Biology and Evolution* **34:** 1016–1020.

**Werner F. 1900.** Reptilien und Batrachier aus Sumatra, gesammelt von Herrn Gustav Schneider jr. im Jahre 1897–98. *Zoologische Jahrbücher abtheilung für Systematik, Geographie und Biologie der Thiere* **13:** 479–508.

**Werner F. 1910.** Über neue oder seltene Reptilien des Naturhistorischen Museums in Hamburg. II. Eidechsen. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* **27:** 1–46.

**Wheeler QD**, **Raven PH**, **Wilson EO. 2004.** Taxonomy: impediment or expedient? *Science (Washington)* **303:** 285.

**Whiting AS**, **Bauer AM**, **Sites Jr JW. 2003.** Phylogenetic relationships and limb loss in sub-Saharan African scincine lizards (Squamata: Scincidae). *Molecular Phylogenetics and Evolution* **29:** 582–598.

**Whiting AS**, **Sites Jr JW**, **Bauer AM. 2004.** Molecular phylogenetics of Malagasy skinks (Squamata: Scincidae). *African Journal of Herpetology* **53:** 135–146.

**Wiegmann AFA. 1834.** *Herpetologia mexicana, seu descriptio amphibiorum Novae Hispaniae: quae itineribus comitis de Sack, Ferdinandi Deppe et Chr. Guil. Schiede in Museum Zoologicum Berolinense pervenerunt*. Berlin: CG Lüderitz.

**Winston JE. 1999.** *Describing species: practical taxonomic procedure for biologists.* New York: Columbia University Press.

**Xie W**, **Lewis PO**, **Fan Y**, **Kuo L**, **Chen MH. 2011.** Improving marginal likelihood estimation for Bayesian phylogenetic model selection. *Systematic Biology* **60:** 150–160.

**Zheng Y**, **Wiens JJ. 2016.** Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Molecular Phylogenetics and Evolution* **94:** 537–547.

**Ziegler T**, **Schmitz A**, **Heidrich A**, **Vu NT**, **Nguyen QT. 2007.** A new species of *Lygosoma* (Squamata: Sauria: Scincidae) from the central Truong Son, Vietnam, with notes on its molecular phylogenetic position. *Revue Suisse de Zoologie* **114:** 397–415.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

**Table S1** Table showing the taxonomic and genetic sampling for this study. GenBank numbers for each gene are listed in the columns.

**Table S2** Table showing the museum number (or collector number when the museum number was not available) and country of origin for each specimen in our morphological dataset. AA=Anchalee Aowphol (at ZMKU), ACD=Arvin Diesmos (at PNM), BNHM=Bombay Natural History Museum, CAS=California Academy of Sciences, CES= Center for Ecological Sciences at the Indian Institute of Science, FMNH=Field Museum of Natural History, KU=University of Kansas Museum of Natural History, MCZ=Museum of Comparative Zoology, MVZ=Museum of Vertebrate Zoology, PNM=Philippines National Museum, UNIMAS=Institute of Biodiversity and Environmental Conservation, USNM=National Museum of Natural History, ZMKU=Zoological Museum of Kasetsart University.

**Table S3** Table with values (minimum–maximum) for mensural, meristic and qualitative characters for each species in *Lygosoma*, *Mochlus*, *Riopa*, and ***Subdoluseps* gen.nov** included in our morphological dataset. Means and standard deviations for mensural characters are shown in parentheses when the number of samples included is three or higher. Measurements and counts for juveniles and individuals suspected of being misidentified are excluded from this table. SVL = snout–vent length, AGD = axilla–groin distance, MBW = midbody width, TL = tail length, TW = tail width, HL = head length, HW = head width, HD = head depth, END = eye–nares distance, SNL = snout length, IND = internarial distance, MBSRC = midbody scale row count, PVSRC = paravertebral scale row count, FinIIILam = finger three lamellae, ToeIVLam = Toe four lamellae, SuprL = supralabials, InfrL = infralabials, SO = supraocculars, SC = supercilliaries, lower eyelid state transp. disc = transparent disc. Definitions of each character are found in text

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