USING INTEGRATED APPROACHES TO STUDY THE SYSTEMATICS OF SCINCID LIZARDS IN THE LOWER SUNDA SHELF

by

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Dedication

In Remembrance of His Majesty King Bhumibol Adulyadej.

This dissertation is dedicated to the late king of Thailand who devoted his entire life to the Thai people. Guided by his mercifulness, he created numerous royal-initiatives to enhance scientific research and promote a better life for the people of Thailand. Many of these projects also manage natural resources and include wildlife conservation.

I dedicate this work to my family, for their unwavering support, and also to the members of the Thammachoti, Charunrochana na Ayudhaya, Sanit and Swangjitr families.

Abstract

USING INTEGRATED APPROACHES TO STUDY THE SYSTEMATICS OF SCINCID LIZARDS IN THE LOWER SUNDA SHELF

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Scincid lizards are one of the most diverse group of squamate reptiles, found from tropical to temperate habitats worldwide. In the tropical rain forests of Java, Sumatra, and other parts of the Sunda Shelf biological hotspot a higher diversity of these lizards is expected, particularly in comparison to adjacent terrains. Lack of exploration and cryptic diversity of skinks in these areas might amount for the disproportionate low numbers. Recently, large-scale herpetological exploration of Java and Sumatra has been done as a collaboration between the University of Texas at Arlington, the Indonesian Institute of Sciences, and Brawijaya University. Large numbers of amphibians and reptiles, including skink specimens, have resulted from these concerted effort, and are now available for study in herpetological collections. With these new samples, the systematics of skinks in Java and Sumatra is reviewed, using integrated molecular and morphological approaches. Mitochondrial and nuclear loci have been used to estimate a concatenated data phylogeny estimate, as well as, a coalescent species tree, a time calibrated phylogeny, and genetic distance molecular species delimitation. Meristic and mensurable morphological characters have been used in discriminant functional analyses, skull anatomy has been compared, and ecological niche modeling examined for taxonomic consideration. We have studied in detail the Common Sun Skinks of the *Eutropis mutifasciata* complex, the Asian diminutive forest skinks of the genus *Tytthoscincus,* and the forest skinks in the genus *Sphenomorphus*. The results reveal hidden diversity of species in Java and Sumatra, and the occurrence of a new genus and two new species allied to the *Sphenomorphus* group, two new species of *Tytthoscincus*, resurrection of a junior synonym and elevating to species level several subspecies of *Eutropis* and *Tytthoscincus*. Finally, we transfer several species of *Sphenomorphus* to *Tytthoscincus*. The systematic revision of skinks in Java and Sumatra revealed an underestimated diversity, finding that can lead to a reassessment of conservation priority areas and their management.

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Chapter 1

General Introduction

Scincid lizards or skinks are some of the most diverse squamate reptiles. They are found in many habitats, from tropical to temperate, and from low to high elevations. There are more than 120 genera and 1500 species. They were recognized as single family, Scincidae Oppel (1811), but now they are part of the Scincomorpha with nine families including, Acontidae Gray (1839), Ateuchosauridae Hedges (2014), Egerniidae Welch (1982), Eugongylidae Welch (1982), Lygosomidae Mittleman (1952), Mabuyidae Mittleman (1952), Ristellidae Hedges (2014), Sphenomorphidae Welch (1982), and Scincidae Oppel (1811). Skinks are mostly terrestrial and fossorial, but many are arboreal, and some semi-aquatic. Their size and shape is also diverse, they can be limbless or with well develop limbs, or small to large. Skinks are recognized by their large shield-like scales on the head and their cycloid scales on the body (Pianka and Vitt 2003). In terms of internal anatomy, they have a secondary palate in the roof of the mouth, separating respiratory and digestive tracks (Greer 1989). In addition, skinks are also important in the ecosystem, as part of the food chains, they are prey or predators. For example, they are predators to many insects and invertebrates, and they are prey for snakes, birds and small mammals (Vitt 2016). Even though the taxonomy, morphology and ecology of skinks has been studied many times, this has happened mostly in developed countries or well explored developing nations where they occur. There are still many areas of the globe, inaccessible, where skinks have had very little attention.

The Sunda Shelf has been considered an important biodiversity hotspot, recognized as on of the eight most important of those spots (Myers et. al. 2000). Located in Southeast Asia it consists of Peninsular Malaysia, Borneo, Java, and Sumatra (Figure 1.1). The Sunda Shelf has been intermittently connected to mainland Southeast Asia and many other Islands over geologic time, and is surround by several other biological hotspots. It relates to the Indochinese or Indoburmese Peninsula, Wallacea, and the Philippines. Given that this area is a biodiversity hotspot, it should be expected to have a high diversity of skinks. There are more than 130 species of skinks recorded from Sunda Shelf, so far. Most of them are recognized from Peninsular Malaysia and Borneo, with 45 and 46 species, respectively, and only 20 and 18 species have been found in Java and Sumatra, respectively. The difference in species richness among these areas must be due to a lack of exploration on the later two islands and also probably due to hidden diversity. During the past decade, most taxonomic studies on skinks from the Sunda Shelf has been done mostly in the Malaysian landmases in Borneo and Peninsular Malaysia (e.g., Inger et al. 2001; Grismer 2011). Only few taxonomic studies have involved Java and Sumatra (Iskandar 1994; Bucklitsch et al. 2012).

Java and Sumatra are two of the largest islands in the Sunda Shelf, and politically part of the Republic of Indonesia. There are few studies on skinks of Java and Sumatra due to limited historical collections, particularly after this nations independence. Most known species were described a long time ago bases on morphological data alone, and genetic data is not available for most of them. Because most of the skinks in Java and Sumatra are fossorial and terrestrial, they are difficult to find, making the Scincidae one of the least-known squamate families. Previous studies have suggested that montane skinks in the Sunda Shelf have a high potential of endemisim, with species distribution limited to small montane areas and being isolated from each other, even when these montane areas are very close (Karen et al. 2016). However, sometimes the morphological characters distinguishing closely related species of skinks are subtle and conserved (Barley et al. 2013).

Species delimitation in skinks is challenging using only morphological traits, and might lead to an underestimate of diversity when species have low morphological diferentiation but high genetic divergence. Some species however, have high variability in morphology, but low genetic variation, leading to overestimation of diversity. These two situations lead to problems in systematic studies (Barley et al. 2013). In the past, differences in morphology were assumed to be due to reproductive isolation, and leading to a classical recognition of different species (Mayr 1942). This approach alone can be incorrect, when faced with morphological conservatism, and in particular among similar habitats or sympatric species. This scenario might be because external morphology can be under similar selective pressure (Bickford et al. 2007), and molecular data might provide better alternatives to investigate species delimitation.

Genetic data can be used appropriately for taxonomic and systematic studies, as we can use genetic data to examine phylogenetic relationships and genetic distance between sister lineages. However, in some case we see conflict between genetic analyses, for example, in the case of incomplete lineages sorting (Heled and Drummond 2009). A gene tree of one locus can indicate some conflicting arrangement, when compared to that of another gene tree, from another locus. In this case we have to use coalescent-based methods or species-trees, to solve this problem. This method, theoretically evaluates the likelihood of competing species delimitation hypotheses base on an assumed evaluation process. This can be advantageous in genetic studies but, in some cases, especially for our Sumatran and Javan skinks, the genetic data is not available. Therefore, we need to use an integrative approach using morphology and genetic data.

A combined data phylogeny has integrated the advantages of both morphology and genetic based phylogenies, although apart, both have their own advantages (Hillis and Wiens 2000). It seems that a molecular-based phylogeny is more powerful due to advancements in molecular techniques. However, the greatest advantage of morphology is allowing much more taxonomic sampling, if including historical specimens and others difficult to obtain. Therefore, it is difficult to conclude which one is better and, if the goal is to get the best estimate of phylogeny, combining data might be best. In the past, combining data phylogeny has been performed by maximum parsimony approaches, however, the Bayesian inference of phylogeny using Markov chain Monte Carlo (MCMC) estimation of posterior probability distributions has been made available for combining data types (Lewis 2001; Nylander et al. 2004).

Species distributions are also important in systematics, they can be used to explain historical biogeography and evolution. However, with limited skink collections, we cannot infer accurate distributions. Species niche modeling provides a good tool to infer species distributions when having limited sampling. Ecological niche modeling or species distribution modeling uses distributional data on a geographic information system (GIS) for each species and environmental data (i.e., climate and geography) to create geophysical area model where species have a high probability to be found (Vid and Cardwell). This model generates potential distributions which fill the gap of our known distributions. Not only illustrating the species distribution but also predicting where we can find the new closely related species. The fragmentations of species distribution resulting from geographic breaks can be use as evidences for gene pool separation.

this can refer to ecology's role in speciation (McCormack et al. 2010). Reptiles is definitely suitable for niche modeling since they are ectotherms which their physiology are variable and corresponding to environmental factors. In last decade the studies of niche modeling in reptiles were obviously increase (hepeto book). Specially in high endemism areas or in biological hotspot (Raxworthy et al. 2003). There are a few studies on skinks (Wogan and Richmond 2015). Interestingly species niche modeling can use to study ecological speciation in skink (Richmond and Reeder 2002). Several species of skink have moving limited. They just live in a particular small area and some of them is very rare therefore the niche modeling will demonstrate where we can find them by predict the suitable habitat. In Java and Sumatra recently had a couple of niche modeling studies on Crocodiles and Agamid lizards (Shaney et al. in prep).

The common sun skink, *Eutropis multifasciata* complex (Kuhl, 1820), is a complex species that have been found throughout Asia Pacific. It ranges from East India, Burma, Indochina, Malay Peninsula, Java, Sumatra, Borneo, the Philippines, Wallacea, and Papua New Guinea. Since it has wide distribution, it was described as multiple species only to be later synonymized to *E. multifasciata,* including *Plestiodon sikkimenesis* (Gray 1853), *Tropidolepisma macrurus* (Bleeker 1860), *Euprepes sebae* (Duméril and Bibron 1839), *Mabuia monticola* (Annadale 1905). Martens (1927 and 1956) described the subspecies consist of *Eutropis multifasciata balinensis* from Bali Island and *Eutropi multifasciata tjendikianesis* from Karimundjawa Archipelago. However recently, one of them (*E. m. balinensis*) has been questioned since weak evidence from genetic data. (Mausfeld and Schmitz 2003). Several studies have investigated the molecular systematics in the genus*,* but their geographic sampling of *E. multifasciata* has been inadequate since they have all lacked samples from the type locality of

Western of Java. Recently Amarasinghe et al. (in press) revisited the taxonomic status of this species groups and designated the neotype of *E. multifasciata* from Banten, Java. This studied also refused two subspecies base on only morphological evidences. This might be underestimated diversity of this complex since *Eutropis* has been known as morphological conserve.

The Asian diminutive skink, *Tytthoscincus* Linkem, Diesmos and Brown (2011) is a genus of small forest skink. The members had been described as part of the genus *Sphenomorphus* Fitzinger (1843). The members of *Tytthoscincus* have rage from Peninsular Malaysia, Sumatra, Java, Borneo, The Philippines, and Sulawesi. The key characters of *Tytthoscincus* that distinguish from *Sphenomorphus* and other related genera are small body size, snout vent length less than 45 mm, Temporal scales are similar in size and shape with lateral body scales and small limb and digit. The small skink like *Tytthosincus* is high potential to be an endemism since it is leaf-litter specialist and vagility limit. Several of *Tytthoscincus* desdcribed in Sunada Shelf were endemic in a single montane area or in single island (Grismer 2011; Karin et al. 2016). The *Tytthoscincus* presently includes 21 species (Uetz and Hošek 2014). There are 17 species of *Tytthoscincus* have been found in Sunda Shelf but only one species has been recorded in Java and Sumatra which is *Tytthoscincus temmincki* (Duméril & Bibron 1839). Therefore, with only one species was recorded in Java and Sumatra, we hypothesized the cryptic diversity of *Tytthoscincus* in Java and Sumatra.

The forest skink, *Sphenomorphus* Fitzinger (1843) is one of the most diverse genus of skinks. It has been known as non-monophyletic group (Linkem et al. 2011) and recognized as catch all genus. Recently previous study, the *Sphenomorphus* skinks were transferred to other genera including *Insulasaurus, Olosaurus, Parvoscincus, Pinoyscincus, Scincella* and *Tytthoscincus* (Linkem et al. 2011). Currently there are more than 120 species of *Sphenomorphus* range from India subcontinent, Southeast Asia mainland, Peninsular Malaysia, Sumatra, Java, Borneo, The Philippines, Wallacea, Lesser Sunda, Papua and Pasific Islands. There are 43 species of *Sphenomorphus* in Sunda Shelf and most of them were described from Peninsular Malaysia and Borneo (Grismer et al. 2017). Only 7 Species have been found in Java and Sumatra and most of them were described from late 18th to early 19th. The latest species *S. puncticentralis* described by Iskandar in 1994 from Central Java base on only morphological data. There has been no phylogenetic study of Java and Sumatra *Sphenomorphus* yet. The previous studies focused only on morphology-base taxonomy, there are no examination about systematics relationship among species of *Sphenomorphus* in Java and Sumatra. Therefore, the phylogenetic relationship of *Sphenomorphus* in Java and Sumatra is necessary. The phylogenetic relationships and other evidences can be used to clarify taxonomic problems of *Sphenomorphus* in this areas (as it had been resolved in the Philippines skinks before).

As described above different taxa have different problems. we cannot use only one technique solving these all taxonomic problems. Therefore, integrated approach is reasonable idea for taxonomic study of skinks in Java and Sumatra Since previously using only morphology or genetics separately could not solve problems. The morphology is good for taxonomy if the characters are obviously different but not in the case of skinks which have morphological conservation (Barley et al. 2013). Several species of skink are still cryptic even genetics is clearly divergent (Grismer et al. 2017). In the other hand genetic data are also not be able to solve all taxonomic problems since several species of skinks are rare and endemics leading to genetic data limited for these species in remote areas of Java and Sumatra. However, integrated data make taxonomic studies more robust and reliable since they are pluralistic approaches. Padial et al. (2010) present the integrated taxonomic approaches by three main disciplines including morphology, genetics and ecology. They also mentioned that although the traditional taxonomy is useful for many case but new approaches need to be integrated for delimiting species. Therefore, in order to investigate the taxonomic problems of skink in Java and Sumatra, the integrated taxonomy among morphology, genetics and ecology is going to be our object.

In order to examine systematics studies and revise taxonomic problems of skink in Java and Sumatra, I use integrated approaches based on each species group. In chapter two, I examine systeamatics of common sun skinks (*Eutropis multifasciata* complex) by using phylogenetic relationships (concatenated mitochondrial and nuclear gene tree and coalescent species tree), morphometric analysis and molecular species delimitations. In chapter three, I examine systeamtics of diminutive forest skinks (*Tytthoscincus*) by using phylogenetic relationships (concatenated mitochondrial and nuclear gene tree), distinctive morphological characters and ecological niche modeling. In chapter four, I examine systematics of forest skink (*Sphenomorphus*) by using phylogenetic relationships (concatenated mitochondrial and nuclear gene tree), divergent time analysis, distinctive morphological characters, skull comparative anatomy and ecological niche modeling.

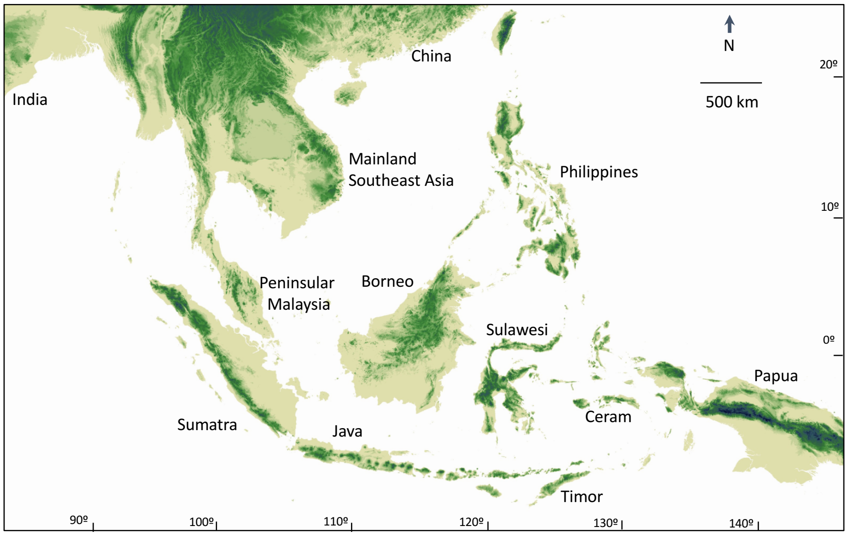

Figure 1.1 Southeast Asia. The Sunda Shelf includes Peninsular Malaysia, Sumatra, Java and Borneo.

Scincid Lizards of Java and Sumatra

Scincidae Gray, 1825

Carlia Gray, 1845

Carlia nigrauris Zug, 2010

Type: SMF 53916 (holotype)

Type locality: Tindjil Island, Banten, Java, Indonesia

Distribution: Endemic to Tindjil Island

Cryptoblepharus Wiegmann, 1834

Cryptoblepharus balinensis Barbour, 1911

Subspecies: *Cryptoblepharus balinensis balinensis* Barbour, 1911

Type: MCZ 7480 (holotype)

Type locality: Boeloeleng, Boeboe, Bali

Distribution: Bali and East Java

Dasia Gray, 1839

Dasia grisea (Gray, 1845)

Type: BMNH 1946.8.20.51

Type locality: Philippines

Distribution: Malay Peninsula, Sumatra, Borneo, Philippines

Dasia olivacea Gray, 1839

Type: ANSP 9531 (holotype)

Type locality: Penang, West Malaysia

Distribution: India, Mainland Southeast Asia, Sumatra, Java, Borneo, Philippines

Emoia Gray, 1845

Emoia atrocostata (Lesson, 1830)

Subspecies: *Emoia atrocostata atrocostata* (Lesson, 1830)

Type: MCZ R-15078 (holotype)

Type locality: Qualan Island, Caroline Islands

Distribution: Indoaustralian archipelago to Papua New Guinea

Eutropis Fitzinger, 1843

Eutropis macrophthalma (Mausfeld & Böhme, 2002)

Type: ZFMK 71717 (holotpe)

Type locality: Java

Distribution: Java

Eutropis multifasciata (Kuhl, 1820)

Subspecies: *Eutropis multifasciata multifasciata* (Kuhl, 1820)

Type: unknown

Type locality: Java

Distribution: India, Mainland Southeast Asia, Sumatra, Java, Borneo, Philippines, Wallacea, Papua

Subspecies: *Eutropis multifasciata tjendikianensis* (Mertens, 1956)

Type: SMF 55147 (holotype)

Type locality: Tjendikian Island, Karimunjava Archipelago

Distribution: Endemic to Tjendikian Island, Karimunjava Archipelago, Java

Subspecies: *Eutropis multifasciata balinensis* (Mertens, 1927)

Type: SMF 22087 (helotype)

Type locality: Gitgit, Bali

Distribution: Endemic to Bali

Eutropis rudis (Boulenger, 1887)

Type: BMNH 1946.8.15.26 (syntype)

Type locality: Matang, Sarawak, Borneo

Distribution: Nicobar Islands, Sumatra, Java, Borneo, Philippines, Sulawesi

Eutropis rugifera (Stoliczka, 1870)

Type: ZSI 2350 (holotype)

Type locality: Camorta, Nicobar Islands, India

Distribution: Nicobar Islands, Malays Peninsula, Sumatra, Java

Lamprolepis Fitzinger, 1843

Lamprolepis leucosticta (Müller, 1923)

Type: ZSM 441/1911 (holotype; lost)

Type locality: Java

Distribution: Java

Larutia Böhme 1981

Larutia sumatrensis (Bleeker, 1860)

Type: BMNH

Type locality: Agam, Sumatra

Distribution: Endemic to Sumatra

Lipinia Gray, 1845

Lipinia relicta (Vinciguerra, 1892)

Type: MSNG (lectotype)

Type locality: Engano Island, Sumatra

Distribution: Mentawai Archipelago, Sumatra, Java

Lipinia vittigera (Boulenger, 1894)

Subspecies: *Lipinia vittigera vittigera* (Boulenger, 1894)

Type: MSNG 55855 (holotype)

Type locality: Sipora, Mentawai, Sumatra

Distribution: Mainland Southeast Asia, Malay Peninsula, Sumatra, Borneo

Lygosoma Hardwicke & Gray, 1828

Lygosoma bampfyldei Bartlett, 1895

Type: BMNH (Syntype)

Type locality: Rejang River, Sarawak, Borneo

Distribution: Sumatra, Borneo

Lygosoma bowringii (Günther, 1864)

Type: unknown

Type locality: Hong Kong

Distribution: Andaman Islands, South China, Mainland Southeast Asia, Sumatra, Java, Borneo, Philippines, Sulawesi

Lygosoma opisthorhodum Werner, 1910

Type: ZMH R01850 (paratype)

Type locality: Somgei Lalah, Indragiri, Sumatra

Distribution: endemic to Sumatra

Lygosoma quadrupes (Linnaeus, 1766)

Type: unknown

Type locality: Java

Distribution: South China, Mainland Southeast Asia, Sumatra, Java, Borneo, Philippines, Sulawesi

Sphenomorphus Fitzinger, 1843

Sphenomorphus anomalopus (Boulenger, 1890)

Type: ZMB 12026 (holotype)

Type locality: Penang, West Malaysia

Distribution: Malay Peninsula, Sumatra

Sphenomorphus cyanolaemus Inger & Hosmer, 1965

Type: FMNH 148567 (holotype)

Type locality: Sungei Seran, Labang, Bintulu, Sarawak, Borneo

Distribution: Malay Peninsula, Sumatra, Borneo

Sphenomorphus malayanum (Doria, 1888)

Type: BMNH 1946.8.3.11

Type locality: Mt. Singalang, Alahan Panjang, Sumatra

Distribution: Vietnam, Malay Peninsula, Sumatra

Sphenomorphus melanopogon (Duméril & Bibron, 1839)

Type: MNHN 1245 (syntype)

Type locality: New Guinea

Distribution: Java, Borneo, Sulawesi, Lesser Sunda, Wallacea, Papau New Ginea

Sphenomorphus modigliani (Boulenger, 1894)

Type: BMNH 1894.12.18.10

Type locality: Sipora, Mentawi Island, Sumatra

Distribution: Sumatra, Borneo

Sphenomorphus necopinatus (Brongersma, 1942)

Subspecies: *Sphenomorphus necopinatus necopinatus* (Brongersma, 1942)

Type: RMNH.RENA 7969

Type locality: Bogor, West Java

Distribution: Endemic to Bogor, West Java

Subspecies: *Sphenomorphus necopinatus garutense* (Brongersma, 1942)

Type: RMNH.RENA 7970

Type locality: Garut, West Java

Distribution: Endemic to Garut, West Java

Sphenomorphus puncticentralis Iskandar, 1994

Type: MZB 1651 (holotype)

Type locality: Mt. Slamet, Baturraden, Purwokerto, Central Java

Distribution: Endemic to Java

Sphenomorphus sanctus (Duméril & Bibron, 1839)

Subspecies: *Sphenomorphus sanctus sanctus* (Duméril & Bibron, 1839)

Type: MHNP 7116

Type locality: Java

Distribution: Malay Peninsula, Sumatra, Java

Subspecies: *Sphenomorphus sanctus tenggeranus* Mertens, 1957

Type: SMI 14470

Type locality: Tengger-Gebirge, Est Java

Distribution: Endemic to East Java

Sphenomorphus scotophilus (Boulenger, 1900)

Type: BMNH 1946.8.16.94

Type locality: Batu Caves, Selangor, West Malaysia

Distribution: Southern Thailand, Malay Peninsula, Sumatra

Sphenomorphus vanheurni (Brongersma, 1942)

Subspecies: *Sphenomorphus vanheurni vanheurni* (Brongersma, 1942)

Type: RMNH.RENA 7967 (holotype)

Type locality: Taman Hidoep, Ijang Mts., Probolinggo, East Java.

Distribution: Endemic to East Java

Subspecies: *Sphenomorphus vanheurni balicus* Mertens, 1957

Type: SMF 23275 (holotype)

Type locality: Gitgit, Bali

Distribution: Endemic to Bali

Tytthoscincus Linkem, Diesmos & Brown, 2011

Tytthoscincus temmincki (Duméril & Bibron, 1839)

Type: MHNP 1344

Type locality: Java

Distribution: Sumatra, Java, Sulawesi

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Chapter 2

The Common Sun Skink, Eutropis multifasciata (Kuhl, 1820), in Java and Sumatra: Discovery of a Species Complex through Integrated Systematics

ABSTRACT: The Common Sun Skink, *Eutropis multifasciata* (Kuhl 1820), originally considered multiple species, is now recognized as a widely distributed scincid that ranges from Northeast India and Indochina, across the Sunda shelf, and into the Philipines and Papua New Guinea. Three subspecies are currently recognized for this taxon, all in or near Java, *E. m. tjendikianensis* (Mertens 1956) from the Karimundjawa Achipelago, *E. m. balinensis* (Mertens 1927) from the island of Bali, and the nominal form, from West Java. The taxonomy of this complex has been based on morphology and controversial, missing type specimens or samples from the type locality. We constructed a molecular phylogeny of *E. multifasciata* employing samples from localities in mainland Asia, Borneo, Sumatra, and Java, including neotopotypic material. With two nuclear (NGFB and R35) and two mitochondrial (16S and ND4) loci, a framework of concatenated and coalescent phylogenetics, and morphological data, we mend the taxonomy and clarify species boundaries using molecular species delimitation methods. We recover four main geographic clades, different species, within Sumatra and Java, a Northern Sumatra clade, and the three subspecies previously recognized from Java and its adjacent satellite islands. The Northern and Central Sumatra, Borneo, Peninsular Malaysia, and mainland Asia populations we recognize as *E. sikkimensis* (Gray 1853). The Southern Sumatra and West Java populations correspond to *E. multifasciata*. Populations from Central Java and the

Karimundjawa Archipelago correspond to *E. tjendikianensis* (Mertens 1956). Finally, the East Java and Bali populations correspond to *E. balinensis* (Mertens 1927).

Key words: *Eutropis balinensis*; *Eutropis sikkimensis*; *Eutropis tjendikianensis*; Molecular phylogenetics; Scincidae; Species delimitation; Species tree; Sunda Shelf

THE COMMON Sun Skink, *Eutropis multifasciata* (Kuhl 1820), is widely distributed throughout the Indo-Malayan region, ranging from Northeastern India and South China, through Indochina, the Malay Peninsula, the Greater and Lesser Sundas, the Maluku islands, and reaching the Philippines and Papua New Guinea to the east (Grismer 2011; Dutta-Roy et al. 2012; Barley et al. 2015a; Karin et al. 2016). Largely habitat generalists, sun skinks can be found from low to mid elevations, in primary and secondary forests as well as agricultural and urban areas (Grismer 2011; Das 2015), and they have even been dispersed by humans into North America (Meshaka et al. 2004) and Australia (Ingram 1987).

The Common Sun Skink was first formally described by Heinrich Kuhl, as *Scincus multifasciatus* in 1820, but without any type designation. Related or synonymous taxa were described shortly after, such as *Euprepes sebae* by André Marie Constant Duméril and Gabriel Bibron in 1839, *Tropidolepisma macrurus* by Pieter Bleeker in 1860, and *Plestiodon sikkimensis,* by John Edward Gray in 1853. To add taxonomic confusion, the taxon described by Gunther (1864) as *E. monticola* from India, possibly from the eastern Himalayas, Sikkim, was later associated to *Mabuya multifasciata* (see Smith 1935:269), through a series of dorsal scale miscounts involving both Annandale (1905) and Theobald (1876:52). In 1927, Robert Mertens described a form from Bali, as *M. m. balinensis*. He mentioned that this subspecies has different characters from typical *M. multifasciata,* having a yellowish lateral body-band and a reddish snout-tip. Mertens continued working with these lizards, in 1930 he stated that the type locality of *M. multifasciata* should be in Java, and in 1956 he described *M. m. tjendikianensis,* from the Karimundjawa Achipelago in the Java Sea (between Java and Borneo). He mentioned that *M. m. tjendikianensis* differs from the *forma typica* of *M. multifasciata* by its smaller size and females possessing a bright yellow lateral band. In 2002 and 2003, Mausfeld et al. presented evidence to place *M. multifasciata,* and other associated taxa in Asia, in the genus *Eutropis* Fitzinger 1843, no longer in *Mabuya* Fitzinger 1826. Figure 2.1 presents a map with the type localities of the taxa just discussed, subspecies and junior synonyms of *E. multifasciata*.

Mausfeld and Schmitz (2003) continued working on the phylogeography of the genus *Eutropis*, suggesting the origin of *E. multifasciata* in Myanmar and South China, and not recognizing the validity of *E. m. balinensis* due to a lack of genetic differentiation. However, they did not mention their opinion on the status of *E. m. tjendikianensis*. Furthermore, several recent studies on *E. multifasciata* using genetic data, but lacking type material, do not offer an opinion about these two subspecies: (1) Datta-Roy et al. 2012 studied phylogeography of *E. multifasciata* using samples from India and Southeast Asia, Peninsular Myanmar; (2) Barley et al. (2015a,b) also studied the biogeography of *Eutropis* in Southeast Asia, mainly in the Philippines and including *E. multifasciata*; and finally, (3) Karin and Karin et al. (2016) looked at *Eutropis* biogeography in Borneo, including one sample from Java and one from Sumatra. These works suggest that more samples from Java, Sumatra, and the two subspecies described by Mertens are still needed to solve the taxonomy of these fascinating lizards.

Other widely distributed species in the genus *Eutropis* have had an intricate and dynamic taxonomic history due to the ample presence of cryptic taxa driven by a conserved fossorial morphotype. Moreover, a number of these were first described during the early 1900s, solely based on descriptive morphological characters as opposed to more robust morphometric and genetic data, which are more accurate at delimiting species boundaries. With the modern capability of rapidly collecting thousands of base-pairs of DNA and using morphometric techniques, many *Eutropis* species have been either resurrected from synonomy or erected anew (Das et al. 2008; Amarasinghe et al. 2016a,b; Batuwita 2016).

The islands of Java and Sumatra in the iconic Sundaland biodiversity hotspot (Myers 2000) are well known for their squamate diversity (Harvey et al. 2014; Iskandar et al. 2017; Wostl et al. 2017). Yet, in the last decade only few studies have investigated the taxonomy and systematics of skinks in this area (Iskandar and Erdelen 2006). Recently some new research started looking at the systematics of the *Eutropis* skinks in the area, Amarasinghe et al. (2017) studied the systematics of *Eutropis rugifera* (Stoliczka 1870) including samples from Java, Sumatra, and adjacent areas; and recently, Amarasinghe et. al. (in press) assigned a neotype for *E. multifaciata,* from Western Java, paving the way for researchers to finally clarify the taxonomy and systematics of this wide-spread and morphologically conserved species lizard. In an attempt to uncover putative cryptic diversity, herein we use mitochondrial and nuclear genetic markers, as well as traditional morphometric data, to revisit the phylogenetic relationships of *E. multifasciata,* with a large number of additional specimens from Java and Sumatra.

MATERIALS AND METHODS

Fieldwork and Sample Collection

We collected skinks during field surveys in Java and Sumatra, between January 2013 and July 2016, recording GPS coordinates as WGS84 datum with a handheld global positioning system device (Garmin® GPSMAP 64s). Specimens were euthanized with 10% Benzocaine according to humane approved protocols (UTA IACUC A12.004). Then, tissues were collected from thigh muscle or liver, to be placed in cell lysis buffer solution (0.5 M Tris/0.25% EDTA/2.5% SDS, pH = 8.2) for further DNA analysis and permanent storage. Specimens were fixed using 10% formalin and transferred to 70% ethanol for storage in museum collections. The preserved specimens are now deposited at the Museum Zoologicum Bogoriense (MZB-LIPI) and the Amphibian and Reptile Diversity Research Center of the University of Texas at Arlington (ARDRC-UTA).

DNA Extraction, PCR Amplification and Sequencing

We extracted genomic DNA using Serapure magnetic beads (Rohland and Reich, 2012). To investigate phylogenetic relationships, we amplified two mitochondrial loci, NADH dehydrogenase subunit 4 (ND4) and 16S ribosomal RNA (16S), and two nuclear loci, nerve growth-factor beta (NGFB) and RNA fingerprint protein 35 (R35). Primer sets of all loci are shown in Table 2.1. The ND4 thermocycler protocol was modified from Mausfeld et. al. (2000) as follows: 35 cycles of amplification with 45 s of denaturation at 94°C, 60 s of annealing at 50°C and 120 s of extension at 74°C. The 16S thermocycler protocol was modified from Mausfeld and Schmitz (2003) as follows: 33 cycles of amplification with 45 seconds of denaturation at 94°C, 45 s of annealing at 55°C, and 90 s of extension at 72°C. We used the nuclear touchdown protocol for NGFB and R35 amplifications, after Don et al. (1991) and Streicher et al. (2009). All polymerase chain reaction products were visualized in 1% agarose gel and purified using Serapure magnetic beads, before sequencing at the Genome Core Facility at the University of Texas at Arlington using the ABI PRISM 3100xl Genetic Analyzer (Applied Biosystems).

Resultant DNA sequences were trimmed and cleaned using Sequencher 5.1 (Gene Codes, Ann Arbor, MI, USA), and aligned in MEGA7 (Kumar et al. 2016) by ClustalW (Larkin 2007). We translated nucleotide to amino acid sequences to verify the absence of stop codons and proper alignment, and additionally edited them by eye for accuracy. We deposited all sequences in GenBank (Table 2.2).

Phylogenetic Analysis

We used Partition Finder v1.1.0 (Lanfear et al., 2012) to infer the best partition scheme and substitution models. The best scheme had five partitions: HKY+I for 16S, NGFB codon 1 and NGFB codon 3; HKY+G for ND4 codon 1; TrN+I for ND4 codon 2 and R35 codon 3; HKY+G for ND4 codon 3; and K80 for NGFB codon 2, R35 codon 1 and R35 codon 2.

To infer phylogenetic relationships, we performed two independent analyses including Parsimony, Maximum Likelihood and Bayesian. For maximum likelihood analysis (ML), we used RAxML v8.00 (Stamatakis 2014), with partition models resulting from Partition Finder, and also through the CIPRES Science Gateway and using its default parameters. The nodal support for ML was provided by bootstrapping, we considered bootstrap value higher than 70 as indicating strong support (Hillis and Bull 1993). For Bayesian Inference analysis (BI), we used MrBayes v3.2.3 (Ronquist and Huelsenbeck 2003). We ran the Bayesian analysis for 5 x 10^6 generations with 4 chains and a temperature of 0.5. We set the burn in value at 25%, discarding the first 2500 generations. We visually examined the convergence of posterior likelihood values using Tracer v1.5 (Rambaut and Drummond 2007) and ascertained that all ESS values were > 200. The nodal support for BI was assessed through posterior probabilities, we considered posterior probability values higher than 0.95 to indicatie strong support (Alfaro et al. 2003; Huelsenbeck and Rannala 2004; Mulcahy et al. 2011). We used Figtree v1.3.1 (Rambaut, 2007) for visualizing trees.

Additionally, to account for anticipated discordances between individual gene-trees, we performed species tree analysis using *Beast v2.1.2 (Drummond et al. 2012), under an HKY model and using a strict molecular clock. We used the Yule Model as a tree prior and selected the Piecewise linear and constant root as population size model. We visualized and manipulated the resultant species tree in Densitree v2.2.2 (Bouckaert and Heled, 2014).

Morphology and Inferring Species Boundaries

We used both morphological and molecular data to infer species boundaries. For our morphological analyses and for descriptive purposes, we used meristic and mensurable characters, standard morphometric characters modified from Greer (1982), Greer et al. (2000), Das et al. (2008) and Linkem et al. (2010). In addition, other descriptive characters such as color patterns and shape of the head scales were examined. For our morphological investigation we measured 15 characters and took meristic data from a further 23 characters. All measurements were taken by a single person (PT) using a Mitutoyo digital virnear calier, at the highest precision = 0.05.

Mensural characters include; snout–vent length (SVL) measured from the tip of the snout to the cloacal opening; tail length (TL) measured from the cloacal opening to the tip of the tail; axilla–groin distance (AGD) measured from the posterior margin of the forelimb insertion to the anterior margin of the hindlimb insertion; head length (HL) measured from the anterior margin of the ear opening to the tip of the snout; head width (HW) measured at the widest part of the temporal region; snout–forelimb length (SFL) measured from the anterior margin of the forelimb insertion to the tip of the snout; internarial distance (IND) measured between the dorsal margin of the two nares; interoccular distance (IOcD) measured between anterior corner of the eye ; rostrum length (RostL) measured from the anterior margin of the eye to the tip of the snout; interorbital distance (IOrD) width of orbital region at mid orbit, measured the length between middle of the left ear and right ear; eye diameter (EyD) measured at widest point on eye; tympanum diameter (TD) measured at widest point on the ear; forelimb length (FLL) measured from base of palm to elbow on the forelimb; hind limb length (HLL) measured from knee to ankle on the hindlimb; Tail width (TW) measured at its base (ventral side).

We counted the scale including number of paravertebral scales (PVSR) define how paravertebrals here; number of dorsoventral scales between the parietals, and the number of dorsal scales at the level of the cloaca; number of ventral scale (VSR) between the chin shields and preanal scales; number of midbody scale rows (MBSR) scale rows around the middle of the body usually at the center between hindlimb and forelimb; number of subdigital lamellae on Finger I (1st FiSDL); number of subdigital lamellae on Finger II (2nd FiSDL); number of subdigital lamellae on Finger III (3rd FiSDL); number of subdigital lamellae on Finger IV (4th FiSDL); number of subdigital lamellae on Finger V (5th FiSDL); number of subdigital lamellae on Toe I (1st ToSDL); number of subdigital lamellae on Toe II (2nd ToSDL); number of subdigital lamellae on Toe III (3rd ToSDL); number of subdigital lamellae on Toe IV (4th ToSDL); number of subdigital lamellae on Toe V (5th ToSDL); number of supralabials (SL) between rostral and temporal; number of infralabials (IL) between mental and lower temporal; number of loreal scales (L); number of enlarged supraoculars (SO); number of enlarge scale on lower eyelid (LE); number of chin shields (CS); number of preocular (PrOc); number of postocular (PoOc); number of supracilliaries (SCil);

We also assessed forty qualitative characters as in species descriptions below including head scales shape and degree of contact, scales shape texture and coloration.

Specimens were checked for sexual maturity by dissection, because only mature individuals were included in the statistical analyses, although other life stages were included for the description of the species, particularly with respect to their meristic data. We considered as mature females those individuals with enlarged and yolked ovarian or oviducal eggs or those with distended and/or well developed oviducts, with thick walls. Males were considered mature when with well develop testes or hemipenes. The total number of mature specimens in our analyses was 42, 19 males and 23 females. We measured specimens using a Mitutoyo digital vernier caliper with a 0.05 mm precision. The morphological data set of mature individuals was then sorted by sex, before performing discriminant analyses (canonical variate analyses, CVA) using Past v3.14 (Hammer et. al. 2001). In order to reduce the number of characters, since the number of characters must be lower than the number of samples in discriminant analysis, we first performed CVAs for the meristic data (18 characters actually we counted 23 characters but five characters do not vary among individual including SL, IL, SO, L, CS therefore we removed them for morphometric analysis but we used in species description) and morphometric data (15 characters), separately. Then, we selected only the 18 most informative characters from both analyses, encompassing both meristic and morphometric traits, and then, we performed a final CVA analyses using only these characters.

To examine species boundaries using molecular data we selected the mitochondrial protein coding locus (ND4), to perform tree-based and distance-based species-delimitation. This included Multi-rate Poisson Tree Process (mPTP; Kapli et al. 2017) and the Automatic Barcode Gap Discovery (ABGD; Puillandre et al., 2012). For both analyses, we used the tree file produced by the BEAST runs. For the mPTP analysis, we removed the outgroup, and kept default settings for all other parameters. The ABGD analysis was run on the online server, with default settings. We ran the analyses using both the Jukes-Cantor (JC69) and Kimura (K80) TS/TV = 2.0, models.

RESULTS

Phylogenetic Reconstruction and Genetic Distances

Our concatenated data set recovered a phylogenetic tree which divided *Eutropis multifasciata* and its subspecies into four well supported clades (Fig. 3.2), although the relationships among these are not well supported. A northern clade consists of populations currently known as *E. m. multifasciata*, from northern Sumatra, Borneo, Philippines, and peninsular and mainland southeast Asia, including a sample from the type locality of *Plestiodon sikkimensis* in northeast

India (BI: 0.92, ML: 46). A second clade, a southwestern clade, is also currently known as *E. m. multifasciata*, and includes populations from Southern Sumatra—Lampung, and Western Java (BI: 0.79, ML: 86). This southwestern clade includes the neotype from Banten, Java (Amarasinghe et. al., in press). A third clade, southcentral, includes populations assignable to the subspecies *E. m. tjendikianensis* (see below) from Central Java and from islands to the northeast, including Ceram in the Moluccas and Luzon in the Philippines (BI: 0.71, ML: 95). The fourth clade, southeastern, contains populations assignable to the subspecies *E. m. balinensis* (see below), from East Java and Bali (BI: 0.91, ML: 94).

The coalescent species tree analysis (Fig. 3.3) recovered a topology comparable to that produced by the concatenated method (Fig. 3.2), with phylogenetically distinct and genetically distant northern, southwestern, southcentral, and southeastern main groups. However, there was support for the relationships among the main clades. The southwestern clade of *E. m. multifasciata* was depicted as sister to a clade comprising of the southcentral and southeastern clades. This last relationship, between the southcentral and southeastern clades, needs to be interpreted with caution, given a low posterior support, 0.56, as opposed to the high support for the remaining major internal clades (≥ .96).

One striking detail of our results is that the northern *E. m. multifasciata* clade is not only phylogenetically distinct but also genetically distant (raw distances based on the ND4 locus, Table 2.3) from the other lineages, with more than 5.76% raw genetic distance. Additionally, a substantial 3.13%–4.13% raw genetic distance is found between the three distinct clades occurring in Java.

Morphological and Molecular Species Delimitation

To support our phylogenetic hypotheses suggesting four species encompassed in our sampling of the *Eutropis multifasciata* complex in Sumatra and Java we used morphological and molecular species delimitation. Our morphological species delimitation using CVA on the 18 most informative characters from both the meristic and morphometric data sets and on the sexes separated were able to distinguish among the four groups/putative species (Table 2.4). The male CVA scatter plot consisting of the first two axes completely discriminates among these groups (Fig. 2.4A). The eigenvalue and percentage of variation explained for the first axis are 14.59 and 65%, respectively, with the strongest loadings by SVL (1.7661), AGD (0.8775), SFL (0.592), and PVSR (-0.5654). The eigenvalue and percentage of variation explained by the second axis are 6.25 and 28%, respectively, with the strongest loadings by SVL (-2.0847), AGD (-0.9167), PVSR (0.6994), and HL (-0.4880). For the third axis, we get an eigenvalue of 1.58 and a 7% variance explained. The highest loadings for this third axis are from PVSR (0.9295), 4th TSDL (0.4089), 3rd FSDL (0.3489), and AGD (-0.3241).

The female CVA results are similar to those for the males, separating the four species. Figure 2.4B shows the scatter plot for the first two axes. The first axis presents an eigenvalue of 65.42 and explains 67% of the variance. The highest loadings on the first axis are by SVL (-1.2471), AGD (-0.7232), SFL (-0.3296), and HL (-0.2337). The eigenvalue of the second axis is 25.39 and explains 26% of the variance. The highest loadings for this second axis are by AGD (-0.2292), VSR (-0.1722), SVL (-0.1400), and SFL (-0.0902). The third axis had an eigenvalue of 7.01 and an explained 7% of the variance, with SVL (-2.4616), AGD (-1.4712), SFL (-0.6960), and HL (-0.5320) having the highest loadings. In summary, CVAs for both males and females separate dramatically between the four-putative species hypothesized by the phylogenetic analyses. Eight characters are the main discriminators among the species, SVL, AGD, SFL, HL, PVSR, VSR, 4th TSDL, and 3rd FSDL.

Our molecular species delimitation models support our concatenated and species tree phylogenies and discriminant analyses results. The mPTP analysis supports a four-species model, with the clades supported by the previous analyses. In addition, the results for ABGD showed six partitions with a prior maximal distance (*P*) range from 0.0010 to 0.0129. The initial partitions supported two species, northern/southwestern and southcentral/southeastern. However, the recursive partitions were stable at supporting our hypothesis with four species.

DISCUSSION

We found that our phylogenetic reconstruction techniques, using a concatenated gene-tree and a coalescent base species-tree with two nuclear and two mitochondrial genes, support the same four primary clades. These provide a hypothesis in which *E. multifasciata* is a complex of four candidate species in Sumatra and Java, distinct from each other. A northern clade is separate from the groups that occur in Java, southwestern, southcentral and southeastern. And within the Javan group, the three currently recognized subspecies are supported as distinct, based on geography, namely *E. m. multifasciata*, *E. m. tjendikianensis*, and *E. m. balinensis*. Since the Javan population bearing the name *E. multifasciata* is distinct from those to the north, we resurrect the name *E. sikkimensis* for the later populations. From this point on we will recognize these as different species, and will explain the taxonomic molecular and morphological support for these, type affinities, and the extent of the ranges of these species. These four groups are also support Also, from this point forward we follow the results of our coalescent species-tree, our preferred topology because of having higher internal node supports as compared to those of the concatenated-matrix analysis. According to our preferred topology, *E. tjendikianensis* is sister to *E. balinensis,* both sister to *E. multifasciata,* and these three, as a clade, sister to *E. sikkimensis*.

Our phylogenetic relationships are similar to those depicted by the excellent but still unpublished thesis of Karin (2016), where he found the same major groups that we find and two more, one from S. Sulawesi and the Philippines, and one from Bukit Kana, Sarawak. Karin's (1996) relationships, using the mitochondrial gene ND2 vary between his BI and ML analyses and his time-tree. His time-tree is more similar to our preferred topology, with *E. sikkimensis* (his *E. multifasciata* from Indochina, West Malaysia, Sumatra, Borneo and Central/West Philippines clade)*,* sister to a clade of *E. multifasciata* (his *E. multifasciata* from Java, Sulawesi and S. Philippines clade)*, E. balinensis* (his *E. multifasciata* from Bali clade)*,* and *E. tjendikianensis* (his *E. multifasciata* from N. Philippines and Sulawesi clade). He also mentions that *E. balinensis* is probably also found in Java. Barley et al. (2013, 2015b) also found that *E. multifasciata* from mainland Southeast Asia (India, Myanmar) differs from those populations in the islands of the Philippines and Sulawesi.

Our findings also support those of Mausfeld and Schmitz (2003) based on mtDNA and regarding *E. multifasciata*. They found two major clades of *E. multifasciata*, one from mainland Southeast Asia consisting of samples from Myanmar, China and Kalimantan (Borneo), and another of "insular" clades, consisting of samples from Java, Bali, Ceram, and the Philippines. We found that those samples from mainland southeast Asia and Borneo correspond to *E. sikkimensis*, samples from West Java to typical *E. multifasciata*, those samples from Luzon and

Ceram group with our *E. tjendikianensis* from Central Java, and samples from Bali group with our *E. balinensis*. Mausfeld and Schmitz (2003) did not recognize *E. m. balinensis,* due to low genetic differentiation from other populations. However, their work was based only on the 16S and 12S genes, non-protein coding mitochondrial molecules that are relatively slow and likely with incomplete lineage sorting. However, our ND4 protein coding sequences show 3.13%–4.13% divergence among Javan species, with Javan species forming a monophyletic clade, which makes biogeographic sense. Grismer et al. 2017 also indicated 3.6% divergence of ND2 protein coding sequences as species boundary of sister species of skinks in the genus *Tytthoscincus* in Peninsular Malaysia. In addition, Schmitt et al. (2000) in their excellent work using allozymes and morphology to analyze the variation of *E. multifasciata* along the Banda Arcs of southeast Indonesia did not comment on the validity of subspecies. Their samples were distributed from Bali to Yamdena and displayed very little genetic differentiation, not even to recognize subspecific differentiation. The authors did not compare any samples beyond the Banda Arc. All of their samples belong to the Lesser Sunda islands and the southern Maluku islands, we consider them all to be *E. balinensis*.

All previous studies had little or no genetic data from Java, including the type localities of the three previously described and recognized subspecies of *E. multifasciata*, making any possibilities of solving the taxonomy of the group impossible. This study brings genetic data from topotypic *E. multifasciata,* the neotype. In addition, it includes near topotypic *E. m. balinensis* and *E. m. tjendikianensis*, this last for the first time. All of these subspecies form a monophyletic clade, with significant phylogenetic support and high genetic distance between themselves.

In order to validate and elevate to species level *E. sikkimensis*, *E. tjendikianensis* and *E. balinensis* we examined morphological data to confirm our taxonomy suggested by our genetic data. Previous studies have used discriminant analysis (DA or CVA in case of multiple groups) in taxonomic studies, suggesting this to be a good tool for finding morphological characters useful in differentiation (De Queiroz 1997, Viscosi and Cardini 2011). In addition, discriminant analysis was used for examining species boundaries in *Eutropis* (Barley et al. 2013). After detecting cryptic species with molecular data Barley et al. (2013) also distinguished between most of these species of the *Eutropis* complex in the Philippines through the use of discriminant analysis, except for some with highly conserved external morphology. Similarly, Schmitt et al. (2000) also looked for differences among Banda Arc populations of *Eutropis*, finding little variation.

Because we had a priori molecular knowledge of population differentiation and putative species and we wanted to maximize morphological demarcation among these, we choose discriminant analysis (CVA) instead of principal component analysis (PCA). We used both morphometric data and meristic data, as discriminant analysis is also suitable for meristic data while PCA is not (Keck and Near 2013), and previously used in taxonomic studies (Ronals 1936; Buholzer; 1978; Agrawal et.al. 2008). Our CVA results, separating sexes, show clear separation among species, contrary to previous works (e.g., Schmitt et al 2000, Barley et al. 2013). Our species are closely related from each other, they can be considered as incipient species, but they still show morphological differentiation (Table 2.5). Our putative species are confirmed and we provide a key to the species of the *E. multifasciata* complex in Java and Sumatra based on some of these characters used (below).

Molecular species delimitations are objective approaches to indicate species boundaries, they model speciation events. A previous study used ND4 to delimit species of squamates and suggested that mPTP and ABGD were the most stable methods and suitable for single locus delimitation (Blair and Bryson 2017). As a suggested, here we used mPTP, which is a tree-based approach, and ABGD, which is a distance-based approach, to examine species boundaries. The mPTP model is applied from a PTP model, which uses maximum likelihood to model substitutions on branches process to evaluate speciation (Zhang et al. 2013). The mPTP method uses multiple exponential distributions for delimiting species considering unique evolutionary histories (Kaply et al. 2017). Our mPTP results support our putative four species, *E. sikkimensis*, *E. multifasciata*, *E. tjendikianensis,* and *E. balinensis*. In addition, the ABGD model uses a species barcode gap—when intra-specific divergence is smaller than inter-specific divergence—to distinguish species (Puillandre et al. 2012). Although there is no agreement as to how to delimit species on ABGD, we can decide species boundary base on stability of the initial and recursive partitions. The initial partitions always show at least two species separating, *E. sikkimensis* from *E. multifasciata* sensu lato, and the recursive partitions were always stable with full support of the four species across all rage of intraspecific divergence priors (P). Puillandre et al. 2012 also suggested that although initial partition shows a number of species close to that of classical taxonomy, recursive partitions were better in heterogeneities. In case of genetic distance, our *E. multifasciata* complex also heterogeneities since *E. sikimensis* speperates from other sister species in Java about 5.76% to 8.01% and our three species in Java speperate from each other about 3.13% to 4.13% of genetic distance. Our different approaches to species delimitation and differentiation show concordant results, and with confidence we distinguish *E. sikkiemensis*, *E. multifasciata*, *E. tjendikianensis,* and *E. balinensis* as full species.

Based on our preferred phylogeny, the distribution of *E. sikkimensis* from Sumatra to mainland Southeast Asia and Borneo might be explained by land connection in the Miocene (20-10 Mya). This timing is supported by Karin et al. (2016). At that time, Java was not yet land positive, but then gradually emerged as several islands, starting from the west. These islands led to colonization and isolation of *E. multifasciata* populations, the three lineages now present in Java. In the late Miocene to Early Pliocene, 10–5 Mya, connections occurred between the Malay Peninsula, Borneo, and Sumatra, a time in which southern Sumatra was connected to west Java. This last event explains why *E. multifasciata* is present in southern Sumatra and western Java, a pattern similar to that of other species of herpetofauna (Hamidy and Matsui 2017). However, the relationships of the Sumatran and Javanese populations with those in the Philippines, Sulawesi, and the Maluku and Lesser Sunda islands are more difficult to explain due to our limited data and geologic data of the region.

With our phylogenetic relationships and species delimitation evidence and supported by the general linage species concept (de Queiroz 1998) we recognize and support the four putative-species discussed above. We resurrect a synonym and elevate to species level three subspecific taxa in accordance to the taxonomic priority rules of the International Commission and Code on Zoological Nomenclature (ICZN 1999). We also take into account the results in the works of Schmitt et al. (2000) and Karin (2016) to supplement our knowledge on the extent of the distribution of the putative species involved. The priority name for the northern populations—mainland southeast Asia, peninsular Malaysia, northern Sumatra, Borneo and the western

Philippines—is *E. sikkimensis* (Gray), a species described in 1853 from the state of Sikkim in northeast India (close to the state of Assam, where genetic data was available). The southwestern populations—southern Sumatra (Province of Lampung), western Java (Province of West Java and Banten), western Sulawesi (provinces of Southern, Central and Northern Sulawesi), and the Zamboanga Peninsula of Quezon in the Philippines—all correspond to *E. multifasciata* (Kuhl 1820), the first form described from this complex and from which we have included neotype genetic data. *Eutropis tjendikianensis* (Mertens 1956) represents the southcentral populations—from the Karimunjawa islands of the coast of Central Java (type locality), Central Java, Eastern Sulawesi and the northern Moluccas to at least Seram, and Luzon, in the northern Philippines. *Eutropis balinensis* (Mertens 1927) inhabits East Java, Bali (type locality with genetic data), and the Banda Arc to at least the island of Yamdena. Below we diagnose, describe, and provide synonomies and a key for *E. balinensis, E. multifasciata, E. sikkimensis,* and *E. tjendikianensis*. We also provide the standard measurements of all type specimen of the common sun skink species complex (Table 2.6). We hope that our study will raise our understanding of biodiversity and biogeography in the Sunda Shelf and across important biogeographic areas, and at the same time, that it will spark further research in systematics in this poorly known biological hotspot.

Systematic Accounts

Eutropis sikkimensis (Gray 1853)

(Figs. 2.5A, 2.6A, Tables 2.5–2.6)

Euprepes sebae Dumeril and Bibron 1839:692, in part; Smith 1935:269 designated a lectotype from Batavia (specimen 2956-2837) to avoid confusion, becoming a synonym of *E. multifasciata* (Kuhl 1820), the syntypes included multiple species and the authors description seemed unjustified.

Plestiodon sikkimensis Gray 1853:388. [Misspelled as *Plestrodon sikkimensis*]

Tropidolepisma macrurus Bleeker 1860:328.

Mabuia multifasciata (Kuhl 1820): Boulenger (1887:186), in part; De Rooij (1915:162), in part.

Mabuia monticola Annandale 1905:143.

Mabuya multifasciata multifasciata (Kuhl 1820): Smith (1935:268), in part.

Mabuya multifasciata (Kuhl 1820): Taylor (1963:950), in part; *Mabuya multifasciata* Hendrickson (1966:65), in part; Grandison (1972:82), in part; Manthey and Grossmann (1997:271), in part; Cox et al. (1998:110) in part; Ziegler (2002:199), in part; Malkmus et al. (2002:276), in part.

Eutropis multifasciata (Kuhl 1820): Mausfeld and Schmitz (2003:161), in part; Nguyen et al. (2009:249), in part; Das (2010:233), in part; Grismer (2011:570), in part; Chan-ard et al. (2015:107), in part.

Eutropis multifasciatus (Kuhl 1820): Hecht et al. (2013:535), in part; Ziegler et al. (2015:28). [Misspelling]

Holotype.—BMNH 1946.8.19.3. A juvenile (SVL = 38.0 mm) from Sikkim Himalaya [Sikkim State], India; Collected by Dr. Joseph Hooker.

Diagnosis.—A relatively large species of the *Eutropis multifasciata* complex (males to 111.3 mm, females to 121.2 mm, SVL)*,* However from Grismer 2011, Male SVL can reach 137 mm and female SVL can reach 132 mm. similar in size to *E. multifasciata*; snout tip usually not reddish; with postnasal scales; lower eyelid transparent, with 5 enlarged shields, sometimes 4 to 6; adult males and females with orange lateral bands; sides of body with prominent and dark dorsolateral band in females, light ocelli on lower flanks; body robust; prominent keels on upper body dorsals 3–5; anterior and posterior limbs barely overlap when adpressed.

Comparison with Southeast Asian *Eutropis* and *Toenayar*.—*E. sikkimensis* differs from *E. longicaudata, E. macularia, E. rugifera* and *T. novemcarinata* in having postnasal scales; from *E. indeprensa* in having no stripe from labia to forelimbs; from *E. rudis* in having 42–47 paravertebral scale rows (vs. 34–38).

Most *E. sikkimensis* lack reddish color on snout tip, rostral and first supralabial (present in most *E. multifasciata*, *E. tjendikianensis* and *E. balinensis*); have orange lateral bands, when bands present in adult males and females (vs. yellow in most males and orange in most females of *E. multifasciata*, yellow in both sexes of *E. tjendikianensis,* and with both orange and yellow in *E. balinensis*); from *E. tjendikianensis* and *E. balinensis* additionally differs in having 5 (sometimes 4, 6, or rarely 7) lower eyelid enlarged scales (vs. 4, rarely 5); additionally from *E. balinensis* differs in having 42–46 paravertebral scale rows in males (vs. 48–55).

Description.—Based on six adult males and seven adult females. All measurement ranges for adult individuals are shown in Table 5, those for the type in Table 2.6. Supranasals usually separate, rarely in contact; postnasals present; frontonasal broader than long; frontal longer than broad; prefrontals in contact; supraoculars 4; frontoparietals in contact; pineal eye present on interparietal; parietals in contacts; pair of nuchals 1, with keels; loreals 2, subequal; enlarged scales of lower eyelid usually 5, rarely 4 or 6; tympanum sunk in oval ear opening, anterior lobular scales 4, at most; supralabials 6, fifth largest, under eye; supracilliaries 6, rarely 7; preoculars 2, lower is largest; mental present; postmental present; pairs of chin shields 2; infralabials 6; dorsals with prominent keels, usually 3 keels, rarely 4 or 5; ventrals smooth, sometimes striated; upper part of lateral scales keeled, like dorsals, lower part smooth, like ventrals; preanals slightly enlarged; subcaudals not enlarged; midbody scale rows 32–33 in males, 31–34 in females; paravertebral scale rows 42–46 in males, 43–47 in females; ventral scale rows 54–59 in males, 57–62 in females; finger I subdigital lamellae 6–7, both sexes; finger II subdigital lamellae 10–11 in males, 10–12 in females; finger III subdigital lamellae 12–13 in males, 12–14 in females; finger IV subdigital lamellae 12–14, both sex; finger V subdigital lamellae 8–9 in males, 8–10 in females; toe I subdigital lamellae 7–8 in males, 6–8 in females; toe II subdigital lamellae 12–14 in males, 12–13 in females; toe III subdigital lamellae 14–16, both sexes; toe IV subdigital lamellae 16–19 in males, 16–20 in females; toe V subdigital lamellae 10–13 in males, 11–13 in females.

Color in life.—Dorsum in males, uniform brown, gray, or bronze color, in females uniformly colored, like males, or having 6–8 black longitudinal lines; flanks in males uniform, similar to dorsum but with orange band, females with thick and dark dorsolateral band above and light ocelli below, some females with orange lateral band; venter uniform grey or white, yellow throat in some females; forelimbs and hindlimbs similar in color to body, just slightly darker.

Distribution.—*Eutropis sikkimensis* ranges from northeastern India, through south China and mainland southeast Asia (Myanmar, Thailand, Laos, Cambodia, Vietnam and Peninsular Malaysia), through Borneo and the western and central islands of the Philippines, and in northern and central Sumatra (excluding the province of Lampung). It is found in many different types of habitats, from low (0 m) to high in elevation (1724 m).

Eutropis multifasciata (Kuhl 1820)

(Figs. 2.5B, 2.6B, Tables 2.5–2.6)

Scincus multifasciatus Kuhl 1820:126.

Euprepes sebae Duméril and Bibron 1839:692, in part; Gravenhorst (1851:332), in part; Smith 1935:269 designated a lectotype from Batavia (specimen 2956-2837) to avoid confusion, becoming a synonym of *E. multifasciata* (Kuhl 1820), the syntypes included multiple species and the authors description seemed unjustified.

Mabuya multifasciata (Kuhl 1820): Fitzinger (1826:52);

Mabuia multifasciata (Kuhl 1820): Boulenger (1887:186), in part; De Rooij (1915:162), in part; Dammerman (1929:65), in part. [Misspelling]

Mabuya multifasciata (Kuhl 1820): Smith 1935:268), in part; Taylor (1963:950), in part; *Mabuya multifasciata* Hendrickson (1966:65), in part; Grandison (1972:82), in part;

Manthey and Grossmann (1997:271), in part; Cox et al. (1998:110) in part; Ziegler (2002:199), in part; Malkmus et al. (2002:276), in part.

Eutropis multifasciata (Kuhl 1820): Mausfeld and Schmitz (2003:161), in part; Nguyen et al. (2009:249), in part; Das (2010:233), in part; Grismer (2011:570), in part; Chan-ard et al. (2015:107), in part.

Eutropis multifasciatus (Kuhl 1820): Hecht et al. (2013:535), in part. [Misspelling]

Neotype.—MZB 11912 (designated by Thasun et al. in press). An adult male from Jalan Tanah, trail from Cilitung to the Pulosari Waterfall, Pandeglang, Banten Province (previously West Java), Indonesia, 525 m (Lat -6.32756, Long 105.95988), collected by Irvan Sidik, Ahmad Muammar Kadafi, and Eric N. Smith on 20 December 2013.

Diagnosis.—A relatively large species of the *Eutropis multifasciata* complex (males to 116.9 mm, females to 118.1 mm, SVL), similar in size to *E. sikkimensis*; tip of snout reddish; with postnasal scales; lower eyelid transparent, with 5 enlarged shields, sometimes 6; adult males with yellow lateral bands, rarely orange, in females orange only; sides of body with prominent and dark dorsolateral band in females, light ocelli lower on flanks; body robust; prominent keels on upper body dorsals 3–5; anterior and posterior limbs barely overlap when adpressed.

Comparison with Southeast Asian *Eutropis* and *Toenayar*.—*E. multifasciata* differs from *E. longicaudata, E. macularia, E. rugifera* and *T. novemcarinata* in having postnasal scales; from *E. indeprensa* in having no stripe from labia to forelimbs; from *E. rudis* in having 42–47 paravertebral scale rows (vs. 34–38).

Most *E. multifasciata* with reddish snout tip, rostral and first supralabial (vs. most *E. sikkimensis* with no reddish snout tip); yellow lateral bands in males, when colored lateral bands present, rarely orange (vs. always orange in males of *E. sikkimensis,* when present); lower eyelid enlarged scales 5–6 (vs. 4 in most *E. tjendikianensis*, rarely 5); females with orange lateral bands, when present (vs. yellow lateral bands in females of *E. tjendikianensis*); larger overall body size (vs. smaller body size in *E. tjendikianensis* and *E. balinensis*); paravertebral scale rows 42–46 in males (vs. 48–55 in male of *E. balinensis*); females with no brightly colored bands, with thick and prominent dark dorsolateral bands (vs. faded dark dorsolateral bands in females of *E. balinensis*); having light ocelli only on lower part of flanks (vs. ocelli uniformly distributed on flanks of female *E. balinensis*).

Description.— Based on eight adult males and six adult females. All measurement ranges for adult individuals are shown in Table 2.5, those for the type in Table 2.6. Supranasals usually separate, rarely in contact; postnasals present; frontonasal broader than long; frontal longer than broad; prefrontals in contact; supraoculars 4; frontoparietals in contact; pineal eye present on interparietal; parietals in contact; a pair of nuchals present, with keels; loreals 2, subequal; enlarged scales on lower eyelid usually 5, rarely 4 or 6; tympanum sunk in oval ear opening, anterior lobular scales 4, at most; supralabials 6, fifth largest, under eye; supracilliaries 6, rarely 7; preoculars 2, lower is largest; mental present; postmental present; infralabials 6; dorsals with prominent keels, usually 3 keels, rarely 4 or 5; ventrals smooth, sometimes striated; upper part of lateral scales keeled, like dorsals, lower part smooth, like ventrals; preanals slightly enlarged; subcaudals not enlarged; midbody scale rows 31–34 in males, 32–34 in females; paravertebral scale rows 42–45 in males, 44–47 in females; ventral scale rows 53–61 in males, 54–59 in females; finger I subdigital lamellae 6–7 in males, 5–6 in females; finger II subdigital lamellae 10–12 in males, 10–11 in females; finger III subdigital lamellae 12–14 in males, 12–13 in females; finger IV subdigital lamellae 12–15 in males, 13–14 in females; finger V subdigital lamellae 8–9, both sexes; toe I subdigital lamellae 7–8, both sexes; toe II subdigital lamellae 11–13, both sexes; toe III subdigital lamellae 15–16 in males, 15–17 in females; toe IV subdigital lamellae 17–19, in both sexes; toe V subdigital lamellae 12–13, both sexes.

Color in life.—Dorsum in males uniformly gray or bronze, females uniformly colored, like males, or having 6–8 black longitudinal lines; flanks in males uniform in color, similar to dorsum, usually with a yellow band, rarely orange, females with thick and dark dorsolateral band above and light ocelli below, some females with orange lateral band; snout tip, rostral and first supralabial reddish; venter in males and females, uniform beige, grey, or white; forelimbs and hindlimbs similar in color to body, just slightly darker.

Distribution.—*Eutropis multifasciata* inhabits the province of Lampung in south Sumatra, and the provinces of Banten and West Java. It is also found in south, western, central and northern Sulawesi, and in the Zamboanga Peninsula in the southern Philippines. *E. multifasciata* has been found in many different types of habitats, from low (0 m) to high elevation (1548 m).

Eutropis tjendikianensis (Mertens, 1956)

(Figs. 2.5C, 2.6C, Tables 2.5–2.6)

Euprepes sebae Dumeril and Bibron 1839:692, in part; Smith 1935:269 designated a lectotype from Batavia (specimen 2956-2837) to avoid confusion, becoming a synonym of *E. multifasciata* (Kuhl 1820), the syntypes included multiple species and the authors description seemed unjustified.

Mabuia multifasciata (Kuhl 1820): Boulenger (1887:186), in part; De Rooij (1915:162), in part; Dammerman (1929:65), in part. [Misspelling]

Mabuya multifasciata multifasciata (Kuhl 1820): Smith 1935:268), in part, by implication.

Mabuya multifasciata (Kuhl 1820): Smith 1935:268), in part; Taylor (1963:950), in part; *Mabuya multifasciata* Hendrickson (1966:65), in part; Grandison (1972:82), in part; Manthey and Grossmann (1997:271), in part; Cox et al. (1998:110) in part; Ziegler (2002:199), in part; Malkmus et al. (2002:276), in part.

Mabuya multifasciata tjendikianensis Mertens 1956:253, 255.

Eutropis multifasciata (Kuhl 1820): Grismer (2011:570), in part; Chan-ard et al. (2015:107), in part.

Eutropis multifasciata tjendikianensis Mertens 1956: Mausfeld and Schmitz (2003:167); Nguyen et al. (2009:250).

Eutropis multifasciatus (Kuhl 1820): Hecht et al. (2013:535), in part. [Misspelling]

Holotype.—SMF 55147. An adult female form Tjendikian island, Karimunjawa Archipelago, Central Java, Indonesia. Collected by A. Hoogerwerf on 17 February 1955. Original description mentions holotype residing at the Museum Zoologicum Bogoriense, MZB.

Diagnosis.—A relatively small species of the *Eutropis multifasciata* complex (males to 102.9 mm, females to 106.1 mm, SVL)*,* similar in size to *E. balinensis*; snout tip reddish in most individuals; postnasal scales present; lower eyelid transparent, with 4 enlarged shields, rarely 5; yellow bands in adult males and female with colored flanks; dark dorsolateral band faded in females, light ocelli bellow; body robust; prominent keels on upper body dorsals 3–5; anterior and posterior limbs barely overlap when adpressed.

Comparison with Southeast Asian *Eutropis* and *Toenayar*.—*E. tjendikianensis* differs from *E. longicaudata, E. macularia, E. rugifera* and *T. novemcarinata* in having postnasal scales; from *E. indeprensa* by having no stripe from labia to forelimbs; from *E. rudis* in having 42–47 paravertebral scale rows (vs. 34–38).

Most *E. tjendikianensis* with reddish snout tip (vs. usually with no reddish snout tip in *E. sikkimensis*); a yellow band when with bright colored flanks (vs. orange band when colored flank in *E. sikkimensis*); smaller body size (vs. larger in *E. sikkimensis* and *E. multifasciata*); enlarged scales on lower eyelid 4, rarely 5 (vs. 5, rarely 6 in *E. multifasciata,* and rarely 4, 6 and 7 in *E. sikkimensis*); females with yellow lateral bands, when with bright flanks, and faded dark dorsolateral band, when present (vs. orange and/or dark and prominent lateral bands in female *E. multifasciata*); males with 42–46 paravertebral scale rows (vs. 48–55 in male *E. balinensis*), female with 45–46 paravertebral scale rows (vs. 46–50 in female *E. balinensis*).

Description.—Based on two adult males and five adult females. All measurement ranges for adult individuals are shown in Table 5, those for the type in Table 2.6. Supranasals usually separate, rarely in contact; frontonasal broader than long; frontal longer than broad; postnasals are present; prefrontals in contact; supraoculars 4; frontoparietals in contact; pineal eye present on interparietal; parietals in contacts; pair of nuchals 1, with keels; loreals 2, subequal; enlarged scales of lower eyelid usually 4, rarely 5; tympanum sunk in oval ear opening, anterior lobular scales 4, at most; supralabials 6, fifth largest, under eye; supracilliaries 5 or 6; preoculars 2, lower is largest; mental present; postmental present; infralabials 6; dorsals with prominent keels, usually 3 keels, rarely 4 or 5; ventrals smooth; upper part of lateral scales keeled, like dorsals, lower part smooth, like ventrals; preanals slightly enlarged; subcaudals not enlarged; midbody scale rows 32–33 in males, 32–33 in females; paravertebral scale rows 43–45 in males, 45–46 in females; ventral scale rows 57–58 in males, 53–58 in females; finger I subdigital lamellae 6, both sexes; finger II subdigital lamellae 10 in males, 9–10 in females; finger III subdigital lamellae 12–13 in both sexes; finger IV subdigital lamellae 13 in males, 12–13 in females; finger V subdigital lamellae 8 in males, 8–9 in females; toe I subdigital lamellae 7–8 in males, 7 in females; toe II subdigital lamellae 10–11 in males, 10–12 in females; toe III subdigital lamellae 15 in males, 14–15 in females; toe IV subdigital lamellae 16–17 in males, 16–18 in females; toe V subdigital lamellae 11–12 in males, 10–12 in females.

Color in life.—Dorsum in males uniform brown or olive green, females like males or having 4–6 black longitudinal lines, usually fusing with each other; flanks in males uniform, similar to dorsum but with yellow band, females with a faded dark dorsolateral band above and light ocelli below, some female with yellow lateral band; snout tip, rostral and first supralabial, reddish; venter in males and female uniformly beige, yellow or grey; forelimbs and hindlimbs similar in color to body, just slightly darker or yellowish.

Distribution.—*Eutropis tjendikianensis* is known from Central Java, the island of Tjendikian in the Karimundjawa Archipelago, Central Sulawesi, Ceram, and the island of Luzon in the northern Philippines. In Central Java we have found this species in primary forest and at a mid-elevation (688 m), but the type locality is from near sea-level.

Eutropis balinensis (Mertens, 1927)

(Figs. 2.5D, 2.6D, Tables 2.5–2.6)

Euprepes sebae Dumeril and Bibron 1839:692, in part.

Mabuia multifasciata (Kuhl 1820): Boulenger (1887:186), in part; De Rooij (1915:162), in part; Dammerman (1929:65), in part. [Misspelling]

Mabuya multifasciata balinensis Mertens 1927:181: Mertens (1930:147); Smith (1935:268), in part [by implication].

Mabuya multifasciata multifasciata (Kuhl 1820): Smith (1935:268), in part.

Mabuya multifasciata (Kuhl 1820): Taylor (1963:950), in part; *Mabuya multifasciata* Hendrickson (1966:65), in part; Grandison (1972:82), in part; Manthey and Grossmann (1997:271), in part; Cox et al. (1998:110) in part; Schmitt et al. 2000:241), in part, discussed as *Mabuya mutifasciata baliensis* [*sic.*]; Ziegler (2002:199), in part; Malkmus et al. (2002:276), in part.

Eutropis multifasciata (Kuhl 1820): Mausfeld and Schmitz (2003:161), in part; McKay (2006:68), in part, discussed as *Eutropis multifasciata baliensis* [*sic.*]; Nguyen et al. (2009:249), in part; Grismer (2011:570), in part; Chan-ard et al. (2015:107), in part.

Eutropis multifasciatus (Kuhl 1820): Hecht et al. (2013:535), in part. [Misspelling]

Eutropis multifasciata balinensis (Mertens 1927): Das (2010:233).

Mabuya multifasciata subspecies incerta. Mertens 1956:253, 255: from Seruni and Genting islands in the Karimundjawa Archipelago.

Eutropis multifasciata (Kuhl 1820): Somaweera 2017:82

Holotype.—SMF 22087. An adult male from Gitgit, 500 m, north Bali, Indonesia. Collected by Robert Mertens on 1 August 1927.

Diagnosis.— A relatively small species of the *Eutropis multifasciata* complex (males to 103.6 mm, females to 94.5 mm, SVL), However from Schmitt et al. 2000, this species in Lesser Sunda male can reach 120 ± 0.00 mm and female can reach 109.67 ± 8.08 mm) similar in size to *E. tjendikianensis*; snout tip reddish in most individuals; postnasal scales present; lower eyelid transparent, with 4 enlarged shields, rarely 5; yellow bands in adult males and females with colored flanks, rarely orange; dark dorsolateral band faded in both sexes; light ocelli numerous across flanks, particularly in females; body robust; prominent keels on upper body dorsals 3–5; anterior and posterior limbs barely overlap when adpressed.

Comparison with Southeast Asian *Eutropis* and *Toenayar*.—*E. balinensis* differs from *E. longicaudata, E. macularia, E. rugifera* and *Toenayar novemcarinata* in having postnasal scales; from *E. indeprensa* in having no stripe from labia to forelimbs; from *E. rudis* in having 46–55 paravertebral scale rows (vs. 34–38).

E. balinensis differs from other *E. multifasciata* complex species in having more paravertebral scale rows, 46–55 (vs. 42–47 in *E. sikkimensis* and *E. multifasciata*, and 43–46 in *E. tjendikianensis*); most *E. balinensis* with reddish snout tip (vs. usually with no reddish snout tip in *E. sikkimensis*; enlarged scales on lower eyelid 4, rarely 5 (vs. 5, rarely 6 in *E. multifasciata*, and rarely 4, 6 and 7 in *E. sikkimensis*); females with faded dark dorsolateral bands (vs. prominent and dark when present in female *E. multifasciata* and *E. sikkimensis*).

Description.— Based on five adult males and six adult females. All measurement ranges for adult individuals are shown in Table 5, those for the type in Table 2.6. Supranasals usually separate, rarely in contact; frontonasal broader than long; frontal longer than broad; postnasals are present; prefrontals in contact; supraoculars 4; frontoparietals in contact; pineal eye present on interparietal; parietals in contacts; pair of nuchals 1, with keels; loreals 2, subequal; enlarged scales of lower eyelid usually 4, rarely 5; tympanum sunk in oval ear opening, anterior lobular scales 4, at most; supralabials 6, fifth largest, under eye; supracilliaries 6; preoculars 2, lower is largest; mental present; postmental present; infralabials 6; dorsals with prominent keels, usually 3 keels, rarely 4 or 5; ventrals smooth, sometimes striated; upper part of lateral scales keeled, like dorsals, lower part smooth, like ventrals; preanals slightly enlarged; subcaudals not enlarged; midbody scale rows 32–34 in males, 34–36 in females; paravertebral scale rows 48–55 in males, 46–50 in females; ventral scale rows 56–65 in males, 56–61 in females; finger I subdigital lamellae 6–8 in males, 6 in females; finger II subdigital lamellae 10 in both sexes; finger III subdigital lamellae 12–13 in both sexes; finger IV subdigital lamellae 14–15 in males, 13–14 in females; finger V subdigital lamellae 8–9 in males, 8 in females; toe I subdigital lamellae 7–9 in males, 7–8 in females; toe II subdigital lamellae 11–12 in males, 11 in females; toe III subdigital lamellae 15–16 in males, 13–15 in females; toe IV subdigital lamellae 18–19 in males, 16–18 in females; toe V subdigital lamellae 12–14 in males, 11–12 in females.

Color in life.— Dorsum in males, uniform brown or olive green; in females uniformly colored, like males, or having 6–8 black longitudinal lines; flanks in males uniform, similar to dorsum but usually with a yellow or rarely orange band, females with a faded dark band and numerous light ocelli; snout tip, rostral and first supralabial, reddish; venter in males and females uniformly bright yellow, throat whitish; forelimbs and hindlimbs similar in color to body, just slightly darker or yellowish.

Distribution.—*Eutropis balinensis* is distributed from the province of East Java to at least the island of Yamdena, across the Banda Arc islands, and also from Seruni and Genting islands of the Karimundjawa Archipelago. It has been found in many habitats, from low (0 m) to high elevation (1527 m).

KEY TO ADULT SPECIES OF THE COMMON SUN SKINK COMPLEX INHABITING JAVA AND SUMATRA

1a. Typically, tip of snout reddish 2

1b. Typically, snout not reddish at tip, flanks with orange bands, when colored bands present, found in central and northern Sumatra ....***E. sikkimensis***

2a. Typically, with five, rarely six, enlarged lower eyelid scales, females with prominent dark dorsolateral bands, light ocelli on lower part of flank, found in southern Sumatra—Lampung, and western Java—Banten and West Java .... ***E. multifasciata***

2b. Typically, with four, rarely five, enlarged lower eyelid scales, females never with dark and prominent dorsolateral bands, light ocelli above and below on flanks 3

3a. Paravertebral scale rows 43–45 in males and 45–46 in females, found in Central Java and Tjendikian Island in the adjacent Karimundjawa Archipelago...............***E. tjendikianensis***

3b. Paravertebral scale rows 48–55 in males and 46–50 in females, found in East Java and the adjacent Karimundjawa Archipelago...***E. balinensis***

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APPENDIX

Specimens Examined

E. sikkimensis (n = 13).—INDONESIA: Aceh: Aceh Selatan: Gunung Putri Tidur, 467 m, 3.2921 °S, 97.19642 °E, UTA-R 64106 (female); Aceh Tenggera: Gunung Bandahara, 352 m, 3.63485 °S, 97.71897 °E, UTA-R 64108 (female); Pidie Jaya, 1108 m, 4.86024 °S, 96.21368 °E, UTA-R 64109 (female); Sumatra Utara: Dairi Sumut: Desa Silalahi, 976 m, 2.79804 °S, 98.52049 °E, UTA-R 64113 (male); Tapanuli Selatan: Utaimbaru, 463 m, 1.75922 °S, 99.13827 °E, UTA-R 64115 (female); Karo, 1471 m, 3.22664 °S, 98.50005 °E, UTA-R 64116 (male);

Dairi: Kampung Silalahi, 1019 m, 2.7982 °S 98.52515 °E, UTA-R 64118 (female); Deli Serdang, 239 m, 3.37724 °S, 98.5975 °E, UTA-R 64122 (male); Sumatra Barat: Kabupaten Pasaman Barat, 454 m, 0.11623 °S, 99.92268 °E, UTA-R 64123 (female); Andalas University Forest, 341 m, -0.91137 °S, 100.47246 °E, UTA-R 63032 (male); Sumatra Selatan: Lahat: Gunung Dempo, 1322 m, 3.98674 °S, 103.16644 °E, UTA-R 63017 (male); Sumatra Selatan: Maura Enim: Desa Segamit, 1510 m, 4.19649 °S, 103.46299 °E, UTA-R 63018 (female); Bengkulu: Road from Pagar Alam to Manna, 929 m, 4.10028 °S, 103.11941 °E, MZB 13492 (female).

E. multifasciata (n = 14).—INDONESIA: Lampung: Kabupaten Pasawaran, 43 m, 105.22708 °S, 105.22708 °E, UTA-R 64087 (male); UTA-R 64089 (male); Kabupaten Tanggamus, 777 m, 5.32536 °S, 104.57709 °E, UTA-R 64093 (male); UTA-R 64094 (female); UTA-R 64095 (male); 747 m, 5.31267 °S, 104.56848 °E; UTA-R 64096 (female); Hills south of Ngarip, 603 m, 5.34553 °S, 104.53824 °E, UTA-R 64098 (female); Kabupaten Lampung Barat, 1008 m, 4.93542 °S, 103.855 °E, UTA-R 64099 (female); Banten: Pandeglang, 525 m, 6.32756 °S, 105.95988 °E, MZB 11912 (male), NEOTYPE; UTA-R 64072 (male); MZB 11913 (female); Java Barat: Bandung: Gunung Tilu, 1453 m, 7.14837 °S, 107.51986 °E, MZB 11915 (female); Java Tengah: Cilacap, UTA-R 64126 (male); Nusakambangan, UTA-R 64129 (male).

E. tjendikianensis (n = 7).—INDONESIA: Java Tengah: Wonosobo, UTA-R 64139 (male); Dusun Candi, Kec. Selomerto UTA-R 64141 (female); NK0295 (female); NK0296 (male);

Sungai Curuk Winong: Desa Winongsari: Kec. Kaliwiro, NK0351 (female); Baturaden, Kebun Raya Baturaden, 688 m, 7.31187 °S, 109.23544 °E, MZB 13873 (female); MZB 13878 (female);

E. balinensis (n = 9).—INDONESIA: Java Timur: Malang, UTA-R 64144 (male); UTA-R 64142 (female); MZB 9724 (female); Lebakharjo, 89 m, 8.31119 °S, 112.90756 °E, UTA-R 64148 (female); Banyuwangi, UTA-R 64150 (female); Wonosoba: Tamangung, 1434 m, 7.35139 °S, 110.0332 °E, MZB 13875 (male); Bondowoso, 115 m, 7.76804 °S, 113.70995 °E, MZB 9728 (female); NK0959 (male); Road between Jampit and Sempol, 1527 m, 8.07491 °S, 114.1388 °E, ENS13634 (male).

LIST OF TABLE

Table 2.1 List of primers used for mitochondrial and nuclear amplification.

Primer Name	Sequence	Reference
16SA	5’ CGC CTG TTT ATC AAA AAC AT 3’	Palumbi et al. 1991
16SB	5’ CCG GTC TGA ACT CAG ATC ACG T 3’	Palumbi et al. 1991
ND4	5’ CAC CTA TGA CTA CCA AAA GCT CAT GTA GAA GC 3’	Mausfeld et. al. 2000
LEU	5’ TTT TAC TTG GAK TTG CAC CA 3’.	Mausfeld et. al. 2000
R35f	5’ GAC TGT GGA YGA YCT GAT CAG TGT GGT GCC 3’	Leaché et al. 2009
R35r	5’ GCC AAA ATG AGS GAG AAR CGC TTC TGA GC 3’	Leaché et al. 2009
NGFB_f2	5’ GAT TAT AGC GTT TCT GAT YGG C 3’	Townsend et al. 2008
NGFB_r2	5’ CAA AGG TGT GTG TWG TGG TGC 3’	Townsend et al. 2008

Table 2.2 List of voucher specimens, localities, and Genbank numbers used in molecular analyses of species of the *Eutropis multifasciata* complex.

Species	Locality	Voucher No.	GenBank Accession Number			
			16S	ND4	NGFB	R35
E. sikkimensis	India, Assam	CES 09/925	JQ767964.	-	-	-
E. sikkimensis	Philippines, Panay	KU 302890	JF497984	JF498466	JF498223	JF498340
E. sikkimensis	Thailand, Maehongsorn	KU Z32896	AB028788	-	-	-
E. sikkimensis	Laos, Champassak	FMNH 255530	DQ238897	-	-	-
E. sikkimensis	Myanmar, Mwe Hauk Village	CAS 2120916	AY159088	-	-	-
E. sikkimensis	Indonesia, West Kalimantan	ZFMK 65791	AY159086	-	-	-

E. sikkimensis	Malaysia, Sarawak	FMNH 269170	KX231451	-	-	-
E. sikkimensis	Thailand, Chaiyaphume	UTA-R 64135	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. sikkimensis	Indonesia, Aceh	UTA-R 63019	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. sikkimensis	Indonesia, Aceh	UTA-R 63022	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. sikkimensis	Indonesia, Sumatra Utara	UTA-R 64112	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. sikkimensis	Indonesia, Sumatra Utara	UTA-R 64114	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. sikkimensis	Indonesia, Sumatra Barat	UTA-R 64124	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. sikkimensis	Indonesia, Sumatra Barat	UTA-R 63032	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance

E. sikkimensis	Indonesia, Jambi	MZB 9736	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. sikkimensis	Indonesia, Jambi	UTA-R 64125	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. sikkimensis	Indonesia, Sumatra Selatan	UTA-R 63017	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. sikkimensis	Indonesia, Sumatra Selatan	UTA-R 63018	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. sikkimensis	Indonesia, Bengkulu	UTA-R 63026	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. multifasciata	Indonesia, Banten	ZFMK 50187	AY159087	-	-	-
E. multifasciata	Indonesia, Lampung	UTA-R 64091	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. multifasciata	Indonesia, Lampung	UTA-R 64098	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. multifasciata	Indonesia, Banten	UTA-R 64072	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance

E. multifasciata	Indonesia, Java Barat	MZB 11915	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. multifasciata	Indonesia, Java Barat	UTA-R 64075	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. tjendikianensis	Indonesia, Ceram	ZFMK 70628	AY159085	-	-	-
E. tjendikianensis	Philippines, Luzon	USNM 54394	AY159084	-	-	-
E. tjendikianensis	Indonesia, Java Tengah	UTA-R 64136	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. tjendikianensis	Indonesia, Java Tengah	UTA-R 64137	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. balinensis	Indonesia, bali	ZFMK 76381	AY159082	-	-	-
E. balinensis	Indonesia, Java Timur	UTA-R 64147	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. balinensis	Indonesia, Java Timur	NK0498	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
E. rugifera (outgroup)	Indonesia, Java Tengah	NK0354	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance

Table 2.3 Pairwise raw genetic distances of ND4 among species of the *Eutropis multifasciata* complex.

Species	p-distance
E. sikkimensis - E. multifasciata	6.51–7.76%
E. sikkimensis - E. tjendikianensis	6.88–8.01%
E. sikkimensis - E. balinensis	5.76–7.01%
E. multifasciata - E. tjendikianensis	3.13–3.75%
E. multifasciata - E. balinensis	3.38–4.13%
E. tjendikianensis - E. balinensis	3.50–3.88%

Table 2.4 Discriminant scores and loading values for CVA analyses of species of the *Eutropis multifasciata* complex; SVL: snout vent length; AGD: axilla groin distance; HL: head length; HW: head width; RSTL: rostral length; SFL: snout forelimb length; LE: lower eyelid scales; PVSR: paravertebral scale rows; VSR: ventral scale rows; MBSR: midbody scale rows; FSDL: finger subdigital lamellae; TSDL: toe subdigital lamellae.

	Male			Female		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
SVL	1.7661	-2.0847	0.0624	-1.2471	-0.1400	-2.4616
AGD	0.8775	-0.9167	-0.3241	-0.7232	-0.2292	-1.4712
HL	0.4537	-0.4880	0.0556	-0.2337	-0.0565	-0.5320
HW	0.3110	-0.2671	-0.2295	-0.0676	0.0549	-0.2654
RSTL	0.1583	-0.2143	-0.1824	-0.0659	-0.0595	-0.2918
SFL	0.5925	-0.9946	0.0911	-0.3296	-0.0902	-0.6960
LE	0.0004	0.0341	-0.0327	-0.0734	0.0060	-0.1007
PVSR	-0.5654	0.6994	0.9295	0.0403	-0.0010	0.3733
VSR	-0.2810	0.1279	0.1726	-0.0819	-0.1726	0.1824
MBSR	-0.0331	-0.1070	0.2682	-0.0082	-0.0121	0.2652
2nd FSDL	0.0172	-0.0801	0.0022	-0.0567	-0.0659	-0.0289
3rd FSDL	-0.0568	0.0509	0.3489	-0.0271	-0.0656	-0.0076

4th FSDL	-0.1156	0.0043	0.3206	-0.0677	0.0071	0.0347
1st TSDL	0.0567	0.0388	0.1143	-0.0329	0.0235	0.0079
2nd TSDL	0.1675	-0.1084	0.0453	-0.0506	-0.0274	-0.0899
3rd TSDL	0.0356	0.0407	0.0315	-0.0767	0.0526	-0.1698
4th TSDL	-0.0793	0.0460	0.4089	-0.0682	0.0162	-0.1183
5th TSDL	-0.0392	-0.1642	0.0809	-0.0617	-0.0017	0.0164
Eigenvalue	14.5880	6.2637	1.5835	65.4220	25.3940	7.0122
Percentage	65.02	27.92	7.058	66.87	25.96	7.188

Table 2.5 Measurements (mm) and characters of species of the *Eutropis multifasciata* complex.

Characters	*E. sikkimensis*		*E. multifasciata*		*E. tjendikianensis*		*E. balinensis*	
	male	female	male	female	male	female	male	female
	n = 6	n = 7	n = 8	n = 6	n = 2	n = 5	n = 5	n = 6
SVL	98.81–111.28	99.39–121.16	100.16–116.92	87.46–118.08	93.98–102.86	70.34–106.13	98.65–103.55	74.33–94.53
AGD	45.81–51.99	46.94–64.81	48.95–55.71	43.42–58.16	47.16–47.54	32.01–5596	48.05-51.03	33.01–46.35
HL	21.15–24.85	19.45–25.70	23.16–25.72	17.70–22.85	18.64–22.56	15.11-20.44	19.86–21.63	14.59–18.76
HW	15.28–18.54	12.75–17.67	16.50–19.14	12.40–16.30	14.76–18.66	11.12–15.82	16.15–16.42	10.55–14.56
SFL	35.73–40.11	31.67–39.72	39.22–46.22	30.80–41.52	34.80–40.57	26.54–36.66	34.97–36.66	25.98–34.71
IND	3.95–5.81	3.80–4.90	4.08–5.24	2.96–5.19	3.38–4.17	2.90–4.14	3.44–3.80	2.24–4,10
IOcD	9.16–9.99	8.03–10.18	8.33–9.48	6.99–8.40	8.56–8.62	6.26.-9.05	7.24–1.98	6.00–8.38
RostL	8.36–10.11	8.30–11.30	8.86–10.95	7.02–8.71	8.18–9.57	6.01–9.72	7.15–7.60	5.85–8.41

IOrD	13.67–18.84	12.87–16.14	14.72–17.55	11.38–15.25	15.51–15.88	6.65–14.92	13.91–14.89	9.79–13.10
EyD	5.85–7.21	4.51–7.37	5.96–7.14	5.27–7.00	4.45–6.14	4.67–5.77	5.64–5.78	4.13–5.38
TD	1.19–2.09	0.88–2.00	1.44–2.62	1.04–1.80	1.52–2.15	0.98–1.63	1.43–1.77	1.18–1.44
FLL	30.96–37.94	30.29–39.22	34.15–37.94	31.79–36.41	32.86	28.38	30.63–32.22	23.94–27.35
HLL	46.81–50.19	41.75–56.33	46.07–52.76	42.48–50.48	42.84	36.91	31.40–31.90	31.87–38.62
TW	14.42–16.92	13.10–19.44	14.66–18.08	12.16–18.87	12.69–15.82	10.08–14.82	14.66–15.04	8.15–13.96
PVSR	42–46	43–47	42–45	44–47	43–45	45–46	48–55	46–50
VSR	54–59	56–62	54–61	54–59	57–58	53–58	56–65	56–61
LE	5 (6,7)	5 (4,6)	5 (6)	5 (6)	4	4 (5)	4 (5)	4 (5)
4th FSDL	12–14	12–14	12–15	13–14	13	12–13	14–15	13–14
4th TSDL	16–19	17–20	16–19	17–19	16–17	15–18	18–19	16–18
Snout-tip color	Brown (Red)	Brown (Red)	Red (Brown)	Red (Brown)	Red (Brown)	Red (Brown)	Red (Brown)	Red (Brown)

Lateral band	Orange	Orange	Yellow (Orange)	Orange (Yellow)	Yellow (Orange)	Yellow	Yellow (Orange)	Yellow (Orange)
Lateral light ocelli	-	Below	-	Below	-	Below and above	Below	Below and above
Dark dorsolateral Stripe	-	Prominent	-	Prominent	-	Faded	-	Faded

Table 2.6 Character comparisons among type specimens of the valid species recognized within the *Eutropis multifasciata* complex, namely, *Plestiodon sikkimensis* Gray 1853, *Scincus multifasciatus* Kuhl 1820, *Mabuya multifasciata tjendikianensis* Mertens 1956, *Mabuya multifasciata balinensis* Mertens 1927; The morphometric data (in mm.) modified from Amarasingue et al. in press; type specimens include adult males, a female, and a juvenile.

	E. sikkimensis	*E. multifasciata*	*E. tjendikianensis*	*E. balinensis*
Voucher	BMNH 1946.8.19.3	MZB 11912	SMF 55147	SMF 22087
Status	Holotype	Neotype	Holotype	Holotype
Type locality	Sikkim, India	Banten, Indonesia	Tjendikian, Indonesia	Bali, Indonesia
Sex/maturity	Juvenile	Male/adult	Female/adult	Male/adult
Snout vent length	104.0	38.0	87.1	109.6
Head length	26.7	12.9	22.4	27.1
Head width	16.6	6.5	13.2	14.6
Snout length	9.3	3.1	7.8	10.0
Orbit diameter	8.1	1.8	5.2	7.0

Eye tympanum length	6.2	3.1	5.9	7.7
Axilla–groin length	49.77	18.2	46.5	53.0
Femur length	17.0	5.9	14.5	16.7
Tibia length	17.4	6.2	11.9	14.8
Midbody scale rows	34	32	32	32
Paravertebral scale rows	43	44	43	48
Ventral scale rows	55	53	58	53
Lamellae on 4th toe	17	19	19	18

FIGURE CAPTIONS

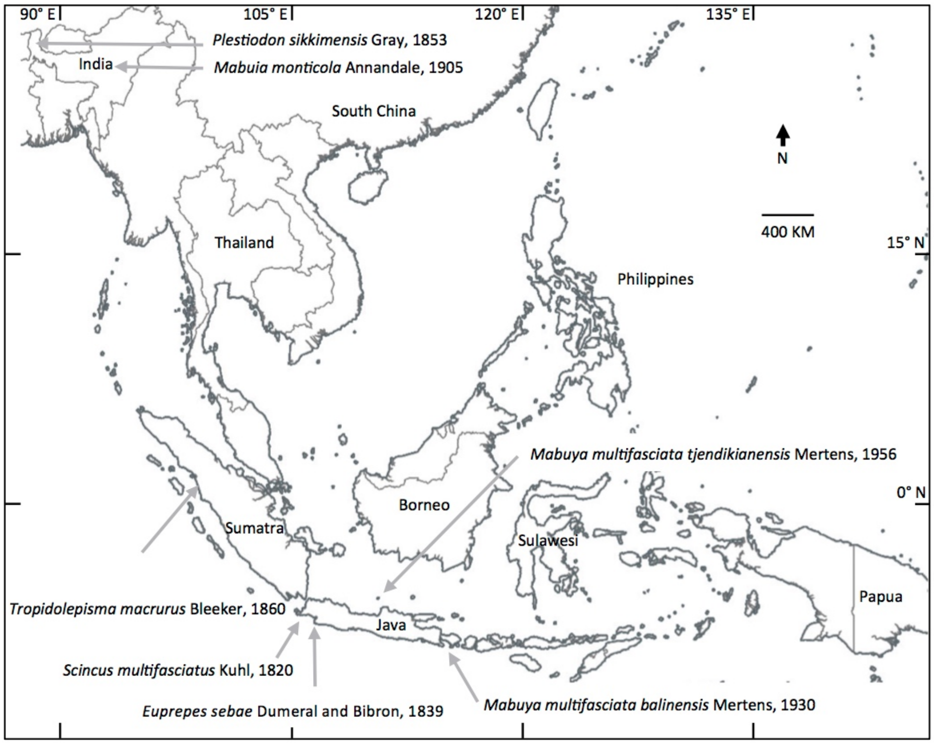

Figure 2.1 Type localities associated to the *E. multifasciata* complex of species. Java and adjacent areas possess type localities of all subspecies currently recognized, including, *E. m. multifasciata* from western Java, *E. m. tjendikianensis* from the Karimunjawa Archipelago, and *E. m. balinensis* from Bali.

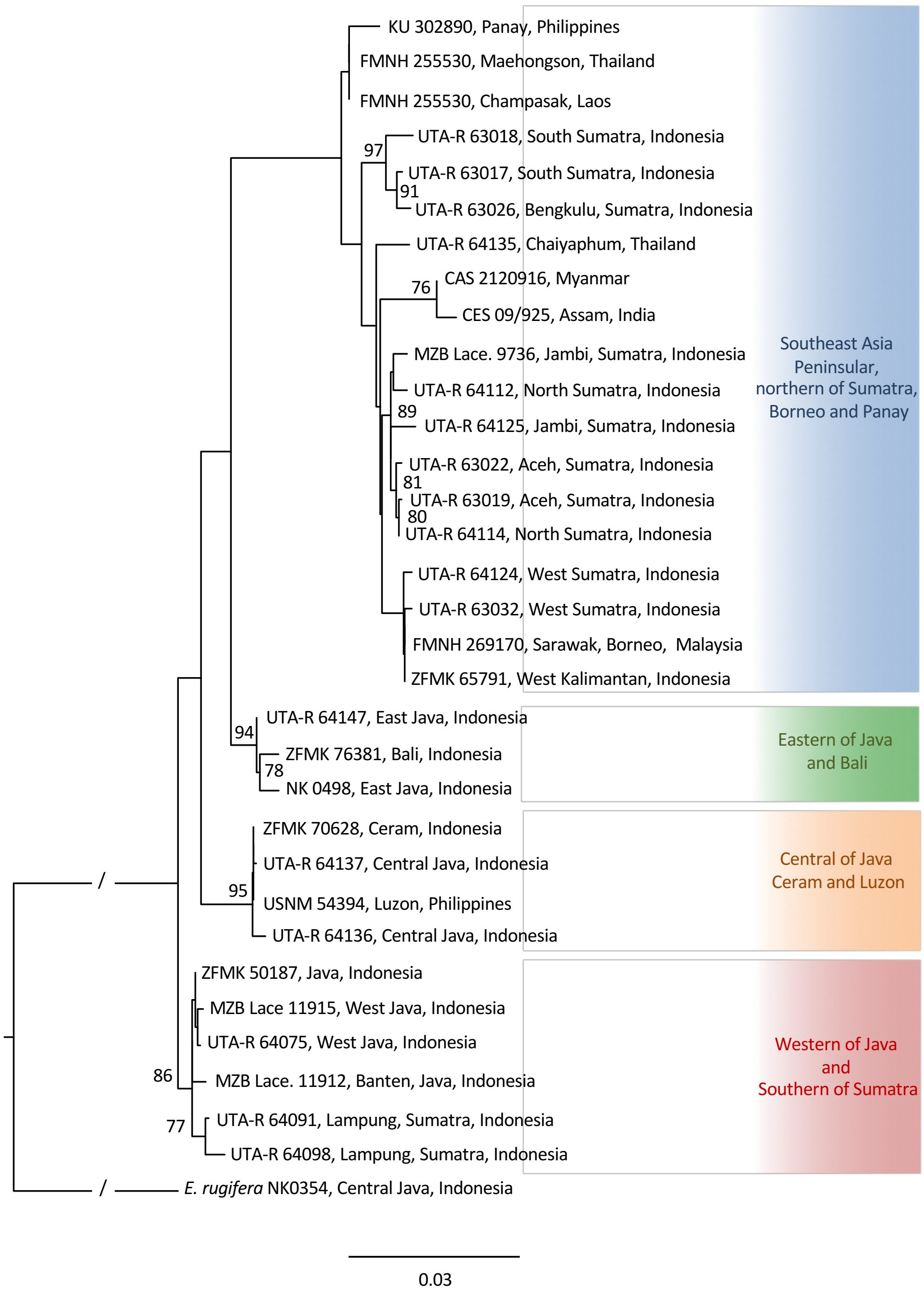

Figure 2.2 Maximum Likelihood phylogeny for members of the *E. multifasciata* complex, based on 2613 base pairs of mitochondrial and nuclear DNA, notice paraphyletic clades of *E. m. multifasciata* with regards to geographic distribution.

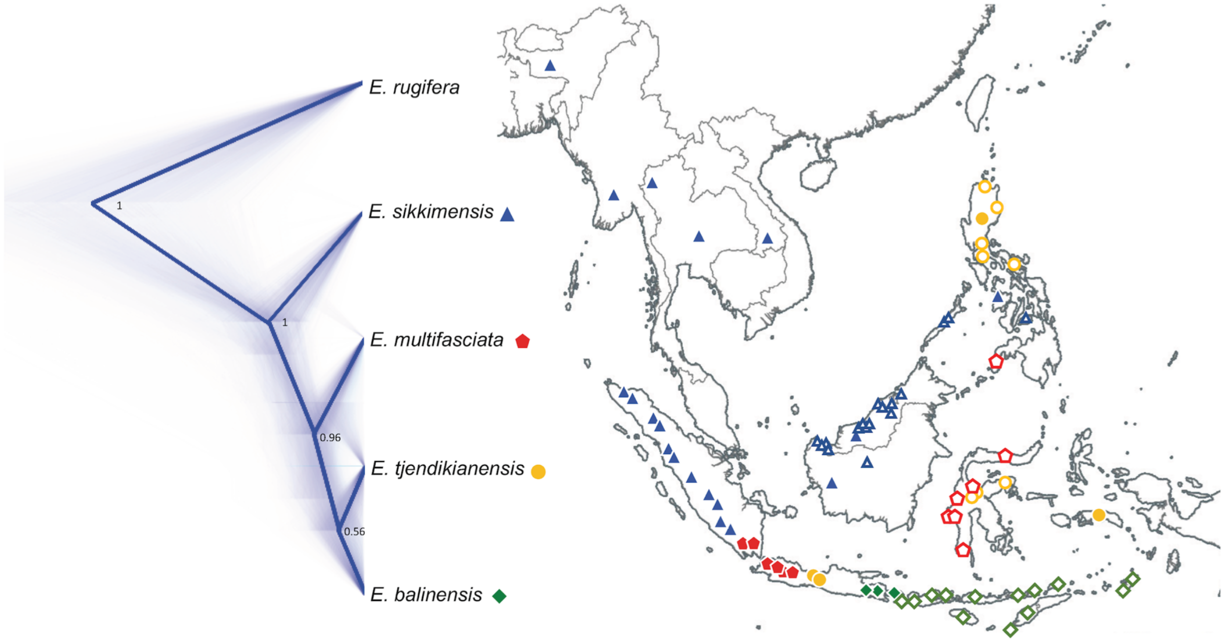

Figure 2.3 Bayesian inference species tree of members of the *E. multifasciata* complex showing deep separation between populations that can be assigned to *E. sikkimensis, E. multifasciata, E. tjendikianensis* and *E. balinensis*. Map shows in solid symbols the origin of samples used in our molecular analyses, hollow symbols represent those used in the work of Karin (2016) and Schmitt et al. (2000).

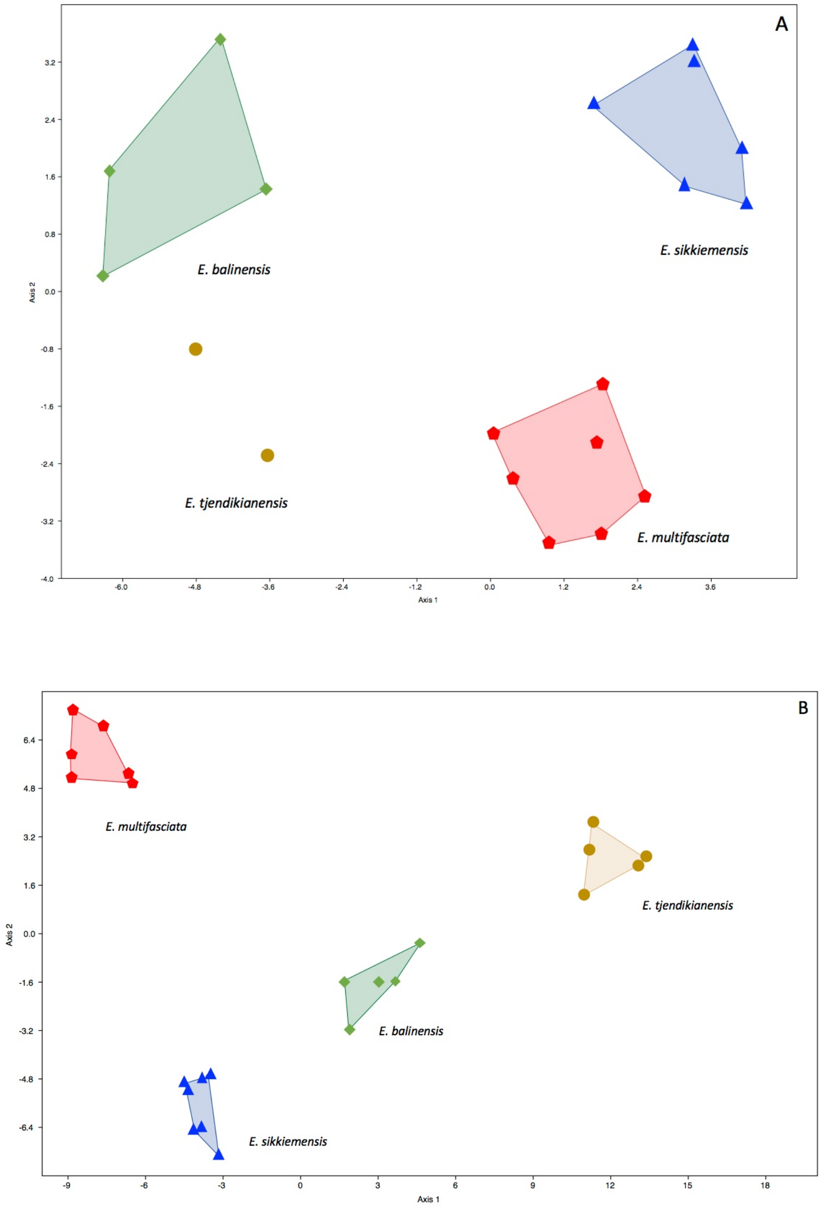

Figure 2.4 Morphometric discriminant analyses (CVA) on male (A) and female (B) samples of species of the *E. multifasciata* species complex.

Figure 2.5 Adult male examples for the species recognized within the *E. multifasciata* species complex; *E. sikkimensis* MZB 14459 from north Labuhan Batu Regency, North Sumatra (A); *E. multifasciatus* UTA-R 64072 from trail between Cilitung and Pulosari Waterfall, Pandeglang Regency, Banten, Java (B); *E. tjendikianensis* UTA-R 64139 from Curug Winong Water fall, Central Java (C); *E. balinensis* UTA-R 64147 from Jampit, Bondowoso, East Java (D).

Figure 2.6 Adult female examples for the species recognized within the *E. multifasciata* species complex; *E. sikkimensis* UTA-R 64115 from Tapanuli Selatan, Utaimbaru, North Sumatra (A); *E. multifasciatas* MZB 9749 from Mount of Rajah Basa, Lampung, South Sumatra (B); *E. tjendikianensis* NK0296 from Wonosobo, Central Java (C); *E. balinensis* UTA-R 64151 from Bondowoso, East Java (D).

Chapter 3

Taxonomic revision of diminutive Asian skinks (Squamata: Scincidae: *Tytthoscincus*) with two new species from Java and Sumatra and a note on their montane distribution

Abstract

We describe two new species of diminutive Asian skinks from the Sunda Shelf, one from the Province of Aceh in northern Sumatra and another from the Province of East Java. Even though the islands are part of the Sundaland biodiversity hotspot, there is little known about the skink diversity of these two massive islands. The two new species, *Tytthoscincus* sp. nov. 1 and *T.* sp. nov. 2 are morphological and genetically distinctive from *T. temmincki* which surprisingly, is the only species of *Tytthoscincus* currently recognized from Java and Sumatra. We also investigated the phylogenetic relationship between the two new species, all other skinks in the genus *Tytthoscincus* and the closely related and morphologically similar genus *Sphenomorphus* that occur on the Sunda Shelf. Our results show the two new species herein described are morphologically and genetically distinct from other *Tytthoscincus* and *Sphenomorphus* species. In the course of our work we also transfer *S. necopinatus* and *S. vanheurni* to the genus *Tytthoscincus,* based on molecular and morphological evidence. The discovery of these two new species indicates that the diversity of skinks on the Sunda Shelf, especially on Java and Sumatra is underestimated, and taxonomic investigation of the forest skinks in these areas is still required.

Key words: Ecological Niche Modeling, Endemic species, Sunda Shelf, Systematics

Introduction

The diminutive Asian skinks in the genus *Tytthoscincus* Linkem, Deesmos and Brown, 2011 were formerly considered part of the genus *Sphenomorphus* Fitzinger, 1843. In their evaluation of *Sphenomophus* from the Philippines, Linkem *et al.* (2011) recognized that this lineage as a distinct genus. The diminutive Asian skinks have a large distribution that encompasses Peninsular Malaysia, Borneo, Sumatra, Java, Sulawesi, Maluku and the Philippines (Karin *et al.* 2016; Linkem *et al.* 2011). Currently 21 species of *Tytthoscinus* are recognized (Uetz & Hosek 2018) fourteen of which were originally recognized as members of the genus *Sphenomorphus* and seven of which were recently described as *Tytthoscincus* (Karen et al. 2016; Grismer et al. 2016; Grismer et al. 2017a; Grismer et al. 2017b). *Tytthoscincus* are distinguished from *Sphenomorphus* and other related genera by their small body size (SVL less than 45 mm), slender body, temporal scales similar in size and shape, to laterals, forelimbs and hind limbs that do not overlap when adpressed (Linkem *et al.* 2011).

Currently, there are 21 recognized species including: *T. aesculeticola* (Inger, Lian, Lakim & Yambun 2001), *T. atrigularis* (Stejneger 1909), *T. batupanggah* Karin, Das & Bauer 2016, *T. biparietalis* (Taylor 1918), *T. bukitensis* (Grismer 2007), *T. butleri* (Boulenger 1912), *T. hallieri* (Lidth De Jeude 1905), *T. ishaki* (Grismer 2006), *T. jaripendek* Grismer, Wood, Quah, Anuar, Ngadi, Mohd Izam & Ahmad 2017, *T. kakikecil* Grismer, Wood, Quah, Anuar, Ngadi, Mohd Izam & Ahmad 2017, *T. langkawiensis* (Grismer 2008), *T. leproauricularis* Karin, Das &

Bauer 2016, *T. martae* Grismer, Wood, Quah, Anuar, Ngadi, Mohd Izam & Ahmad 2017, *T. panchorensis* Grismer, Muin, Wood Jr, Anuar & Linkem 2016, *T. parvus* (Boulenger 1887), *T. perhentianensis* (Grismer, Wood & Grismer 2009), *T. sibuensis* (Grismer 2006), *T. temasekensis* Grismer, Wood, Lim & Liang 2017, *T. temengorensis* (Grismer, Ahmad & Onn 2009), *T. temmincki* (Duméril & Bibron 1839) and *T. textus* (Müller, 1894). Most are known from Peninsular Malaysia (twelve species) and Borneo (five species) only one species, *T. temmincki,* has been recorded from Java and Sumatra (Uetz & Hosek 2018). The paucity of species on Java and Sumatra, two of the largest landmasses in the region, suggests that there may be several undescribed species still hidden on the islands. Historically, *T. temmincki* was recognized as a member of the genus *Sphenomophus,* infrequently encountered in the montane jungle of Java, Sumatra, and Sulawesi (Boulenger 1887 and De Rooij 1915). Brongersma (1942) revisited the taxonomic status of *T. temmincki*. He found that specimens collected from Java and Sumatra are morphologicaly distinct between and subsequently described *S. necopinatus*from Bogor, West Java and its subspecies *S. n. garutense* from Garut, west Java, and *S. vanheurni* from Probolinggo, East Java. From his work at that time, *T. temmincki* had been splited into *T. temmincki*, *S. necopinatus necopinatus*, *S. n. garutense*, *S. vanheuni.* Later, Mertens (1957) described the subspecies as *S. vaheurni balicus* from Bali Island. These are the only taxonomic studies of *Tytthoscincus* on Java and Sumatra until now.

Species of *Tytthoscincus* occur in a variety of forested environments from swamp to montane (Grismer *et al.* 2016). The species that live in montane jungles have a high potential form an endemic species because of their specialized habitat, and limited vagility (Grismer 2011; Karin *et al.* 2016).

Java and Sumatra are part of the Sundaland biological hotspot (Myer 2000) and known for their high diversity of squamates (Harvey *et al.* 2017b; Iskandar & Erdelen 2006; Shaney *et al.* 2016). In addition, as part of the Pacific ring of fire, Java and Sumatra, have a long volcanic history (Verstappen 1973) resulting in the formation of numerous isolated peaks, each with the potential of housing endemic species of skink

The aim of this study is to investigate the species diversity of skinks in the genus *Tytthoscincus* and estimate their phylogenetic relationships. In the course of this work, we describe two new species*, T. sp. 2*. from Aceh Province, northern Sumatra and *T. sp. 1* from eastern Java. We also transfer *Sphenomorphus necopinatus* and *S. vanheurni* to *Tytthoscincus* and discuss the distribution of species on isolated volcanic highlands of Java shedding some light on the biodiversity in Java and Sumatra.

Materials and methods

We collected the specimens used for this study during visual encounter surveys conducted both day and night in 2013 and 2015 as part of in herpetological expeditions of Java and Sumatra undertaken as a collaboration between three institutes, the University of Texas at Arlington, USA, the Indonesia Institute of Science, and the University of Brawijaya. We euthanized specimens by cardiac injection using 10% benzocaine solution, according to the IACUC protocol control (UTA IACUC A12.004). Prior to sacrifice, we took photos of the animals, after euthanasia we took photos of dorsal, ventral and lateral sides. A piece of tissue was taken from the leg or liver and stored in cell lysis buffer (0.5 M Tris/0.25% EDTA/2.5% SDS, pH = 8.2) for further molecular analysis. We fixed specimens with 10% formalin and stored them in 70% ethanol. We deposited preserved specimens in Museum Zoologicum Bogoriense (MZB) and Amphibian and Reptile Diversity Research Center of the University of Texas at Arlington (UTA). We identified specimens primary base on external morphology by comparing them with characters in the original descriptions and other descriptive articles (de Rooj 1915; Grismer 2011; Manthey & Grossman 1997). We compared our specimens with type specimens of small skinks found on Java, Sumatra and adjacent areas to confirm species identification. The type specimens examined include *T. temmincki* (MHNP 1344-Holotype), *S. necopinatus* (RMNH.RNEA 7969-Holotype and BMNH 1948.1.8.17-Palatype), *S. n. glutense* (RMNH.RENA 7970-Holotype, RMNH.RENA 7963-Paratype and RMNH.RENA 7964-Paratype), *S. vanhernei* (RMNH.RENA 7967-Holotype), *S. v. balicus* (SMF 23275- Holotype), *S. cophias* (BMNH 1946.8.3.15-type), *S. malayanus* (MSG 27869-lectotype) and *S. modiglaiani* (BMNH 1946.8.16.98-type) The type locality of these species in Java and Sumatra are in Fig. 3.1. If we were unable to match our specimens with any described species, we propose them as new.

For our morphological investigation we measured 15 characters and took meristic data from a further 26 characters. All measurements were taken by a single person (PT) using a Mitutoyo digital vernear caliper, at the highest precision = 0.05. Morphometric characters were modified from Linkem *et al.* (2010) and Karen *et al.* (2016). All bilateral characters were quantified on the right side. Mensural characters include; snout–vent length (SVL) measured from the tip of the snout to the cloacal opening; tail length (TL) measured from the cloacal opening to the tip of the tail; axilla–groin distance (AGD) measured from the posterior margin of the forelimb insertion to the anterior margin of the hindlimb insertion; head length (HL) measured from the anterior margin of the ear opening to the tip of the snout; head width (HW) measured at the widest part of the temporal region; head height (HH) at the center of eye; snout–forelimb length (SFL) measured from the anterior forelimb insertion to the tip of the snout; internarial distance (IND) measured between the dorsal margin of the two nares; inter-occular distance (IOcD) measured between anterior corner of the eye ; rostrum length (RostL) measured from the anterior margin of the eye to the tip of the snout; interorbital distance (IOrD) measured the length between middle of the left ear and right ear; eye diameter (EyD) measured at widest point on eye; tympanum diameter (TD) measured at widest point on the ear; forelimb length (FLL) measured from anterior margin of forelimb to the 4th finger; hind limb length (HLL) measured from anterior margin of hindlimb to the 4th toe; Tail width (TW) measured at its base (ventral side).

Scale counts included the number of paravertebral scales (PVSR) counted dorsal scales between the parietals and the cloacals; number of scales (VSR) counted ventral scales between the 3rd chin shields and the precloacals; number of subcaudal (SC) counted scales from posterior margin of the cloacal to tip of the tail; number of midbody scale rows (MBSR) counted scales around the body at the center of the trunk; number of subdigital lamellae on finger I (1st FiSDL) counted lamellae under the first finger; number of subdigital lamellae on finger II (2nd FiSDL) counted lamellae under the second finger; number of subdigital lamellae on finger III (3rd FiSDL) counted lamellae under the third finger; number of subdigital lamellae on finger IV (4th FiSDL) counted lamellae under the fourth finger; number of subdigital lamellae on finger V (5th FiSDL) counted lamellae under the fifth finger; number of subdigital lamellae on toe I (1st

ToSDL) counted lamellae under the first toe; number of subdigital lamellae on toe II (2nd ToSDL) counted lamellae under the second toe; number of subdigital lamellae on toe III (3rd ToSDL) counted lamellae under the third toe; number of subdigital lamellae on toe IV (4th ToSDL) counted lamellae under the fourth toe; number of subdigital lamellae on toe V (5th ToSDL) counted lamellae under the fidth toe; number of supralabials (SL) counted scales between the rostral and the postsupralabial; number of number of postsupralabials (PS) counted scales between the supralabial and the temporal; number of infralabials (IL) counted scales between the mental and the first lateral. number of loreal scales (L) counted scales between the nasal and the preoccular; number of enlarged supraoculars (SO) counted enlarged scales above ocular bulk; number of chin shields (CS) counted enlarged scales between the postmental and the first ventral; number of preocular (PrOc) counted scales between the loreal and anterior margin of eye; number of postocular (PoOc) counted scales between posterior margin of eye and the temporal; number of supracilliaries (SCil) counted scale above eye and below supraoculars; number of primary temporal scales (1st Tmp) counted scales on first row after postocular or postsupralabial; number of secondary temporal scales (2nd Tmp) counted scales on second row after postocular or postsupralabial; Number of longitudinal black dot lines on dorsals; number of longitudinal black dot line on subcaudals. Number of row of single dorsal scale at apex of 4th toe (unpaired DT) counted number of unpaired and paired scale rows on the distal end of dorsal surface of the fourth toe.; number of row of pair dorsal scale of 4th toe (paired DT) counted number of paired scale rows on the distal end of dorsal surface of the fourth toe. We also assessed forty-five qualitative characters including degree of overlap of addpressed limbs, head scales shape and degree of contact, scale shape, texture, and coloration.

We extracted the genomic DNA from tissue samples using a Serapure magnetic bead suspension (Rohland and Reich 2012). The DNA extraction starts by transferring 50 µl of dissolved-tissue in cell lysis buffer dilute with 50 uL of Ultrapure water and incubating at 55 °C with 20 µl protenase K for 2 hours to ensure digestion. After that the solution was mixed with 180 µl of Serapure bead. After that the solution was cleaned twice with 80 µl of 70% EtoH and resuspended in 50 ul of Tris pH 8.5 with 0.1% of Tween 20.

We amplified a fragment of the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and a fragment of the RNA fingerprint protein 35 (R35) as a representative of a nuclear locus. For the ND2 locus, we used the primers METF1 (5'-AAGCTTTCGGCCCATACC-3') for the forward reaction (Macey et al. 1997) and CO1R1 (5'-GACTGTGGAYGAYCTGATCAGTGTGGTGCC-3') for the reverse reaction (Arevalo *et. al.* 1994; Karin *et al.* 2016). For the R35 locus, R35f (5'-GACTGTGGAYGAYCTGATCAGTGTGGTGCC-3') was used as forward primer and R35r (5'-GCCAAAATGAGSGAGAARCGCTTCTGAGC-3') was used as reverse primer (Townsend *et al.* 2008; Leache 2009). The thermal cycling profile for ND2 consisted of an initial step of denaturation for 3 minutes at 95 °C followed by 33 cycles of a 35 second 95 °C denaturation, a 30 second 52 °C annealing, and a 1 minute 72 °C extension then a final 10 minute extension at 72 °C. The thermal cycling profile for r35 consisted of an initial denaturation of 20 seconds at 94 °C followed by twenty cycles of a 30 second 94 °C denaturation, a 30 second 50 °C annealing, and a 1 minute 72 °C extension followed by holding 6 steps: 30 seconds at 94 °C, 30 seconds at 54 °C, 1 minute at 72°C, 30 seconds at 94 °C, 30 seconds at 52° C, 1 minute at 72° C then kept on 20 similar cycles with the annealing temperature reduce to 50° C and then a final 10 minutes extension at 72 °C. The PCR amplification products were visualized on a 10 % agarose gel.

PCR products were purified by the same method used for the genomic DNA extraction. The purified products were submitted for Sanger sequencing to the Genome Core Facilities at the University of Texas at Arlington with an ABI PRISM 3100xl Genetic Analyzer (Applied Biosystems). After that we checked and trimmed the DNA sequences in Sequencer5.1 (Gene Codes, Ann Arbor, MI, USA). All new sequences are deposited on GenBank under accession numberx XXXX-XXXX (Table 3.1).

In order to examine the phylogenetic relationship of *Tytthoscincus* from Java and Sumatra, we aligned the sequences generated for this study with available sequences of *Tytthoscincus* from GenBank in MEGA7 (Kumar, Stecher, and Tamura 2016) using the Clustal W algorithm (Larkin 2007). We used Partition Finder 1.1.0 (CITATION) to identify the best model of molecular evolution and best partitionining scheme for each gene using the greedy algorithm. The best partitioning scheme had five partitions including TVM+I+G for ND2 1st codon position; HKY+I+G for ND2 2nd codon position; K81uf+G for ND2 3rd codon position; K80+I for R35 1st and 2nd codon positions; HKY+G for R35 3rd codon position.

We used both maximum likelihood (ML) and Bayesian inferences (BI) to estimate phylogenetic relationships. For ML we used RAxML v8.00 (Starmatakis 2014) with bootstrapping 1,000 pseudoreplicates in CIPRES Science Gateway online server (v3.2; Miller *et al.* 2010) and in case of BI we used MrBayes3.2.3 (Ronquist and Huelsenbeck 2003). We ran the Bayesian analysis for 15x 10^6 generations. There were three heated and one cold chains. We ran four independent Bayesian analyses each with four chains. We set the burn in value as 25% therefore discard first 2,500 generations. We visually examined the convergence of posterior likelihood values using Tracer v1.6 (Rambaut and Drummond 2014) and making sure that all ESS values were > 200. We used Figtree (Rambaut 2007) for visualizing and editing the resulting ML and BI trees.

We used Maxent 3.3.3 (Phillips *et al.* 2016) to model suitable *Tytthoscincus* and *Sphenomorphus* habitat across volcanic montane forest of Java. We ran separate analyses for the *S. vanheurnei* group which has been found only in eastern Java and the *S. necopinatus* group (here in we transfer these two species to *Tytthoscincus*) which is believed to be restricted to western Java (Das 2011). We used all confirmed records of *S. necopinatus necopinatus, S. n. garutense*, *S. vanheurni vanheurni, S. v. balicus* from museum collection (MZB) and the literature (Brongerma 1942) and our own data. The geographic data used in this analysis shown in Table 3.2. In case of *S. vanheurni* we chose the most likely coordinates that reflect the collection locality of the "shore of Taman Hidap" in East Java (about 1,900 m. high). We did not include record of *S. v. balicus* for this analysis since they occur in low elevation forests (300–550 m) on Bali Island (Mertens, 1957; VertNet 2018). The original description (Mertens, 1957) present 550 m elevation for holotype (SMF 23275). The data from VertNet present three additional samples from Gunung Kelatakan, Bali (WAM REPT R109338, R109309–10). The Coordinate data of these three specimens is latitude -8.216667; longitude 114.5) indicating about 337 m elevation. This notes on the different in vertical distribution of *S. vanheurni* and *S. v. balicus*. We used all 19 bioclimatic files (30 sec. resolution) available at http://www.worldclim.org/. We formatted files for use in Maxent using the Clip and Raster to ASC tools in ArcMap 10.2 (ESRI, Redlands, USA). Collinearity is not considered to be problematic when using Maxent, and therefore we did not exclude any variables after model testing (Elith *et al.* 2011). We used the Auto Features settings provided, changed the number of iterations to 5000, replicated run type to subsample, and set random test percentage to 25. We assessed the area under the curve (AUC) for each model, to measure model performance using the presence localities provided. AUC models are produced in Maxent only when test values are provided. AUC values closer to 1.0 indicate high performance of the predicted suitability models. We distinguished break points in probability of occurrence at 0.5, 0.6, 0.7, 0.8, and above 0.9 to provide context for levels of habitat suitability across the species' ranges. Everything < 0.5 probability occurrence is not shown as suitable habitat. We used the final models as an additional line of evidence of species boundary and to predict where new species of *Tythhoscincus* may be discovered based on distinct biogeographic breaks in suitable habitat.

Results

In order to clarify the taxomic confusion surrounding the *Tytthoscincus* on Java and Sumatra, we modify the taxonomy of diminutive skinks in Java and Sumatra using several approaches. First, we formally transfer *S. necopinatus* to the genus *Tytthoscincus,* based on the genetic phylogenetic results. Second, we transfer *S. vaheurni* to the genus *Tytthoscincus,* based on morphological similarity to other species of *Tytthoscincus*. Third, we elevate the subspecies *T. n. necopinatus*, *T. n. garutense*, *T. v. vanheurni*, and *T. v. balicus.* to full species, based on distinct morphology, restricted distribution, and niche data.

The ecological niche modeling for the *Tytthoscincus necopinatus* group shows allopatric suitable habitat between *T. necopinatus* and *T. garutense* (Fig. 3.1). *Tytthoscincus necopinatus* is endemic to the Bogor region (Mount Halimun Salak National Park) and has been found from 900–1000 m at Mount Halimun (based on two specimens examined in Lipi and original description). *Tytthoscincus garutense* is only known from 700–1500 m at Mount Galunggung, in the vicinity of Garut and Tasikmalaya (based on two specimens examined in Lipi and original description). These two species have been found in small and isolated areas in West Java and differ in number of paravertebral scale rows, subdigital lamellae on toe 4, suprascilliary scales projecting dorsomedialy, and maximum SVL. Brongersma (1942) also recongnized the subspecies as being distinct, based on these same morphological characters. These two species occupy different niches, occur about 175 km apart, and have limited vagility, suggesting reproductive isolation.

The niche modeling for the *Tytthoscincus vanheurni* group shows allopatric suitable habitat between *T. vanheurni*, *T. balicus* and *T. sp. 1* (herein described as a new species). Fig. 3.2 presents the niche modeling for this species group. Unsurprisingly, this model does not include the current low distribution for *T. balicus* (WAM R109338) at 337 m, at Mount Kelatakan, western Bali. *T. vanheurni* is known only from the highlands (1900 m) of the Ijang Plateau. In contrast, *T. balicus* seems to be a lowland species (300–550) known only from the Bali (Mertens 1957; VertNet 2018). Mertens (1957) found that these two species differ in the number of subdigital lamellae on the 4th toe, paravertebral scale rows, and number of rows of paired scales on the dorsal surface of the 4th toe. Based on our examination of type specimens and one additional specimen of *T. balicus* (examined and photographed for us by R. Somaweera at

Western Australian Museum, WAM R109338, described in Somaweera 2017) we find that in addition to the characters noted by Mertens, these species also differ in pattern, *T. balicus* has a light dorsolateral stripe. Based on genetic, morphological, and ecological niche evidence, we recognize five species of *Tytthoscincus* on Java and Sumatra, *T. temmincki, T. necopinatus, T. garutense, T. vanheurni* and *T. balicus*. As most *Tytthoscincus* from Penninsular Malaysia and Borneo, *T. necopinatus, T. garutense* and *T. vanheurni* are known only from their respective type localities. A map depicting the distribution/type localities of all species of *Tytthoscincus* and *Sphenomorphus* from Java and Sumatra discussed in this work is provided in Fig. 3.3.

Examination of our specimens of *Tytthoscincus* identify two new species. Inclusion in the genus is based on small size, limbs that do not meet when addpressed, and temporal scales that are not larger than dorsal scales (Linkem *et al.* 2011). These two species differ from other genera of skinks in Java and Sumatra by the presence of the following characters: pentadactyl limbs (absent in *Larutia, Carlia* and *Brachemeles*), absence of supranasal scales (present in *Lygosoma*, *Eutropis, Cryptoblepharus, Lamprolepis, Emoia,* and *Dasia*), smooth dorsal scales (keeled in *Tropidophorus*), lower eyelids with a series of small scales (single large disc on lower eyelids in *Scincella*), and temporal scales not enlarged (enlarged in *Sphenomorphus*). Characteristics that differentiate these two new species from other *Tytthoscincus* and *Sphenomorphus* on the Sunda Shelf are given in Table 3.3, and in the respective species descriptions below.

Phylogenetic analyses. The partitioned model-based combing mtDNA (ND2) and nuDNA (R35) show no conflicting results between the BI and the ML analyses (Fig. 3.4), both strongly support *Tytthoscincus* as a monophyletic (BI = 1; ML = 98). The supermatrix consists of

70 sequences of ND2 and 22 sequences of R35. The tree topology is similar to that of Grismer *et al.* 2017a,b, but has slightly different nodal support values. The phylogeny also shows the two new species as distinct, and within *Tytthoscincus*. Our *Tytthoscincus* from Aceh (here as *T. sp. nov. 2*) did not group with *T. jaripendek* and *T. kakikecil,* even though they all share a tympanic depression, and our *Tytthoscincus* from East Java (here as *T. sp. nov. 1*) is also different (BI = 1; ML = 100). However, the relationship between these two new species and others is still poorly supported.

We have also found that *Sphenomorphus neopinatus* is sister to *T. cf. temmincki* (BI = 1; ML = 99), and we transfer this species to *Tytthoscincus.* Moreover, we find that *T. temmincki* is paraphyletic. *Tytthoscincus temmincki* from west Java does not clade with that from GenBank, also from Java (exact location not available). This taxon will need to be revisted at a later date. In addition, the raw pairwise distance of ND2 indicates that both *T. sp. nov. 1* and *T. sp. nov. 2* are more than 21% different from other species of *Tytthoscincus* (see Table 3.4).

Together, the morphological and genetic evidence indicates that these two species are different from all described species of *Tytthoscincus* and *Sphenomorphus*, and are described below.

Taxonomy

Tytthoscincus sp. nov. 1

Holotype. MZB 14404 (field number: ENS 13594; Fig. 3.5). A male from the foothills of the old fumaroles of Gunung Raung, G. Pendu and G. Kendii in the Ijen volcanic complex, Desa Jampit, Kecamatan Sempol, Kabupaten Bondowoso, Jawa Timur, Java, Indonesia, 8.07684 °S 114.14006 °E, 1573 m elevation, 830–900 h. Collected on 10 February 2013 by Eric N. Smith.

Paratypes. MZB 14402, MZB 14403, UTA-R 64201, UTA-R 64202 (paralectotype) and UTA-R 64203. The specimens were collected in the same area and on the same date as the holotype. at 1552–1605 m elevation.

Diagnosis. *Tytthoscincus sp. nov. 1* can be identified by the following combination of characters: adult maximum SVL 52 mm; body truncated; tail long and thick; limbs not overlapping when adpressed; dorsal, ventral and lateral scales smooth; midbody scale rows 32; paravertebral scale rows 78–81; ventral scale rows 67–72; supra-ocular scales 4; parietal scales contacting supraoculars; a last supraciliary projecting to body middorsum; prefrontal scales in contact; loreal scales 2; supranasal scales absent; supralabials 6: infralabials 6; toe 4 keeled lamellae 12; precloacal scale enlarged; blackish paravertebral lines on dorsum 6–8; lateral stripe present, fading below; uniform white dots on flanks; light postorbital stripe absent; light dorsal stripe absent; toe 4 dorsal scale formula = 3+4/4 or 2+5/5, unpaired scales 2 or 3, paired scales 4 or 5.

Comparisons. We compared *Tytthoscincus sp. nov. 1* with other congeners and Javan and Sumatran *Sphenomorphus*. *Tytthoscincus sp. nov. 1* differs from *S. anomalopus*, *S. melanopogon*, *S. cyanolaemus*, *S. puncticentralis*, *S. sanctus*, and *S. scotophilus* in having non-overlapping adpressed limbs (vs. overlapping); from *S. modigliani* in having 12 subdigital lamellae on toe 4 (vs. 15), 78–82 paravertebral scale row (vs. 73), and non-overlapping limbs, when adpressed (vs. barely overlapping); from *S. malayanum* in having 6 supralabials (vs. 7) and 5 infralabials (vs. 7–8); from *S. cophias*, *T. jaripendek*, *T. kakikecil*, and *T. sp. nov. 2* in having a deep tympanum (vs. tympanic depression); from *T. aesculeticola, T. bukitensis, T. leproauricuraris, T. parvus,* and *T. perhentianensis* in having a dark dorsolateral stripe (vs. absent). By having 12 subdigital llamellae on toe 4, *T. sp. nov. 1* differs from *T. textus* (13–15); *T. atrigularis*, *T. biparietalis*, *T. leproauricuraris, T. parvus,* and *T. perhentianensis* (all with 10); *T. temengorensis* (10–11); *T. batupanggah* and *T. sibuensis* (both with 9); *T. panchorensis* (8). By having 78–82 paravertebral scale rows *T. sp. nov. 1* differs from *T. butleri* (60–72); *T. martae* (70–74); *T. temasekensis* (55–65). *Tytthoscincus sp. nov. 1* differs from *T. hallieri* by having enlarged precloacal scales and 32 midbody scale rows (vs. 33–41); and from *T. temmincki*, *T. necopinatus* and *T. garutense* by having paired scales on dorsum of toe 4 (vs. single scales followed by sets of three scales).

Tytthoscincus sp. nov. 1 differs from *T. vanheurni* by having 67–72 ventral scale row (vs. 75), 12 subdigital lamellae on toe 4 (vs. 14–15), keeled subdigital lamellae (vs. smooth), prefrontals in contact (vs. not incontact), 2–3 unpaired scales on dorsum of toe 4, followed by 4–5 rows of paired scales (3+4/4 or 2+5/5 vs 2+4/4), and 5 infralabials (vs. 6). *Tytthoscincus sp. nov. 1* differs from *T. balicus* by having 67–72 paravertebral scale rows (vs. 64), 67–72 ventral scale rows (vs. 59), light dorsolateral stripes absent (vs. light dorsolateral line present). Table 3.5 presents a morphological comparison between *T. sp. nov. 1*, *T. vanheurni* and *T. balicus*, and Figs. 3.6–3.8 show dorsal, ventral, and lateral views of these three tree species.

Description of Holotype. All measurements in mm; male; SVL 49.34; tail length 76.10 (primary tail) axilla–groin distance 26.33; head length 10.49; head width 7.16; snout–forelimb length 17.55; internarial distance 1.65; interoccular distance 3.71; rostral length 3.82; interorbital distance 3.41; eye diameter 3.35; tympanum diameter 1.47; forelimb length 9.46 ; hindlimb length 13.10; rostral wider than long, convex, in broad contact with frontonasal; frontonasal wider than long; prefrontals large, widely in contact; frontal elongate, triangular in shape, in contact with first two supraoculars and one preocular; frontoparietals asymmetrical, in broad contact, contacting second, third, and fourth supraoculars, and parietals, interparietal, and frontal; interparietal diamond-shaped, large, parietal eyespot posterior; parietals large, in contact posterior to interparietal, in contact with fourth supraocular; nuchal scales absent; first row of dorsal scales slightly larger than following scales; nostril in posterior part of nasals, nasal contacting anteriorly with rostral, dorsally with frontonasal, posteriorly with anterior loreal, and ventrally with first supralabial; supralabials 6, first contacting nasal and anterior loreal, second contacting anterior loreal, posterior loreal, and lower preoccular; third to fifth contacting small suboculars, and sixth contacting slightly enlarged temporals; supranasals absent; suture between rostral scale and prefrontal narrower than half of rostral width; two loreals, subequal, taller than wide; preoculars 3, anteriorly contacting posterior loreal, highest bigger than others; supraciliaries 9, posteriormost elongated, projecting dorsaly; temporals slightly enlarged, compared to lateral scales; lower eyelid scaly, without transparent scale; mental wider than long, wider than rostral, contacting postmental and first infralabial; postmental contacting first infralabial; pairs of chin shields 2, first pair in asymmetrical medial contact, contacting first and second infralabials; second pair of chin shields separated by first single ventral scale, contacting second and third infralabials; five infralabials; ear opening oval, tympanum visible, no lubules; body scales smooth, hexagonal; ventrals, dorsals, and laterals subequal; subcaudals not enlarged; scale rows around midbody 32; paravertebral scale rows 81; ventral scale rows 69; enlarged preanal scales 2; body relatively slender, with primary tail; limbs widely separated when adpressed; lamellae keeled; forelimb subdigital lamellae (L/R) in parentheses: I(4/4), II(6/6), III(7/7), IV(8/,8), V(6/6); hindlimb subdigital lamellae (L/R) in parentheses: I(4/4), II(8/8), III(10/10), IV(12/12), V(7/8).

Color in life: Dorsally, the head, body, and tail are dark brown. The dorsolateral stripe is black, beginning posterior to the temporal scales. Above the dorsolteral dark stripes are light stripes. Limbs are darker than the body and with a uniform pattern of light dots, as on the body. Laterally, head scales are almost completely black but with light dotting. The temporal region and flanks of the body are also blackish and with white dots. The dorsolateral stripe is not distinct towards the venter, gradually becomes paler. The coloration transitions gradually from the dorsal surface to the ventral, without a clean demarcation between the two colors. But the light dots are different, paler brown towards the upper flank, white below. The flanks of the tail are similarly colored to the flanks of the body. Ventrally, the gular scales are blackish with abundant white spotting. The abdomen is white with a small median region of light pink and every scale with melanic pigment. Limbs underneath are grey, also with melanic pigment. Tail venter is also grey and with melanic pigment on every scale and with white dots, similar to those in the gular area. Palmar and plantar surfaces are grey.

Color in preservation: In the type series in 70% ethanol the color pattern is similar to that of living specimens. However, the dark areas are paler and the white spotting is beige. Venter changing from white to beige or yellow and with clear melanic pigment and white dots. Internal organs are no longer visible at middle of body. Dorsal and lateral surfaces of head, body, tail, and limbs dark brown, with the dorsolateral stripe being more evident than in life. Light dots on flanks are all beige. The secondary tail is darker than the primary tail.

Variation. Deviation in lepidosis includes the number of paravertebral scale rows (78–82) and ventral scale rows (67–72). The paratype UTA-R 64201 has much more melanic pigment on the lateral and ventral scales, compared to the other specimens; the paratype MZB 14402 has pale yellow ventral scales, instead of white; the dorsal scale formula can also be 2+5/5 or 3+4/4. The paratype UTA-R 64203 has the frontoparietal not broadly in contact, just meeting and not overlapping, like in all other specimens. Variation is shown in Table 3.5.

Distribution and natural history. This species has been found from 1552 to 1605 m in the Ijen volcanic comples of East Java, and it is likely endemic to this orogoraphic feature. This species seems to be semi-fossorial, since all specimens were found in leaf litter and under logs in primary forest or in coffee plantation. The habitat near the collection site of the holotype is shown in Fig. 3.9.

***Tytthoscincus* sp. nov. 2**

Holotype. MZB 14401 (field number: ENS 18790; Fig. 3.10). A male from the base of Gunung Batee Meucica, Kabupaten Aceh Besar, Aceh Darussalam, Sumatra, 5.26157 °N 95.54176 °E, 502 m elevation. Collected 1 August 2016 between 1800–1830 h by Irvan Sidik, Ilham Fonra, Panupong Thammachoti, Goutam C. Sarker, Syarif Udin, and Eric N. Smith.

Diagnosis. *Tytthoscincus sp. nov. 2* differs from most species of *Tytthoscincus* and small *Sphenomorphus* in the Sunda Shelf because it has a tympanic depression. However, this character is also found in *S. cophias, T. jaripendek* and *T. kakikecil,* all found in Peninsular Malaysia. *Tytthoscincus sp. nov. 2* differs from these species in number of midbody scale rows (28), paravertebral scale rows (61), ventral scale rows (59), subdigital lamella on toe 4 (10), supralabials (6), infralabials (6), and having enlarged pectoral scales. Table 6 presents amorphological comparison among species in the Sunda Shelf with a tympanic-depression. Fig. 3.11. compares the tympanic region of four *Tytthoscincus* species, including those described herein.

Comparisons. We compared *Tytthoscincus sp. nov. 2* with other congeners and Javan and Sumatran *Sphenomorphus*. *Tytthoscincus sp. nov. 2* differs from *S. anomalopus*, *S. cyanolaemus*, *S. melanopogon*, *S. modigliani, S. puncticentralis*, *S. sanctus*, and *S. scotophilus* in having non-overlapping adpressed limbs (vs. overlapping or barely overlapping [*S. modigliani*]); and from species with non-overlapping limbs in the genus *Sphenomorphus* and all other *Tytthoscincus* species, *S. malayanum, T. aesculeticola*, *T. atrigularis*, *T. batupanggah*, *T. biparietalis*, *T. bukitensis, T. butleri T. garutense, T. hallieri*, *T. ishaki*, *T. leproauricularis*, *T. sp.*

nov. 1, *T. necopinatus, T. panchorensis*, *T. parvus*, *T. perhentianensis*, *T. sibuensis*, *T. temasekensis T. temengorensis*, *T. temmincki*, *T. textus,* and *T. vanheurni* by having a tympanic depression (vs. recessed tympanum). *Tytthoscincus sp. nov. 2* differs from species with tympanic depressions, *S. cophias, T. jaripedek,* and *T. kakicecil*. From *S. cophias* differs in having a truncated body (vs. elongated); midbody scale rows 28 (vs. 24); paravertebral scale rows 61 (vs. 56); ventral scale rows 59 (vs. 56); supralabials 6 (vs. 7); infralabials 6 (vs. 7); light postorbital stripe present (vs. absent); dark dorsolateral stripe present (vs. absent); from *T. jaripendek* differs in having a truncated body (AGD/SVL = 0.53 vs 0.55–0.57); paravertebral scale rows 61 (vs. 63–65); ventral scale rows 59 (vs. 60–62); infralabials 6 (vs. 5); from *T. kakikecil* differs in having midbody scale rows 28 (vs. 30–33); paravertebral scale rows 61 (vs. 68–73); ventral scale rows 59 (vs. 65–69); infralabials 6 (vs. 5). Table 6 presents morphological comparisons between species with a tympanic depression, *T. sp. nov. 2*, *S. cophias T. jaripendek,* and *T. kakikecil.*

Description of Holotype. All measurements in mm; male; SVL 34.54; tail length 22.62 (secondary tail); axilla–groin distance 18.13; head length 6.04; head width 4.22; snout–forelimb length 11.59; internarial distance 1.32; interoccular distance 2.31; rostral length 2.49; interorbital distance 4.14; eye diameter 2.58; tympanum diameter 0.51; forelimb length 6.85; hindlimb length 12.30; weight in life 0.6 grams; rostral wider than long, convex, broadly contacting frontonasal; frontonasal wider than long; prefrontals large, widely separated; frontal elongated, triangular, contacting first two supraoculars and one preocular; frontoparietals with broad asymmetrical contact, contacting second, third, and fourth supraoculars, parietals, interparietal, and frontal; interparietal diamond-shaped, small, parietal eyespot posterior; parietals large, contacting interparietal and fourth supraocular; nuchal scales absent; nostril in posterior part of nasals, nasal in contact anteriorly with rostral, dorsally with frontonasal, posteriorly with anterior loreal, and ventrally with first supralabial; supralabials 6, first dorsally contacting nasal and anterior loreal, second dorsally contacting posterior loreal, third to sixth contacting suboculars; supranasals absent; suture between rostral scale and prefrontal wider than half of rostral width; loreals 2, subequal, taller than wide; preoculars 3, anteriorly contacting posterior loreal, lowest biggest; supraciliaries 8; last posterior supraciliary elongated, projecting dorsaly; temporals not enlarged, similar to lateral scales; lower eyelid scaly, without transparent scale; mental wider than long, wider than rostral, contacting postmental and first infralabial; postmental contacting first infralabial; pairs of chin shields 3, first pair contacting each other asymmetrically, contacting first and second infralabials; second pair separated by first single ventral scale, contacting second and third infralabials; third pair separated by three ventral scales, contacting third and fourth infralabials; infralabials 6; ear opening fully covered by pigmented scale, tympanum not visible (Fig. 3.11); body scales smooth, hexagonal; ventrals, dorsals and lateral scales subequal; some pectoral scales enlarged; subcaudals not enlarged; scale rows around midbody 28; paravertebral scale rows 61; ventral scale rows 59; precloacal scales slightly enlarged; body relative slender, with secondary tail; limbs widely separated when adpressed; lamellae keeled; forelimb subdigital lamellae (L/R): I(3/3), II(5/6), III(7/7), IV(7/,7), V(5/5); hindlimb subdigital lamellae (L/R): I(4/4), II(6/6), III(9/9), IV(10/10), V(7/7); no paired scale row at dorsal surface of toe 4.

Color in life: The dorsum of the body is reddish brown with light dots uniformly scattered. The head and tail are relatively darke, compared to the body and limbs. The head is dark brown with small light dots on scales. Dorsolateral stripes start after temporals and also have light dots at the edges. Limbs and tail have a uniform pattern of light dots. In lateral view, the head scales are dark brown with light dots in the temporal area, and the body flanks are light brown with no pattern of white dots. Some lateral scales below the dark dorsolateral stripes also have a dark color. The dorsolateral stripes at the middle of body fade laterally, towards the venter. The flanks of the tail are similar in pattern to those of the body. Ventrally the head scales are light beige and with no melanic pigment. The body venter is beige and relative transluscent, with the internal organs visible, although some of its scales have melanic pigment. The limbs are beige, similar to the venter of body. The tail is light beige and have six melanic lines, continues from above preanal scales. The palmar and plantar surfaces are darker the arms and legs.

Color in preservative: In the holotype, in 70% ethanol, the color pattern is similar to that of living specimens, but paler. The venter changing from white or beige to pale yellow, but still having the internal organs visible in the middle of the body. Dorsally and laterally, the head, body, tail, and limbs turn lighter brown or tan, making the light dots easier to see. The dorsolateral stripes are slightly paler, and still fade at the middle of the body. The secondary tail is darker than the original base of the tail.

Distribution and natural history. The holotype and only known specimen was found at mid elevation, 502 m, in Gunung Batee Meucicain, Aceh Besar, Aceh, Sumatra. With a single locality known no ecological niche modeling could be used for prediction the distribution of this species. However, most species in the genus are microendemics, and the lack of more specimens in historical collections agree with this being the case for *T. sp. nov. 2*. The holotype was found at half a meter above the ground on a fallen tree trunk covered by leaf litter at the base of a hillside. The habitat was dipterocarp primary forest close to small stream (Fig. 3.12).

Discussion

This is the first taxonomic revision on *Tytthoscincus* in Java, Sumatra and adjacent areas, since Brongersma (1942) and Mertens (1957), although several new species of *Tytthoscincus* have been described recently from Peninsular Malaysia and Borneo (Grismer *et al.* 2016; Karin *et al.* 2016; Grismer *et al*. 2017a; Grismer *et al.* 2017b), and several species of have been recognized as endemics (Grimer 2011 and Karin *et al.* 2016). Similar to our two new species, these have been found in restricted and isolated areas, with elevation and limited vagility restricting them as endemics.

Tytthoscincus sp. nov. 2 was found at mid elevation in primary forest, in Aceh, in the northernmost part of Sumatra (Hitchcock and Meyers, 2006), where very few recent studies on reptiles have been published (Harvey *et al.* 2017b; Wostl *et al.* 2017). *Tytthoscincus sp. nov. 1* was found in the Ijeng volcanic complex, at relatively high elevation in East Java. We determined ecological niche modeling using our own data and that in the literature for *T. vanheurni*. The model shows that this species group is endemic to isolated single mountains in East and Central Java. Ecological niche modeling is a suitable technique to examine spatial distributions of herpetofauna (Vitt & Caldwell 2013) and our results shed light into the distributions of fossorial skinks in the highlands of Java. Java has 33 volcanic mountains, many isolated from each other and formed from west to east as part of the Sunda Arc (Curray 1989). Diminutive skinks are of limited movility and cannot move from one mountain to other across lowland, as they are restricted to relatively humid and cool leaf-litter. Each montane population is dramatically separated and follows its own evolutionary history, leading to distinct lineage speciation (Nosil 2012).

The climate in Java is heterogeneious, West Java and Banten are similar in climate to Sumatra, dominated, an equatorial climate dominated by east winds leading to more humidity and precipitation. Central and Eastern Java have a mixture of equatorial, monsoon, and tropical savanna climate, leading to more seasonality, drier conditions, and more isolated humid montane forests (JavaIndonesia.org 2018). Tänzler *et al.* 2015 indicated a pattern of separation in beetle between West and East Java, resulting from recent land emergence 10–5 Ma.

Due to the geographic isolation and climate heterogeneity, the fossorial skinks of the highlands of Java seem to have unique evolutionary histories leading to high allopatric speciation among sister lineages. These resulting endemism being specially high Eastern and Central Java, where volcanic mountains are more isolated from each other.

We find similar external morphology between our new species from mid-elevation in Aceh and species from W. Malaysia, all sharing a tympanic despression. This character is so far only found in four species, *S. copias*, *T. jaripendek* and *T. kakikecil*, and *T. sp. nov. 2*. Based on the phylogenetic analysis our new species is not sister to these W. Malaysia species, indicating convergence in the tympanic depression trait. Microhabitat and habits might be the driving force of this convergence, similar to that of other characters found in other groups of skinks (Barley *et al.* 2013).

We formally transfer from *Sphenomorphus necopinatus* to *Tytthoscincus*. Our new species *Tytthoscincus sp. nov. 1* looks superficially similar to *S. vanheurni* and morphological examination confirms that it also belongs in *Tytthoscincus*.

We bring the number of *Tytthoscincus* in Java and Sumatra from a single recognized species to six, *T. garutense*, *T. necopinatus*, *T. temmincki*, *T. sp. nov. 1*, *T. sp. nov. 2*, and *T. vanheurni*, and note the high potential for discovery of more microendemic fossorial skinks in the highlands of Java and Sumatra.

Key to the species of *Tytthoscinscus* and *Sphenomorphus* in Java and Sumatra

1a. Limbs separated when adpress..2

1b. Limbs barely overlap when adpressed..***S. modigliani***

2a. Lacking external ear opening..***T. sp. nov. 2***

2b. Distinct external ear opening 3

3a. Supralabials and infralabials 5–6 4

3b. Supralabials and infralabials 7–8 ....***S. malayanum***

4a. 4th dorsal scale of toe divided 5

4b. 4th dorsal scale of toe not divided 7

5a. Light dorsolateral stripe absent..6

5b. Light dorsolateral stripe present..***T. balicus***

6a. Infralabials 6, and 4th toe SDL 13-15..***T. vanheurni***

6b. Infralabials 5, 4th toe SDL 12..***T. sp. nov.1***

7a. Toe 3 as long as toe 4..8

7b. Toe 4 longer than toe 3 ....***T. temmincki***

8a. Toe 4 subdigital lamellae 11–13, paravertebral scale rows 63–66 .... ***T. necopinatum***

8b. Toe 4 subdigital lamellae 13–15, paravertebral scale rows 66–75 ....***T. garutense***

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Appendix

Specimens examined

T. sp. nov. 1 (n = 6). Indonesia: East Java: Bondowoso: Jampit: Mount of Ijen, 1591 m, -8.07724 S, 114.14472 E, MZB 14402 (female) - paratype, UTA-R 64201 (male)-paratype; 1552 m, -8.07368 S, 114.14225 E, MZB 14403 (female)- paratype; 1578 m, -8.07684 S, 114.14006 E, UTA-R 64202 (male)-paratype, MZB 14404 (male)-holotype; 1605 m, -8.07903 S, 114.14239 E, UTA-R 64203 (female)-paratype.

T. sp. nov. 2 (n = 1). Indonesia: Aceh: Aceh Besar: Mount of Batee Meucica, 502 m, 5.26157 N, 95.54176 E, MZB 14401 (male)-Holotype.

T. temmincki (n = 2) Indonesia: Wets Java: Bundung: Mount of Kencana, 1884 m, -7.29276 S, 107.63394 E, UTA-R 64192; Indonesia: Java, MHNP 1344-Holotype

T. necopinatus (n = 3) Indonesia West Java: Borgor, RMNH.RNEA 7969-Holotype; BMNH 1948.1.8.17-Palatype; Gn. Halimun 950 m -6.7109 S, 106.5191667 E, MZB 7644.

T. garutense (n = 5) Indonesia Indonesia West Java: Mount of Garoet, RMNH.RENA 7970-Holotype; RMNH.RENA 7963-Paratype; RMNH.RENA 7970-Holotype (700-1500 m); Tasikmalaya, Gunung Gulunggung, MZB 9442; MZB 10475

T. vanheurni (n = 1) Indonesia: East Java: Mount of Argopuro (Ijang): Bremi: Taman Hidub, RMNH.RENA 7967-Holotype

T. balicus (n = 2) Indonesia: Bali: Mount of Gitgit, SMF 23275- Holotype; Mount of Kelatakan, WAM R109338 (examined by R. Somavera)

S. cophias (n = 1) Malaysia: Pahang, BMNH 1946.8.3.15-type

S. malayanus (n = 1) Indonesia: Sumatra Barat: Mount of Singalung, MSG 27869 (female)-lectotype

S. modiglaiani (n = 1) Indonesia: Mentawai: Sipora, BMNH 1946.8.16.98-type

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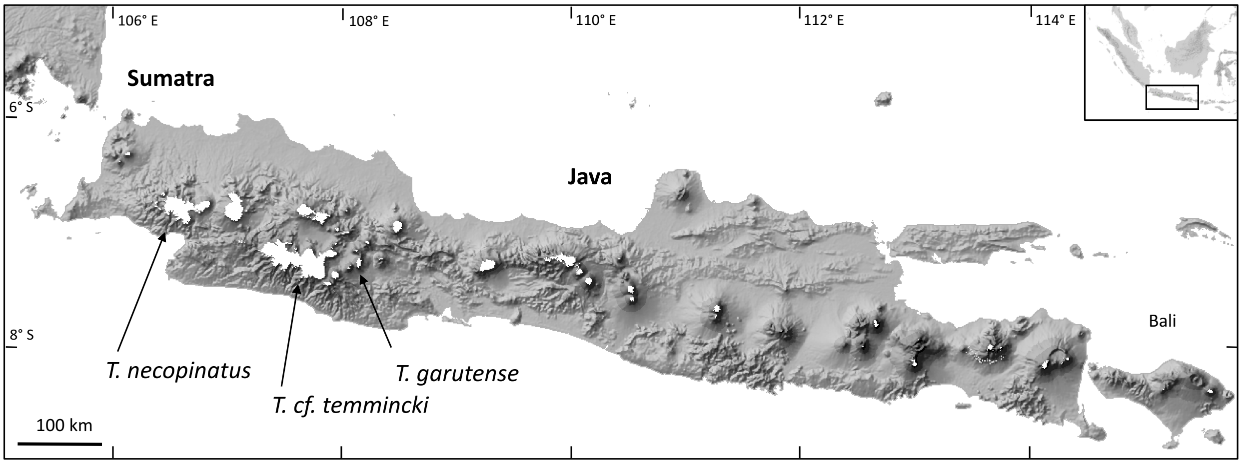

Figure 3.1. Ecological niche modeling distributions showing suitable habitat for montane species in West and Central Java (*T. necopinatus*, *T. garutense* and *T. temmincki*).

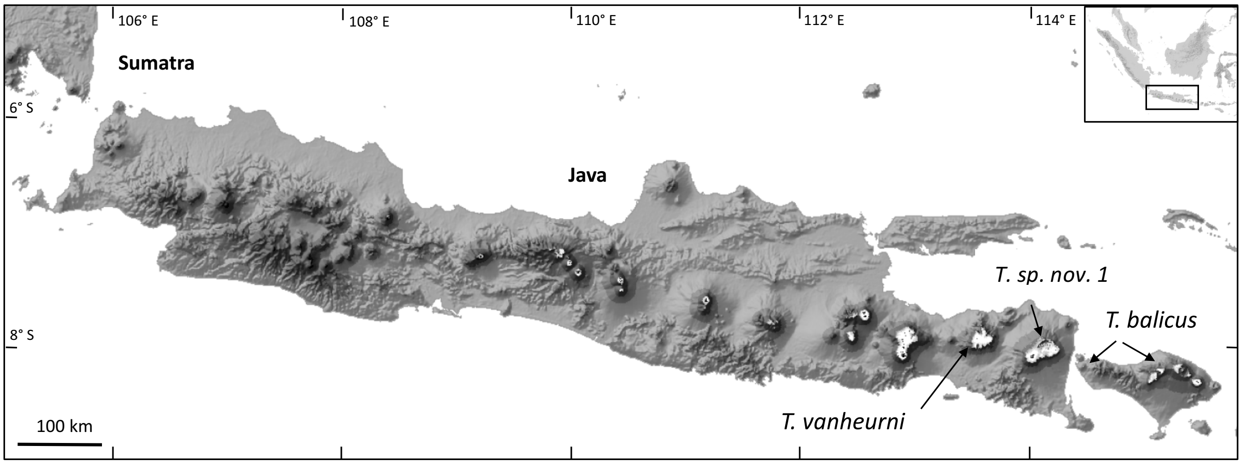

Figure 3.2. Ecological niche modeling distributions showing suitable habitat for montane species in East Java (*T. vanheurni* and *T. sp. nov. 1*) .

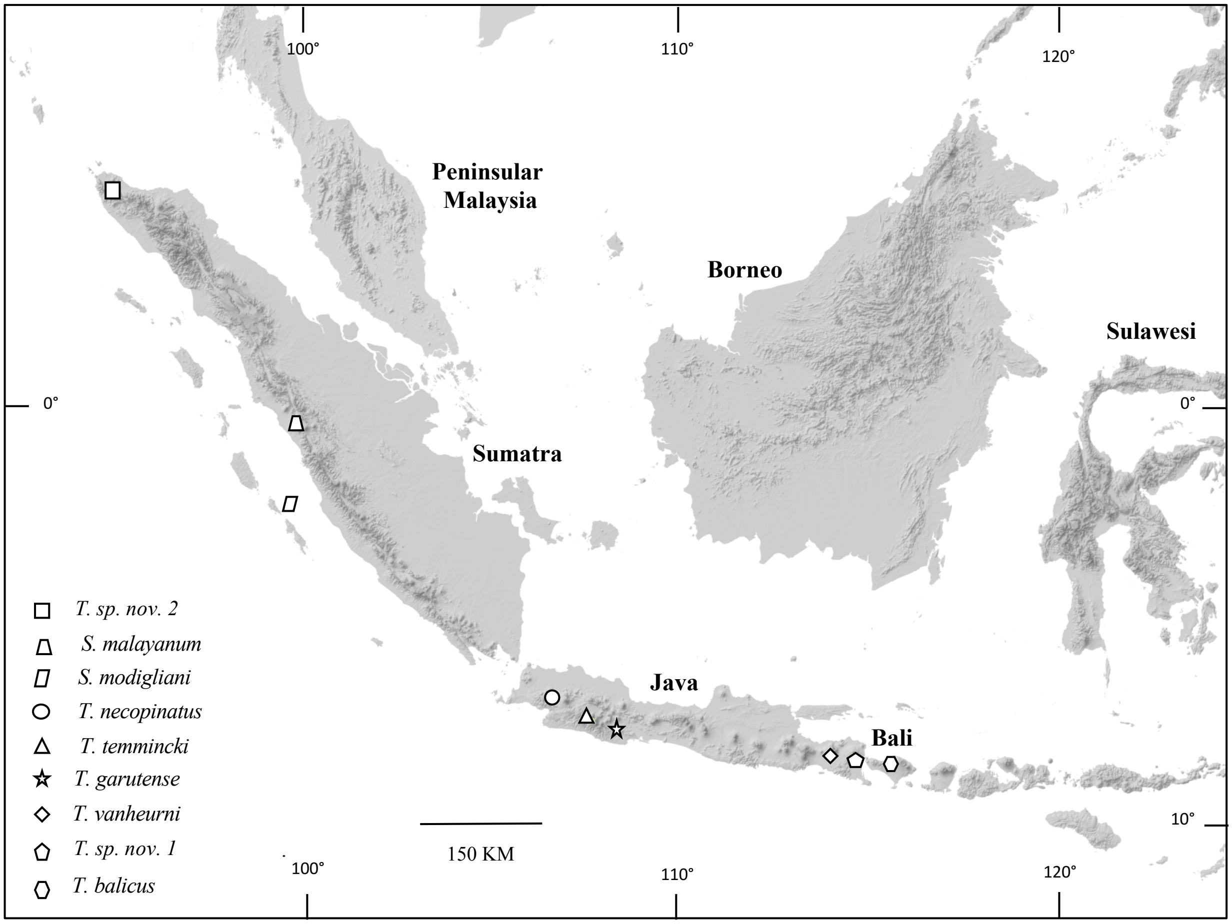

Figure 3.3. Type localities for *Tytthoscincus* and selected *Sphenomorphus* in Java, Sumatra and Bali discussed in this work.

Figure 3.4. Bayesian phylogeny of *Tytthoscincus,* based on concatenated and partitioned mitochondrial and nuclear data. Significant supports presented on nodes, Bayesian (BP ≥ 0.95) and Maximum Likelihood (ML ≥ 70), respectively.

Figure 3.5. Holotype of *Tytthoscincus sp. nov. 1* (holotype, MZB 14404), from the foothills of Gunung Raung, Ijen volcanic complex, Bondowoso, Jampit, East Java, 8.07684 °N, 114.14006 °E, 1573 m elevation.

Figure 3.6. Dorsal views of: A) *Tytthoscincus sp. nov. 1* (holotype, MZB 14404); B) *T. vanheurni* (holotype, RMNH.RENA 7967); and C) *T. balicus* (holotype, SMF 23275).

Figure 3.7. Ventral views of: A) *Tytthoscincus sp. nov. 1* (holotype, MZB 14404); B) *T. vanheurni* (holotype, RMNH.RENA 7967); and C) *T. balicus* (holotype, SMF 23275).

Figure 3.8. Lateral views of: A) *Tytthoscincus sp. nov. 1* (holotype, MZB 14404); B) *T. vanheurni* (holotype, RMNH.RENA 7967); and C) *T. balicus* (holotype, SMF 23275).

Figure 3.9. Habitat of *Tytthoscincus sp. nov. 1*, Gunung Raung, Ijen volcanic complex, Bondowoso, Jampit, East Java, 8.07684 °N, 114.14006 °E, 1573 m elevation.

Figure 3.10. Holotype of *Tytthoscincus sp. nov. 2* (holotype, MZB 14401), from the base of Gunung Batee Meucica, Kabupaten Aceh Besar, Aceh Province, Sumatra, 5.26157 °N, 95.54176 °E, 502 m elevation.

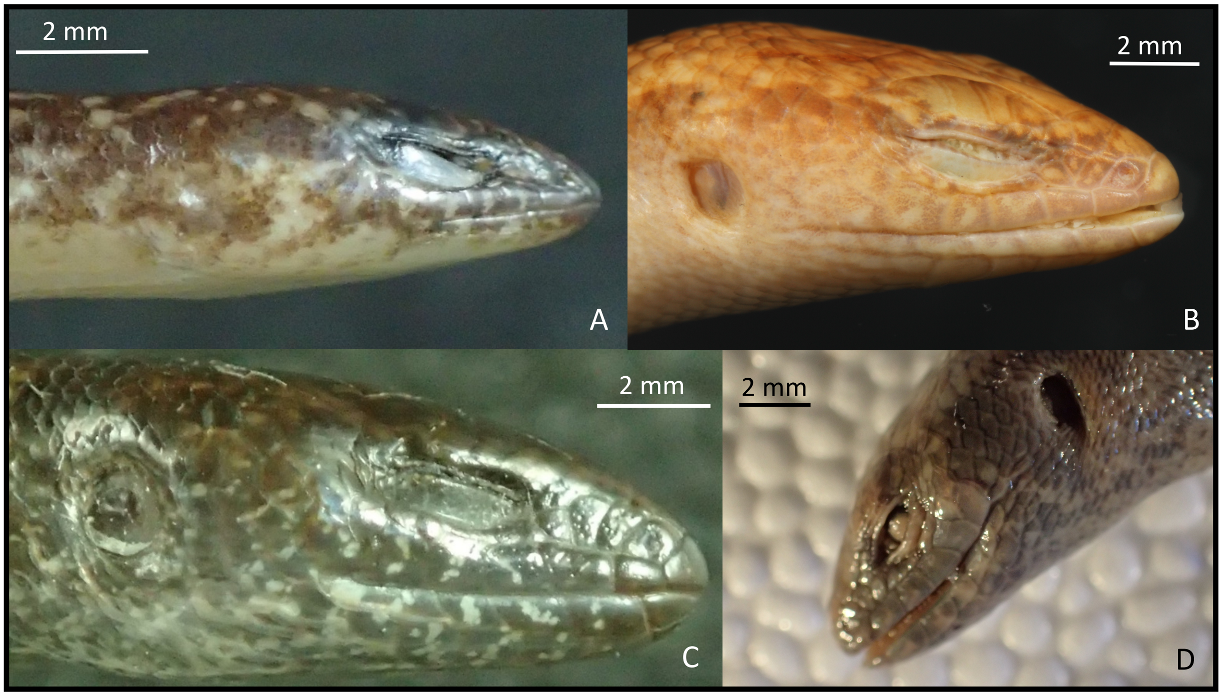

Figure 3.11. Lateral view of head of: A) *Tytthoscincus sp. nov. 2* (holotype, MZB 14401) showing tympanic depression; B) *T. balicus* (holotype, SMF 23275) showing circular tympanum; C) *T. sp. nov. 1* (holotype, MZB 14404) showing circular tympanum; and D) *T. vanheurni* (holotype, RMNH.RENA 7967) showing ovular tympanum.

Figure 3.12. Habitat of *Tytthoscincus sp. nov. 2* at the base of Gunung Batee Meucica, Kabupaten Aceh Besar, Aceh Province, Sumatra, 5.26157 °N, 95.54176 °E, 502 m elevation.

Tables

Table 3.1 Specimens used in phylogenetic analysis, with respective GenBank accession numbers (Karin *et al.* 2016; Linkem *et al*. 2011; Grismer *et al.* 2017a,b; Siler *et al.* 2011; sequences in bold were generated for this study).

Species	Voucher No.	Locality	GenBank No.	
			ND2	R35
Larutia seribuatensis	LSUHC 5168	W. Malaysia, Pahang	HQ907429	HQ907636
Sphenomorphus cyanolaemus	FMNH 239867	Malaysia, Borneo, Sabah	JF498193	JF498436
T. aesculeticola	FMNH 239839	Malaysia, Borneo, Sabah	JF498209	JF498452
T. aesculeticola	SP 06913	Malaysia, Borneo, Sabah	JF498208	JF498451
T. atrigularis	KU 315055	Philippines, Mindanao	JF498210	JF498453
T. atrigularis	KU 315060	Philippines, Mindanao	KU 315060	JF498454
T. batupanggah	CAS 259189	Malaysia, Borneo, Sarawak	KU587720	KU587723

T. batupanggah	ZRC 2.7122	Malaysia, Borneo, Sarawak	KU587722	KU587725
T. bukitensis	LSUHC 11655	W. Malaysia, Pahang	KU872730	-
T. bukitensis	LSUHC 11771	W. Malaysia, Pahang	KY989404	-
T. bukitensis	LSUHC 12226	W. Malaysia, Pahang	KY989403	-
T. bukitensis	LSUHC 12237	W. Malaysia, Pahang	KY989399	-
T. bukitensis	LSUHC 12686	W. Malaysia, Pahang	KY989401	-
T. bukitensis	LSUHC 12687	W. Malaysia, Pahang	KY989402	-
T. bukitensis	LSUHC 12750	W. Malaysia, Pahang	KY989398	-
T. bukitensis	ZRC 2.6245	W. Malaysia, Pahang	KY989400	-
T. butleri	LSUHC 11275	W. Malaysia, Pahang	KY989410	-

T. butleri	LSUHC 11552	W. Malaysia, Kedah	KY989410	-
T. butleri	LSUHC 11784	W. Malaysia, Kedah	KY989411	-
T. butleri	LSUHC 11785	W. Malaysia, Kedah	KU872738	-
T. butleri	LSUHC 11786	W. Malaysia, Kedah	KU872739	-
T. butleri	LSUHC 11802	W. Malaysia, Kedah	KY989412	-
T. butleri	LSUHC 12071	W. Malaysia, Penang	KU872733	-
T. butleri	LSUHC 12429	W. Malaysia, Perak	KY989405	-
T. butleri	LSUHC 12432	W. Malaysia, Perak	KY989406	-
T. butleri	LSUHC 12433	W. Malaysia, Perak	KY989407	-
T. butleri	LSUHC 12516	W. Malaysia, Penang	KY989408	-

T. butleri	LSUHC 6790	W. Malaysia, Kedah	KU872736	-
T. butleri	LSUHC 9204	W. Malaysia, Perak	KU872731	-
T. butleri	LSUHC 9206	W. Malaysia, Kedah	KU872732	-
T. hallieri	FMNH 230184	Malaysia, Borneo, Sabah	JF498212	JF498455
T. ishaki	LSUHC 5165	W. Malaysia, Pahang	KY989413	-
T. ishaki	LSUHC 6150	W. Malaysia, Pahang	KU872735	-
T. ishaki	LSUHC 6151	W. Malaysia, Pahang	KY989414	-
T. jaripendek	LSUHC 11679	W. Malaysia, Pahang	KU872745	-
T. jaripendek	LSUHC 11680	W. Malaysia, Pahang	KU872746	-
T. jaripendek	LSUHC 11681	W. Malaysia, Pahang	KU872747	-

T. jaripendek	LSUHC 11687	W. Malaysia, Pahang	KU872748	-
T. kakikecil	LSUHC 11769	W. Malaysia, Pahang	KY989415	-
T. kakikecil	LSUHC 11770	W. Malaysia, Pahang	KY989416	-
T. kakikecil	LSUHC 11772	W. Malaysia, Pahang	KY989417	-
T. kakikecil	LSUHC 12754	W. Malaysia, Pahang	KY989418	-
T. leproauricularis	ZRC 2.7123	Malaysia, Borneo, Sarawak	KU587721	KU587726
T. leproauricularis	CAS 259190	Malaysia, Borneo, Sarawak	-	KU587724
T. sp. nov. 1	MZB 14402	Indonesia, East Java	**Pending acceptance**	**Pending acceptance**
T. sp. nov. 1	UTA-R 64201	Indonesia, East Java	**Pending acceptance**	**Pending acceptance**
T. sp. nov. 1	MZB 14403	Indonesia, East Java	**Pending acceptance**	**Pending acceptance**

T. sp. nov. 1	UTA-R 64202	Indonesia, East Java	**Pending acceptance**	**Pending acceptance**
T. sp. nov. 1	MZB 14404	Indonesia, East Java	**Pending acceptance**	**Pending acceptance**
T. sp. nov. 1	UTA-R 64203	Indonesia, East Java	**Pending acceptance**	**Pending acceptance**
T. martae	LSUHC12518	W. Malaysia, Pahang	KY989422	-
T. martae	LSUHC 12571	W. Malaysia, Pahang	KY989424	-
T. martae	LSUHC 12688	W. Malaysia, Pahang	KY989419	-
T. martae	LSUHC 12749	W. Malaysia, Pahang	KY989421	-
T. martae	LSUHC 12751	W. Malaysia, Pahang	KY989423	-
T. martae	ZRC 3.6246	W. Malaysia, Pahang	KY989420	-
T. necopinatus	MZB 7644	Indonesia, East Java	**Pending acceptance**	**Pending acceptance**

T. panchorensis	LSUHC 12511	W. Malaysia, Penang	KU872741	-
T. parvus	JAM 6275	Indonesia, Sulawesi	-	JF498457
T. parvus	RMB 4707	Indonesia, Sulawesi	JF498213	JF498456
T. perhentianensis	LSUHC 8705	W. Malaysia, Terengganu	KU872742	-
T. sananus	JAM 8829	Indonesia, Sanana	KY989394	-
T. sibuensis	LSUHC 5583	W. Malaysia, Johor	KU872743	-
T. sp. nov. 2	MZB 14401	Indonesia, Sumatra, Aceh	**Pending acceptance**	**Pending acceptance**
T. temasekensis	LSUHC 12748	W. Malaysia and Singapore	KY989395	-
T. temengorensis	LSUHC 5650	W. Malaysia, Perak	KU872742	-
T. temmincki	BS 10263	Indonesia, Java	KY989396	-
T. temmincki	UTA-R 64192	Indonesia, West Java	**Pending acceptance**	**Pending acceptance**

T. textus	JAM 7497	Indonesia, Sulawesi	KY989397	-
T. sp.	LSUHC 12515	W. Malaysia, Terengganu	MG182075	-

Table 3.2 Geographic data used for ecological niche modeling of the montane species of *Tytthoscincus* in Java.

Species	Vouncher	Latitude	Longitude	Data sources
Tytthoscincus garutense	MZB 9442	-7.25281944	107.9822222	museum data
T. sp. nov. 1	MZB 14402	-8.07724	114.14472	this study
T. sp. nov. 1	UTA-R 64201	-8.07724	114.14472	this study
T. sp. nov. 1	MZB 14403	-8.07368	114.14225	this study
T. sp. nov. 1	UTA-R 64202	-8.07684	114.14006	this study
T. sp. nov. 1	MZB 14404	-8.07684	114.14006	this study
T. sp. nov. 1	UTA-R 64203	-8.07903	114.14239	this study
T. necopinatus	MZB 7644	-6.7109	106.5191667	museum data
T. temmincki	UTA-R 64192	-7.29276	107.63394	this study
T. temmincki	UTA-R 64193	-7.25281	107.61496	this study
T. vanheurni	RMNH.RENA 7967	-7.98101111	113.5347222	Selected from original description

Table 3.3 Morphological characters among species *Tytthoscincus* and selected *Sphenomorphus* from the Sunda Shelf and adjacent areas. Data obtained from original descriptions and from Grismer 2009 and Karin *et al.* 2016. Numbers on column heading refer the following characters: (1) snout–vent length (mm), (2) midbody scale rows, (3) paravertebral scale rows, (4) ventral scale rows, (5) supraoculars, (6) parital in contact with supraocular, (7) posterior supracilliary elongate and projecting dorsomedially, (8) prefrontals in contact, (9) loreals, (10) supralabials, (11) infralabials, (12) subdigital on 4th toe, (13) keeled lamellae texture, (14) enlarged precloacal scales, (15) dark dorsolateral stripe, (16) light post-orbital stripe, (17) light dorsolateral stripe, and (18) tympanic depression. (1 present; 0 absent; - data not available)

Species	Locality	**1**	**2**	**3**	**4**	**5**	**6**
Tytthoscincus							
T. aesculeticola	Borneo	40–43	26–32	-	60–68	4	1
T. atrigularis	Philippines	-	30	-	-	4	-
T. balicus	Bali	33–60	30–31	64	59	4	0
T batupanggah	Borneo	26.8–33.2	30–31	62–66	55–61	4	1
T. biparietalis	Philippines	-	32	-	-	4	
T. bukitensis	W. Malaysia	40.5–44	31–33	73–74	61–74	4	1
T. butleri	W. Malaysia	34–44	31–37	60–72	62–72	4	1
T. garutense	W. Java	27–44	28–32	66–75	58–60	4	1
T. hallieri	Borneo	48–52	33–41	-	63–73	4	0

T. ishaki	W. Malaysia	38–41	30–32	68–73	60–70	4	1
T. jaripendek	W. Malaysia	32.2–33.9	28–30	63–65	60–62	4	1
T. kakikecil	W. Malaysia	24.2–39.2	30–33	67–73	65–69	4	1
T. martae	W. Malaysia	22.4–44	31–35	70–74	61–72	4	1
T. necopinatus	W. Java	25–46.85	28–34	63–84	74	4	1
T. panchorensis	W. Malaysia	35.5	29	68	57	5	1
T. parvus	Sulawesi	-	30	-	-	4	-
T. perhentianensis	W. Malaysia	30	29	65	61	4	1
T. leproauricularis	Borneo	26.8–33.2	30–31	62–66	55–61	4	-
T. sanana	Sanana	32	28	-	-	4	-
T. sibuensis	W. Malaysia	17.7 (Juv)	29	58	52	4	1
T. temasekensis	W. Malaysia	22.5–36.3	27–29	55–65	54–63	4	1
T. temengorensis	W. Malaysia	35.5	30–35	68–70	70–71	4	1
T. temmincki	Java, Sumatra	56	30–37	68–80	62–72	4	1
T. textus	Sulawesi	-	30–32	-	-	5	
T. vanheurni	E. Java	64	31	81	75	4	0
T. sp.1 sp.nov.	E. Java	42.09–52.86	32	78–82	67–72	4	1
T. sp.2 sp.nov.	Aceh, Sumatra	34.54	28	61	59	4	1

Table 3.3 (continue)

Species	Locality	**1**	**2**	**3**	**4**	**5**	**6**
Sphenomorphus							
S. apalpebratus	NE India	42	27–28	62–64	60	5	1
S. alfredi	Borneo	33	26	-	-	4	-
S. buettikoferi	Borneo	35	24	-	-	4	1
S. courcyanum	NE India	35	24	-	-	4	1
S. cophias	W. Malaysia	37	24	56	56	4	1
S. grandisonae	Thailand	30	34	-	71	4	-
S helenae	Thailand	28	30	-	-	4	-
S kinabaluensis	Borneo	45–58	32–38	80–89	73–91	5,6	1
S maculicollus	Borneo	47	35–36	79	84	7	1
S malayanum	Sumatra	52–60	32–33	76–80	74	4	0,1
S. mimicus	Vietnam	36	30	61	-	4	-
S. modigliani	Sumatra	41	32	-	-	4	1
S. murudensis	Borneo	50.4	34	71	74	6	1
S. puncticentralis	Java	45	29	64	-	5	1
S. sanctus	Java	40–45	32–34	71		5	1
S. scotophilus	W Malaysia	50	28–31	67–74	-	5	1
S. schlegeli	Komoda	32	22	-	-	4	-
S. sheai	Vietnam	35.2	20	53	54	4	1

S. senja	W. Malaysia	60–65	32	72–73	68	4	
S. tanahtinggi	Borneo	48–64	40–42	76–79	-	5	1
S. tenuiculus	Borneo	46	26	57	68	4	1
S. tetradactylus	Vietnam	35	20	48	-	4	0
S. tonkinenesis	Vietnam	37.5–48.8	32–34	65–67	61–67	4	1
S. tridigitus	Vietnam	36.5	18	50	-	4	1

Table 3.3 (continue)

Species	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
Tytthoscincus													
T. aesculeticola	1	0	2	6	5	6–10	-	0	0	0	0	0	-
T. atrigularis	1	1	2	6	5	10	0	-	1	-	0	0	-
T. balicus	1	1	2	6	6	12	0	1	1	0	1	0	1
T batupanggah	1	1	2	6	5	9	0	1	1	1	1	0	0
T. biparietalis	2	1	2	6	6	10	0	-	1	-	0	0	-
T. bukitensis	2	1	2	6	5	12–13	1	0	0	0	0	0	0
T. butleri	1,2	1	1,2	6	5,6	11–13	0,1	1	1	0,1	0,1	0	0
T. garutense	2	0,1	2	6,7	6	13–15	0	1	1	0,1	0	0	0
T. hallieri	-	1	2	-	-	10–15	-	0	1	0	0	0	-
T. ishaki	2	1	2	6	5	11	1	1	1	1	0	0	0

T. jaripendek	1	1	1,2	6,7	5	9	1	1	1	1	0	1	0
T. kakikecil	1,2	1	1,2	6	5,6	10	1	1	1	1	0	1	0
T. martae	1,2	1	2	6	5,6	12–13	1	1	1	1	0	0	0
T. necopinatus	1	0,1	2	6	7	11–13	0	1	1	0	0	0	0
T. panchorensis	1	0	1	6	5	8	1	1	1	-	0	0	0
T. parvus	-	1	-	6		10	0	-	0	-	0	0	-
T. perhentianensis	1	1	2	6	6	10	0	1	0	0	0	0	0
T. leproauricularis	1	0	2	6,7	5	10	0	1	0	0	0	0	0
T. sanana	-	-	-	5	-	9	0	0	0	0	1	0	-
T. sibuensis	2	1	1	6	5	9	1	1	1	0	1	0	0
T. temasekensis	1,2	0,1	2	6,7	5–7	9–11	1	1	1	1	0	0	0
T. temengorensis	1	1	2	6	5	10–11	1	1	1	1	1	0	0
T. temmincki	1	0,1	2	6	4,5	9–10	0	0	1	0	0	0	0
T. textus	-	-	-	5		13–15	-	-	1	-	0	0	-
T vanheurni	1	0	2	6	6	14–15	0	1	1	0	0	0	1
T. sp. nov. 1	1	1	2	6	5	12	1	1	1	0	0	0	1
T. sp. nov. 2	2	0	2	6	6	10	1	1	1	1	0	1	0

Table 3.3 (continue)

Species	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
Sphenomorphus													
S. apalpebratus	-	0	2	5–6	4-5	8–9	0	0	1	0	1	0	-
S. alfredi	-	0	-	6	-	12	0	0	1	0	0	0	-
S. buettikoferi	-	1	-	-	-	21–23	0	1	1	-	0	0	-
S. courcyanum		1	-		-	11	0	-	1	0	1	0	-
S. cophias	-	0	2	7	7	9	1	1	1	0	0	1	0
S. grandisonae	-	1	2	6	5	12	-		1	1	-	0	-
S helenae	0	0	1	-	-	17	0	1	1	0	1	0	-
S kinabaluensis	1	0,1	1	7	7	15–17	0	1	1	0	-	0	-
S maculicollus	1	0	1	6	6	18–23	0	1	0	0	0	0	-
S malayanum	1	1	2	7	7,8	12,13	0	1	0,1	0,1	0	0	0
S. mimicus	-	1	2	7	16	16–17	-	1	1	0	0	0	-
S. modigliani	-	1	-	-	-	15	0	1	1	0	0	0	0
S. murudensis	2	1	2	6	7	17	0	1	1	0	0	0	-
S. puncticentralis	-	1	2	7	7	25	0	1	1	0	0	0	0
S. sanctus	2	1	2	7	6	26–27	-	1	0	0	0	0	0
S. scotophilus	2	0,1	2	7	6	22–23	-	1	1	0	0	0	0
S. schlegeli		1	-	-	-	10	0	1	1	0	1	0	-

S. sheai		0	2	6	5	6	0	-	1	0	1	0	-
S. senja	1	0,1	2	7	6	13–17	0	1	1	1	1	0	0
S. tanahtinggi	0	0,1	4	8,9	7	16–17	0	1	1	0	0	0	-
S. tenuiculus	-	0	-	7	6	21–24	0	1	1	0	0	0	-
S. tetradactylus	-	0	1	6	7	10	0	1	1	0	1	0	-
S. tonkinenesis	-	1	2	7	6	15–19	0	1	1	0	0	0	-
S. tridigitus	-	0	1	6	5	7–8	-	-	1	0	0	0	-

Table 3.4 Average uncorrected pairwise distance among species of *Tytthoscincus* base on the mitochondrial locus (ND2). The new species comparisons shown in bolds.

		1	2	3	4	5	6	7	8	9	10
1	*T. aesculeticola*										
2	*T. atrigularis*	0.24									
3	*T. batupanggah*	0.22	0.25								
4	*T. leproauricularis*	0.27	0.27	0.30							
5	*T. bukitensis*	0.23	0.24	0.24	0.26						
6	*T. butleri*	0.22	0.25	0.22	0.25	0.07					

7	*T. hallieri*	0.24	0.21	0.27	0.26	0.20	0.18				
8	*T. ishaki*	0.22	0.23	0.23	0.24	0.06	0.06	0.19			
9	*T. jaripendek*	0.25	0.22	0.23	0.26	0.17	0.15	0.26	0.17		
10	*T. kakikecil*	0.23	0.22	0.25	0.25	0.14	0.14	0.25	0.14	0.04	
11	***T. sp. nov. 1***	**0.25**	**0.23**	**0.25**	**0.25**	**0.23**	**0.22**	**0.23**	**0.21**	**0.25**	**0.25**
12	*T. martae*	0.22	0.24	0.23	0.25	0.04	0.06	0.20	0.06	0.16	0.14
13	*T. necopinatus*	0.25	0.18	0.25	0.25	0.24	0.22	0.23	0.24	0.24	0.24
14	*T. panchorensis*	0.23	0.22	0.26	0.27	0.19	0.19	0.21	0.20	0.22	0.21
15	*T. parvus*	0.26	0.20	0.25	0.26	0.24	0.25	0.21	0.25	0.21	0.21
16	*T. perhentianensis*	0.22	0.25	0.22	0.24	0.07	0.03	0.20	0.06	0.16	0.13
17	*T. sananus*	0.30	0.21	0.27	0.24	0.25	0.24	0.24	0.23	0.21	0.20
18	*T. sibuensis*	0.26	0.25	0.25	0.30	0.23	0.24	0.24	0.24	0.26	0.24
19	***T. sp. nov. 2***	**0.25**	**0.30**	**0.27**	**0.28**	**0.22**	**0.22**	**0.28**	**0.22**	**0.25**	**0.23**
20	*T. temasekensis*	0.24	0.22	0.24	0.27	0.20	0.20	0.23	0.20	0.21	0.18
21	*T. temengorensis*	0.22	0.25	0.24	0.25	0.09	0.03	0.19	0.07	0.15	0.14
22	*T. temmincki*	0.25	0.22	0.22	0.24	0.21	0.18	0.20	0.18	0.19	0.19
23	*T. textus*	0.23	0.19	0.20	0.27	0.21	0.18	0.18	0.20	0.23	0.21
24	*T.*LSUHC 12515	0.23	0.25	0.24	0.25	0.07	0.05	0.21	0.06	0.16	0.13

Table 3.4 (continue)

	11	12	13	14	15	16	17	18	**19**	20	21	22	23
12	**0.21**												
13	**0.22**	0.24											
14	**0.23**	0.19	0.24										
15	**0.25**	0.24	0.20	0.24									
16	**0.23**	0.06	0.22	0.20	0.24								
17	**0.25**	0.23	0.21	0.20	0.20	0.24							
18	**0.27**	0.23	0.26	0.10	0.24	0.23	0.24						
19	**0.26**	**0.22**	**0.27**	**0.22**	**0.27**	**0.21**	**0.26**	**0.25**					
20	**0.27**	0.18	0.22	0.12	0.23	0.19	0.20	0.12	**0.21**				
21	**0.21**	0.08	0.24	0.20	0.24	0.06	0.25	0.24	**0.22**	0.20			
22	**0.25**	0.19	0.17	0.20	0.21	0.18	0.12	0.23	**0.22**	0.16	0.18		
23	**0.24**	0.18	0.17	0.22	0.19	0.16	0.18	0.23	**0.24**	0.18	0.18	0.14	
24	**0.23**	0.06	0.23	0.20	0.24	0.04	0.23	0.22	**0.22**	0.18	0.05	0.19	0.16

Table 3.5 Summary of diagnostic characters for *T. balicus, T. sp. nov. 1* and *T. vanheurni.*

Char.	*T. sp. nov. 1* MZB 14404	*T. sp. nov. 1* MZB 14402	*T. sp. nov. 1* UTA-R 64201	*T. sp. nov. 1* MZB 14403	*T. sp. nov. 1* UTA-R 64202	*T. sp. nov. 1* UTA-R 64203	*T. vanheurni* RMNH 7967	*T. balicus* SMF 23275
Sex	male	female	male	female	male	female	-	-
SVL	49.34	49.86	50.04	52.86	42.09	47.72	64	33
MBSR	32	32	32	32	32	32	31	30
PVSR	79	79	82	82	78	81	81	64
VSR	69	67	71	69	71	72	75	59
IL	5	5	5	5	5	5	6	6
4th DS	3+4/4	2+5/5	2+5/5	3+4/4	2+3/3	3+4/4	2+4/4	2+5/6
SC	7`1	8`1	8`1	7`1	7`1	7`1	7’1	8`2
4th SDL	12	12	12	12	12	12	14,15	12
Typ	circular	circular	circular	circular	circular	circular	ovular	circular
PI	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes
LDS	No	No	No	No	No	No	NO	Yes

Table 3.6 Summary of morphometric and meristic characters among species with “tympanic depression” of the genus *Tytthoscincus* and *Sphenomorphus*. (data for *S. copias, T. jaripendek,* and *T. kakikecil,* from Grismer *et al.* 2017b)

Characters	*T. sp. nov. 2.* MZB 14401	*T. jaripendek* n = 4	*T. kakikecil* n = 6	*S. cophias* BMNH 1946.8.3.15
Infralabials	6	5	5,6	6
Supraciliaries	8`2	8`1	8`1, 9`1, 9`2	8`1
Prefrontal in contacts	No	Yes/No	Yes	No
Loreals	2	1,2	1,2	2
Tympanum	SPD	SPD	SPD	SPD
Midbody scale row	28	28–30	30–33	23
Paravertebral scale rows	61	63–65	67–73	56
Ventral scale row	59	60–62	65–69	56
Enlarged pectoral scale	Yes	No	Yes	Yes
3rd finger SDL	6	5–6	6	5
4th toe SDL	10	9–10	10	10
TD/HL	0.08	0.11–0.13	0.10–0.12	0.15
HL/SVL	0.17	0.18–0.19	0.18–0.21	0.15

AXG/SVL	0.53	0.55–0.57	0.52–0.65	0.58
FLL/SVL	0.2	0.18–0.21	0.18–0.23	0.17
HLL/SVL	0.35	0.31–0.33	0.30–0.34	0.28
Maximum SVL	34.54	33.9	36.2	35.9

Chapter 4

Systematics of the Forest Skinks (Scincidae: *Sphenomorphus* Fitzinger 1843) with Description of a New Genus and Two New Species from Sumatra

ABSTRACT: In ten species of *Sphenomorphus* in Java and Sumatra, all of them were described more than two decades ago which several new genera still embedded in the genus *Sphenomorphus*. Taking this into account, we are revisiting the taxonomic status of *Sphenomorphus* in Java and Sumatra. We have been studied pluralistic approaches including concatenated of mtDNA and nuDNA phylogeny, combined molecular, morphological and ecological data phylogeny, time-calibrated phylogeny, skull comparative anatomy, and ecological niche modeling. Our integrated results showing the genus *Sphenomorphus* is polyphyletic. Interestingly, one particular group has genetics and morphological distinct from other *Sphenomorphus*. And species distribution modeling indicates members of this particular clade is range only in montane forests of Sumatra. Consequently, we described a new genus and two new species out from *Sphenomorphus* base on genetics, morphological and ecological evidences. The new genus is distinctive from other species of *Sphenomorphus* by several characters including limbs barely touch when adpressed, parietal eyespot absent, thick black dorsolateral stripe with serrate edge, body slender not more than 65 mm, 32–38 midbody scale row, and 15–21 subdigital lamellae on the fourth toe. In conclusion with the integrated approaches, we help out the taxonomic controversial of the genus *Sphenomorphus*. Lastly the other groups of forest dwelling skink in Java and Sumatra still also need to be reviewed.

Key words: Combined data phylogeny; Divergent dating; Ecological niche modeling; Integrated taxonomy; Skull anatomy

THE FOREST dwelling skinks of the genus *Sphenomorphus* Fitzinger 1843 are morphologically, behaviorally, and ecologically diverse (Greer 1989; Das 2015; Grismer 2011). Terrestrial and arboreal species typically have robust limbs, whereas semi-fossorial species exhibit varying degrees of body elongation and limb reduction. With secretive habits and a wide distribution from the Indian Subcontinent to Southeast Asia and New Guinea, many species of *Sphenomorphus* remain rare in collections.

Skinks in this genus share the following characters: supranasal absent; prefrontal present; parietal in contact behind the interparietal; lower eyelids scaly without transparent disc; body scales smooth; digits five; precloacal scales enlarged; arm and leg overlapping when pressed against the flank; and dorsal surface of the fourth toe covered by two or more scale rows for at least one-half of its length (Taylor 1963; Greer and Shea 2004; Grismer 2011; Nguen et al. 2011).

Until recently, *Sphenomorphus* contained multiple unrelated groups of phenotypically similar species, and taxonomists have begun dismembering this large, polyphyletic genus. Cogger (2000) transferred Australian *Sphenomorphous* to *Glaphylomophus*, *Eremiascincus*, and *Eulamprus*. Linkem et al (2011) revised Philippines *Sphenomorphus,* transferred Central American species to *Scincella,* and recognized *Pinoyscincus*, *Parvoscincus*, *Otosaurus*, *Insularscincus* and *Tytthoscincus*. Grismer et al. (2016) then transferred two clades of Malaysian

Sphenomorphus to *Tytthoscincus*. Adding to the taxonomic confusion surrounding this genus, the type species is *Gongylus melanopogon* Duméril and Bibron (1839). However, the type series of this species contains three distinct species Shea (2012).

Following recent revisions of the genus, *Sphenomorphus* currently contains 109 species (Uetz and Hosek 2018): seven on the Indian Subcontinent, 18 in mainland Southeast Asia, 30 distributed across land masses of the Sunda Shelf, five in the Philippines, 15 in Wallacea, and 42 on New Guinea and the Pacific Islands. Within the Sunda Shelf, 12 species occur in Peninsula Malaysia and 18 species on Borneo. In sharp contract, only five species occur on Java and six on Sumatra, strongly suggesting that diversity of *Sphenomorphus* has been greatly underestimated. Recent fieldwork on these islands has reveal similar underappreciated diversity, especially among montane agamids and *Philautus* (Harvey et al. 2014, 2017; Wostl et al. 2017).

In this study, we review the Sumatran and Javan skinks still assigned to *Sphenomorphus*, including the following species whose type localites lie on either Sumatra or Java: *S. malayanum* (Doria 1888), *S. necopinatus* (Brongerma 1942), *S. modigliani* (Boulenger 1894), *S. puncticentralis* (Iskandar 1994), *S. sanctus sanctus* (Dumeral and Bibron 1839), *S. sanctus tenggeranus* Mertens (1957), *S. vanheurni* (Brongersma 1942).

MATERIALS AND METHODS

Fieldwork and Specimens Collection

Teams of herpetologists from Broward College, the University of Texas at Arlington, the Indonesia Institute of Science, and the University of Brawijaya collected skins as part of extensive herpetological surveys on Java and Sumatra from 2013–2015. We used the visual encounter survey method described by Simmons (2002). For each specimen we recorded elevation and GPS coordinates (WGS84 datum) with a handheld global positioning system device (Garmin® GPSMAP 64s) and recorded limited field notes regarding ecology and activity. We euthanized specimens by cardiac injection using a 10% benzocaine solution following accepted animal care protocols (UTA IACUC A12.004). Subsequently, we removed tissue samples from muscle or liver and stored them in a cell lysis buffer (0.5 M Tris/0.25% EDTA/2.5% SDS, pH = 8.2) for further molecular analysis. We fixed specimens in 10% formalin prior to storage in 70% ethanol. We deposited preserved specimens in Museum Zoologicum Bogoriense (MZB) and Amphibian and Reptile Diversity Research Center of the University of Texas at Arlington (UTA). We directly compared new specimens to type specimens (Appendix 1), original descriptions, and accounts in recent revisions of the genus (De Rooij 1917; Grismer 2011; Das 2015).

Morphological Data

To identify species and determine their phylogenetic relationships, we generated a data set of morphological, molecular, and ecological characters. We used some of the morphometric characters of Karin et al. (2016a), Linkem et al. (2010) and Sumarli et al. (2016) and modified other characters as follows. On the right side of each specimen, we used a Mitutoyo digital vernier calliper (to nearest 0.05 mm) to measure snout–vent length (SVL, from the tip of the snout to the cloacal opening); tail length (from the cloacal opening to the tip of the tail); axilla–groin distance (from the posterior margin of the arm to the anterior margin of the leg); head length (from the anterior margin of the ear opening to the tip of the snout); head width (at the widest part of the temporal region); head height (at the center of the eye); snout–arm length (from the anterior insertion of the arm to the tip of the snout; internarial distance (between the dorsal margind of the nares); inter-ocular distance (between anterior cornerd of the eye); rostral length (from the anterior margin of the eye to the tip of the snout); interorbital distance (the length between the middle of the left ear and right ear); diameter of eye (at widest point on eye); tympanum diameter (at widest point on the ear); arm length (from palmar base to shoulder); leg length (from groin to plantar base); length of 4th finger (from proximal end of palmar to tip of claw); length of 4th toe (from proximal end of plantar to tip of claw); tail width (at its base on ventral side).

We scored the following meristic characters on the right side of each specimen: number of paravertebral scale rows between the parietals and a point level with the posterior margin of the cloaca; number of ventral scale rows between the 3rd chin shield and the precloacals; number of enlarged precloacal scales; number of subcaudals from the posterior margin of the the cloacal to the tip of the tail; number of midbody scale rows at the center of the trunk; numbers of lamellae under each toe (Our counts of lamellae begin just distal to the interdigital scales and include the ungual scale); number of supralabials counted between the rostral and the postsupralabial; number of postsupralabials counted scales between the supralabial and the temporal; number of infralabials counted scales between the mental and the first lateral; number of loreals counted between the nasal and preoccular; number of enlarged supraoculars; number of chinshields (=enlarged scales between the postmental and the first ventral); number of preoculars; number of postocular; number of supracilliaries; number of primary and secondary temporal scales. Additionally, we noted degree of overlap of adpressed limbs, snout shape, head scales shape and degree of contact, body scale shape on both dorsal and ventral sides, texture of subdigital lamellae, tympanum shape and position, and color pattern.

For study of skeletal morphology, we generated micro-computed tomography scans of six specimens using settings described in Table 4.3. We scanned specimens at the Shimadzu Center for Environmental, Forensics, and Material Science at The University of Texas at Arlington using an inspeXio SMX-100CT (Shimadzu, Kyoto, Japan). All scans averaged 6 frames per image, averaged across 4 rotations, and collected 1200 views per full rotation. We reconstructed raw X-ray data with Shimadzu's inspeXio software and exported images as a 16-bit TIF stack. We cropped images and rotated them using ImageJ 1.51k (Rasband 1997). We then imported the final image stack into Avizo 8.1.1 (FEI, Hillsboro, Oregon) for viewing, sectioning, and measuring. Raw 16-bit TIFF, videos, and STL shape files stacks are available on Morphosource: [link XX].

Ecological Data

Using our own observations in the field and published accounts of species not collected by us, scored species of *Sphenomorphus* and related genera for a four ecological characters, including behavior, climbing ability, elevation, and use of riparian habitats. For species of a new genus described herein, we used Maxent 3.3.3 (Phillips et al. 2006) to model suitable habitat across Sumatra. We used GPS coordinates (Table 4.4) for confirmed locality records, type localities, and our own survey data to generate a robust dataset prior to modeling. We used all 19 bioclimatic files (30 sec. resolution) available at WorldClim (Hijmans et al. 2005). We formatted files for use in Maxent using the Clip and Raster to ASC tools in ArcMap 10.2 (ESRI, Redlands, USA). Colinearity is not considered to be problematic when using Maxent, and therefore we did not exclude any variables after model testing (Elith et al. 2011). We used the "Auto Features" settings provided, changed the number of iterations to 5000 replicated run types per subsample, and set random test percentage to 25. We assessed the area under the curve (AUC) for each model, to measure model performance using the presence localities provided. AUC models are produced in Maxent only when test values are provided. AUC values closer to 1.0 indicate high performance of the predicted suitability models. We distinguished break points in probability of occurrence at 0.5, 0.6, 0.7, 0.8, and above 0.9 to provide context for levels of habitat suitability across a species' ranges. We did not consider areas with less than a 50% probability of occurrence to be suitable habitat. We used the final models as an additional line of evidence for species delimitation and the prediction of where new species of *Sphenomorphus* may be discovered based on distinct biogeographic breaks in suitable habitat.

Molecular Data

We extracted genomic DNA from tissue samples using a Serapure magnetic bead suspension (Rohland and Reich 2012). The DNA extraction starts by transferring 100 µl of dissolved tissue in cell lysis buffer and incubating at 55 °C with 20 µl protenase K for 2 hours. After that the solution was mixed with 180 µl of Serapure bead in ratio1.8:1 (serapure bead: tissue sample in cell lysis buffer). Thereafter we cleaned the solution twice by rinsing in 80 µl of 70% EtoH and dissolved isolated DNA in Tris pH 8.5 with 0.1% of TWEEN$^{®}$ 20 (Polysorbate 20).

We amplified two mitochondrial loci, NADH dehydrogenase subunit 4 (ND4) and 16S ribosomal RNA (16S) and two nuclear loci, the nuclear nerve growth-factor beta (NGFB) and

RNA fingerprint protein 35 (R35). The primer set of 16S included the 16SA light chain 5’ CGC CTG TTT ATC AAA AAC AT 3’ and 16SB heavy chain 5’ CCG GTC TGA ACT CAG ATC ACG T 3’ (Palumbi et al. 1991). We slightly modified the thermocycler protocol of Vence et al. (2000) and Mausfeld and Schmitz (2003) as follows: 33 cycles of amplification with 45 seconds of denaturation at 94°C, 45 s of annealing at 55°C and 90 s of extension at 72°C. The primer set of ND4 included the ND4 light chain 5’ CAC CTA TGA CTA CCA AAA GCT CAT GTA GAA GC 3’ and LEU heavy chain 5’ TTT TAC TTG GAK TTG CAC CA 3’ (Mausfeld et al. 2000). The ND4 thermocycler protocol was slightly modified from Mausfeld et al. (2000) as follows: 35 cycles of amplification with 45 s of denaturation at 94°C, 60 s of annealing at 50°C and 120 s of extension at 74°C. The primer set of NGFB included NGFB_f2 5’ GAT TAT AGC GTT TCT GAT YGG C 3’and NGFB_r2 5’ CAA AGG TGT GTG TWG TGG TGC 3’ (Townsend et al. 2008). Finally, the primer set of R35 included R35f 5’ GAC TGT GGA YGA YCT GAT CAG TGT GGT GCC 3’and R35r 5’ GCC AAA ATG AGS GAG AAR CGC TTC TGA GC 3’ (Leaché 2009). We used the nuclear touchdown protocol for NGFB and R35 amplifications modified after Don et al. (1991) and Streicher et al. (2009). The thermal cycling profile for Nuclear Touchdown consisted of an initial denaturation, 20 s at 94°C followed by twenty cycles of 30 s of denaturation at 94°C, 30 s of annealing at 50°C, and 1 min extension at 72°C; then 6 cycles of 30 s at 94°C, 30 s at 54°C, 1 min at 72°C, 30 s at 94°C, 30 s at 52°C, and 1 min at 72°C; then 20 similar cycles with the annealing temperature reduced to 50°C and then a final 10 min extension at 72°C.

We checked all polymerase chain reaction products by visualization in 1% agarose gel with GelRed fluorescent stain (Crisafuli et al. 2015). We purified products by Serapure beads in similar protocol with genomic DNA extraction. We sent the purified products to the Genome Core Facility at the University of Texas at Arlington for Sanger Sequencing with an ABI PRISM 3100xl Genetic Analyzer (Applied Biosystems). After that we carefully checked and trimmed the DNA sequences in Sequencer 5.1 (Gene Codes, Ann Arbor, MI, USA). We aligned the sequences in each locus in MEGA 7 (Kumar et al. 2016) by ClustalW (Larkin 2007). Finally, we deposited all sequences in GenBank. We list all samples used in this analysis in Table 4.2.

Phylogenetic Analysis

For phylogenetic analysis of molecular data only, we combined our new sequences with sequences from GenBank. We aligned sequences in MEGA7 (Kumar et al. 2016) by ClustalW (Larkin 2007) and used maximum likelihood and Baysian algorithms to analyze concatenated mitochondrial and nuclear loci (total of 2558 sites). To determine the optimal partition scheme, we used the "Greedy" algorithm v1.1.0 in Partition Finder (Lanfear et al. 2012). The best partitioning scheme had seven partitions: GTR+I+G for 16S and ND4 1st codon positions, TVM+I+G for ND4 2nd codon positions, HKY+I+G for ND4 3rd codon positions, K81+I+G for NGFB 1st codon positions; and R35 1st codon positions, K80+G for NGFB 2nd codon positions, and R35 2nd codon position; K80+G for NGFB 3rd codon positions and K81uf+G for R35 3rd codon positions. For the maximum likelihood analysis, we used RAxML v8.00 (Starmatakis 2014) on the CIPRES Science Gateway online server v3.2 (Miller et al. 2010). The GTR+G model was used in RAxML with bootstrapping 1000 pseudoreplications. To evaluate nodal support for our phylogeny produced by maximum likelihood, we used bootstraping and considered bootstrap value higher than 70 to indicate strong support (Hillis and Bull 1993). For the Baysian analysis, we used MrBayes v.3.2.3 (Ronquist and Huelsenbeck 2003), running the analysis for 15 x 10^6 generations with four analyses and three heated and one cold chains. We set the burn-in value as 25% and discard the first 2500 generations. We visually examined the convergence of posterior likelihood values using Tracer v1.6 (Rambaut et al. 2007), ensuring that all ESS values were > 200. We used Figtree v1.2.2 (Rambaut and Drummond 2008) for editing both the maximum likelihood and Baysian trees.

When analyzing the combined data set of molecular, morphological and ecological characters we used Bayesian phylogenetic inference. The combined data set included 2558 molecular characters described above, 139 external morphological characters, one character of the skull, and four ecological characters (total 2702 characters). We present the morphological and ecological characters in Appendix 2. In term of evolutionary model for genetic data, the result of best partition scheme from Partition Finder were used as models similar to concatenated phylogeny described above. The Mk+G model were used for morphological data and ecological data. The Mk or Markov *k* model of was indicated by Lewis 2001. Therefore it is also called Lewis's model. This model basically generalized from JC69 model. However, Nylander et al. 2004 suggested using Mk+G for combined genetics and morpoholgical data. MrBayes v3.2.3 (Ronquist and Huelsenbeck 2003) were used for Bayesian inference. We run Bayesian analysis for 15x 10^6 generations with 4 chains and a temperature of 0.5. We set the burn in value as 25% therefore discard first 2,500 generations. We visually examined the convergence of posterior likelihood values using Tracer v1.6 (Rambaut et al. 2007) and making sure that all ESS values were > 200. We used Figtree 1.2.2 (Rambaut and Drummond 2008) for editing BI trees. Finally, the combined-data phylogeny was compared with genetics-only phylogeny to check the incongruity between two approaches.

We conducted divergent dating analyses using BEAST v1.8.4 (Drummond and Rambaut, 2012). We used same data set with genetics-only phylogeny. We partitioned each gene separately and applied a GTR+Γ model of evolution, but did not partition by codon following Karin et. al. (2016b). We applied a birth-death prior to tree estimation. For the population size we used a piecewise linear model with constant root prior. We applied an uncorrelated log-normal relaxed molecular clock for all loci. We estimated divergence times based on the two mitochondrial loci. For 16S we applied the following rates: rate = 0.0080, standard deviation = 0.0020, producing to a 95% confidence interval (95% CI) of 0.49–1.13% per mission years. For ND4 we applied the following rates: mean rate = 0.00895, standard deviation = 0.00250, producing a 95% CI of 0.49–1.31% following Karin et al. (2016b) and Barley et al. (2015). These rates covered the estimated mitochondrial rates for a diverse set of previously studied lizards. We applied a uniform distribution of 0.0–0.2 for the clock mean prior and we applied an exponential distribution (mean = 0.05) for the standard deviation of the two nuclear loci. We applied a uniform prior distributed from 0.0–100 (initial = 1) for all substitution parameters. Be sure to add the uniform prior info for the nuclear loci, we placed a uniform prior distributed from 0.0–10 (initial = 0.05) to the gamma shape parameters. We ran the analysis for 100 million MCMC generations with sampling every 10,000 generations. We ensured mixing and convergence of all parameters (ESS > 200) in Tracer v1.6 (Rambaut et al. 2007). We removed the first 25% of trees as burnin (2500 trees) and calculated the maximum clade credibility (MCC) tree in Tree Annotator v.1.8.4. (software package of BEAST v1.8.4). We ran additional analyses with the same prior distributions applied to ND2 and 16S alone and applied a uniform prior to the other (0.0–0.04). Dates were consistent across all runs (results not shown). We visualized the final MCC cladogram in Figtree 1.2.2 (Rambaut and Drummond 2008).

RESULTS

Specimens Identification

We assigned specimens to species based on external morphology (Table 4.1). We found seven species of *Sphenomorphus* in Java and Sumatra: *S. cyanolaemus* from Aceh and Bengkulu, *S. scotophilus* from North Sumatra, *S. sanctus sanctus* from West Java, *S. s. tenggeranus* from East Java, *S. sungaicolus* from West Sumatra, *Sphenomorphus* sp.1 from North Sumatra and *Sphenomorphus* sp.2 from South Sumatra and Lampung. Interestingly, this study is the first record of *S. sungaicolus* from Sumatra. This species was previously known only from peninsular Malaysia (Sumari et al. 2016). Moreover, two unidentified species have high potential to be new species. These unidentified species superficially resemble *S. cameronicus* from Malaysia, but differ in scalations, and initially appeared to be new species.

Phylogeny

Baysian (BI) and maximum likelihood (ML) analysis of the concatenated molecular data recovered identical strongly support phylogenies (Fig. 4.1). Therefore, we only present our Bayesian tree. Topology of our tree resembles those of Karin et al. (2016a) and Linkem et al. (2011). We recovered monophyletic *Insulasaurus*, *Lipinia*, *Papuascincus*, *Scincella*, *Parvoscincus*, *Pinoyscincus* and *Tytthoscincus* within Sphenomorphinae and support the conclusions of these studies that *Sphenomorphus* is not monophyletic. However, we found an unnamed clade basal to other Sphenomorphinae (BI = 0.97; ML = 43), whereas both Linkem et al. (2011) and Karin et al. (2016a) found *Tytthoscincus* to be basal. Different placement of these clades is due to differences in taxon sampling, since our data set includes species not considered by these authors.

In our phylogeny, species still assigned to *Sphenomorphus* belong to three unrelated clades, here referenced by Roman numerals. "*Sphenomorphus* I" contains a group of species from the Malay Peninsula and the Greater Sunda Islands, "*Sphenomorphus* II" contains a group of species from the Philippines and Oceania, and "*Sphenomorphus* III" contains two unidentified species from Sumatra. Within *Sphenomorphus* I, *S. cyanolaemus* is sister to *S. sabanus*; *S. multisquamatus* is sister to *S. variegatus,* and these two species pairs are sister to one another. Next, *S. tersus* is sister to *S. sungaicolus*, and this pair is sister to *S. indicus*. Then, *S. sanctus* is sister to *S. scotophilus,* and this pair clades with *S. maculatus* albeit with low nodal support (BI = 0.81; ML = 53). The *S. sanctus*-*S. scotophilus*-*S. maculatus* group clades with the *S. indicus*-*S. sungaicolus*-*S. tarsus* group, and this larger clade is sister to the *S. cyanolaemus*-*S. sabanus*,-*S. multisquamatus*-*S. variegatus* group is sister to group.

Within *Sphenomorphus* II, *S. fasciatus* is sister to *S. cranei*, *S. scutatus* is sister to *S. solomonis,* and these two pairs are sister to one another. Position of two other members of *Sphenomorphus* II suffers from weak nodal support. *Sphenomorphus melanopogon* lies basal to the apical group of four (BI = 0.58; ML = 57), and *S. concinnatus* is basal to the remaining five members of the clade.

The Bayesian tree (Fig. 4.2) based on combined morphological, ecological, and molecular data closely matches the tree based on concatenated molecular data (Fig. 4.1). The combined tree includes some species for which molecular data are lacking. Our analysis places *S. anomalopus* in *Sphenomophus* I sister to *S. multisquamqtus* and *S. variegatus* but with low nodal support (BI = 0.51). Moreover, nodal support of the *Sphenomophus* I clade fell relative to the molecular tree (BI = 0.87). *Sphenomorphus malayanum* and *S. modigliani* are embedded within *Tytthoscincus* rather than within one of the clades of *Sphenomorphus.* Nonetheless, their placement suffers from low nodal support. *Sphenomorphus malayanum* is sister to *Tytthoscincus sp. nov. 2* (BI = 0.88), and *S. modigliani* is sister to this pair of species (BI = 0.61).

Divergence Time Analysis

The time calibreated phylogeny indicate similar topology with Bayesian inference phylogeny (Fig. 4.3). The divergence of the *Sphenomorphus* III clade from other clades in the Sphenomorpinae is about 35.28 millions years ago (Ma) with 24.01, 60.70 confidence interval (CI). The divergence within *Sphenomorphus* III, we have found Sphenomophus sp. 1 was separated from *Sphenomophus* sp. 2 about 13.28 Ma with 7.33, 24.08 CI. Within *Sphenomorphus* sp.1 the divergent between ENS 14854 and group of ENS15151-ENS14699 is Ma with 1.10, 3.93 CI. Finally, the divergence between ENS15151and ENS14699 is about 1.46 Ma with 0.65, 2.79 CI.

Osteology

We examined skulls from representative species in each of the three clases of *Sphenomorphus*: from clade I, we examined skulls from *S. sanctus*, *S. sungaicolus* and *S. cyanolaemus*, from clade II, we examined *S. melanopogon;* and from clade III, we examined both unidentified species. The skull anatomycomparisons present on Figs. 4.4–4.5. Though the external morphology of skinks is relatively conservative, several osteological characters differ among the groups. First, the epipterygoid in *Sphenomorphus* III forms a right angle (90°) to the sagittal plane, whereas it forms an acute angle in species of the other two groups. *Sphenomorphus* III has a relatively larger braincase and relatively smaller orbits than species of the other groups. Moreover, the dentaries of *S. melanopogon* and *S. scotophilus* contact one another medially, whereas a distinct gap separates these bones in the other four species. The septomaxilla forms a right angle with the sagittal plane in *S. scotophilus* but forms an obtuse angle in the other species. The quadrate process is concealed in *S. scotophilus* while other species the quadrate process is prominent. The foramen magnum has a relatively large and circular in *Sphenomorphus* sp.1, *Sphenomorphus* sp.2, *S. sanctus* and *S. sungaicolus* and is relatively small and ovular in *S. cyanolaemus* and *S. melanopogon*.

Ecological Niche Modeling

Distribution modeling predicts that the two unidentified species in *Sphenomorphus* III will only occur in the highlands of the Barisan Mountain Range on Sumatra (Fig. 6). Nonetheless, modeling identified similar habitat in West Java, suggesting that a related species may occur there. On Sumatra, modeling did not identify suitable habitat in montane forests of northern Aceh and revealed three gaps along the extent of the Barisan Range: (1) a gap around Kabanjahe in North Sumatra between the southern Leuser ecosystem in Aceh and northern part of Lake Toba, North Sumatra; (2) a gap around Padang Sidempaun, West Sumatra; and (3) a gap between Curup, Bengkulu, and Lubuklingau, South Sumatra.

Systematics

Based on our phylogenetic analysis, we propose the following changes to the systematics of Sphenomorphinae. We formally transfer *S. malayanum* and *S. modigliani* to *Tytthoscincus* as *Tytthoscincus malayanum* (Doria 1888) **comb. nov.** and *Tytthoscincus modigliani* (Boulenger 1894) **comb. nov.** *Sphenomorphus* II contains *S. melanopogon*, the type species of *Sphenomorphus*. Nonetheless, the relationship between *S. melanopogon* and other species in this group remains unclear and we know of no major morphological differences between *Sphenomorphus* I and *Sphenomorphus* II. Thus, we continue to recognize a polyphyletic *Sphenomorphus* containing these two clades, pending further study of their constituent species. *Sphenomorphus* III is highly divergent from the other two groups and its two constituent species share unique morphological characters not found in other Sphenomorphinae. Therefore, we propose a new genus for the two species within *Sphenomorphus* III.

SphenomophusIII gen. nov.

(Figs. 7–8)

Type species.—*SphenomophusIII* sp.1 by present designation.

Diagnosis and comparison.—Skinks reaching 65 mm SVL, * mm total length, distinguished from all other Scincidae by the following combination of characters: (1) legs pentadactyl; (2) limbs barely overlapping when adpressed; (3) supranasals absent; (4) post nasal scale absent (5) lower eyelid scaled; (6) dorsal scales imbricate, smooth, nontuberculate; (7) temporals enlarged; (8) parietal eye-spot absent.

Unlike *Larutia*, *Carlia* and *Brachymeles*, *Sphenomorphus* III has pentadactyl limbs, unlike *Lygosoma*, *Plestiodon*, *Eutropis*, *Cryptoblepharus*, *Lamprolepis*, *Emoia*, and *Dasia*, it lacks supranasals; unlike *Scincella* it has a scaly lower eyelid; unlike *Tropidophorous* it has imbricate rather than tuberculate dorsal scales; and unlike *Tytthoscincus* it has enlarged temporal scales.

We know of no single character that will distinguish all *Sphenomorphus* from the new genus. Nonetheless, unlike most *Sphenomorphus* group skinks, *SphenomorphusIII* has limbs that barely overlap when adpressed, has a thick serrate dorsolateral stripe, and lacks a parietal eye-spot (Table 3). Epipterygoids of the new genus form right angles with the sagittal plane, whereas these bones make acute angles in *Sphenomorphus* examined thus far.

Content.—*SphenomorphusIII* sp.1 Thammachoti et al. from South Sumatra, *SphenomorphusIII* sp.2. Thammachoti et al. from North Sumatra, *SphenomorphusIII cameronicus* (Smith, 1924) from the Malay Peninsula.

Remarks. —We place *Sphenomorphus cameronicus* Smith in *SphenomorphusIII,* because it has each of the characters diagnostic of the genus. Like other members of the genus, *SIII. cameronicus* occurs only at high elevations (Grismer 2011)

SphenomorphusIII ***sp.1*** sp. nov.

(Figs. 7–8)

Holotype.—an adult male (MZB 14452, field number ENS 15151), from Mount of Pesawaran, Pesawaran Regency, Lampung, Sumatra, 5.51563° S, 105.07667° E, 1055 m elevation, collected 22 December 2013 by E. Wostl, I. Sidik and A. M. Kadafi (Fig. 9).

Paratype (*n* = 2).— An adult female (UTA-R 64204, field number ENS 14699) from Maura Dua, Remanan Jaya, Mount of Pesagi, Kabupaten Ogan Komering Ulu Selatan, South Sumatra, 4.90589° S, 104.13232° E, 1558 m elevation, collected 17 June 2013 by E. N. Smith, K. A. O'Connell and Dian; an adult female (UTA-R 64205, field number ENS 14854) from a ridge South of Ranau Lake, Kabupaten Lampung Barat, Lampung, Sumatra, 4.96599° S, 103.84954° E, 1087 m elevation, collected 17 June 2013 by A. Hamidy, U. Arifin, U. Smart and Kemal.

Diagnosis.—*SphenomorphusIII sp.1* can be identified by having limbs barely overlapping when addressed, no parietal eye-spot, enlarge temporal scales, a serrate dorsolateral stripe from the posterior margin of the eye to anterior margin of the tail, the anterior loreal divided, dorsal black spots forming an irregular pattern, 32–34 midbody scale rows, 73–74 paravertebral scale rows, 69–70 ventral scale rows, and 16–17 lamellae under the fourth toe.

Comparisons.—*SphenomorphusIII sp.1* is most likely to be confused with its two congeners. Unlike *SphenomorphusIII sp.2* (characters in parentheses), the new species has 32–34 (36) midbody scale rows, 9 (8) supracillaries, 16–17 (18) lamellae under the fourth toe, and dorsal black spots forming an irregular pattern (dorsal black spots arrayed in longitudinal lines,

Fig. 8, Table 4.5). Unlike *SIII. cameronicus,* the new species has a divided anterior loreal (entire) and 16–17 (20–21) lamellae under the fourth toe.

Unlike most Southeast Asia and Sunda Shelf *Sphenomorphus*, the new species has limbs that barely overlap when addressed (limb completely overlapping in *S. anomalopus*, *S. crassus*, *S. cyanolaemus*, *S. haasi*, *S. indicus*, *S. kinabaluensis*, *S. lineopunctulatus*, *S. maculatus*, *S. maculicollus*, *S. melanopogon*, *S. multisquamatus*, *S. murudensis*, *S. praesignis*, *S. puncticentralis*, *S. sabanus*, *S. sanctus*, *S. scotophilus*, *S. stellatus*, *S. sungaicolus*, *S. tanahtinggi*, *S. tonkienensis*, *S. tenuiculus*, *S. tersus*, *S. variegatus*; limbs not overlapping in *S. alfredi*, *S. cophias*, *S. grandisonae*, *S. helenae*). Like the new species, limbs slightly overlap in *S. shelfordi,* however this species has 28–29 lamellae under the fourth toe, whereas *SIII. sp.1* has 16–17. The new species lacks a parietal eye spot and has a thick serrate dorsolateral stripe, whereas *S. modigliani* has a parietal eye spot and lacks a serrate dorsolateral stripe.

Description of Holotype.—Adult male, head longer than wide; dorsal head scales plate-like, smooth; snout pointed in dorsal aspect, rounded in profile; rostral wider than high, visible from above; rostral in broad contact with frontonasal, forming strait suture; supranasal absent; frontonasal wider than long, in contact with upper anterior loreal and prefrontals; prefrontals in contact; frontal elongate, narrow posteriorly; frontal in contact with prefrontals, first and second supraoculars, and frontoparietals; four supraoccular, second widest, followed by two small postsupraoculars; frontoparietal unequaly divided, anteriorly in contact with frontal, laterally in contact with second, third and fourth supraoculars, posteriorly in contact with interparietals and parietals; interparietal diamond-shaped, slightly projecting posteriorly between parietals; no parietal eye-spot; parietals in contact posteriorly, in contact with last supraoccular anteriorly;

first two rows of paravertebral scales fused middorsally, forming vertebral plates; parietal laterally surrounded by six scales; nostril in center of single nasal; suture above nostril present; nasal in contact anteriorly with rostral, dorsally with frontonasal, posteriorly with anterior loreals, ventrally with first supralabial; three loreals; anterior loreal divided; upper anterior loreal in contact with nasal and posterior loreal; upper anterior loreal in contact with frontonasl, prefrontal; lower anterior loreal in contact with first and second supralabials; posterior loreal in contact with upper and lower anterior loreals, preocular scales, first supercilliary, and second and third supralabials; two preoculars; upper preocular smaller than lower preocular; three suboculars contacting supralabials; nine supraciliaries, first largest; two posterior supraciliaries elongate and projecting dorsomedially; seven supralabials; two post-supralabials; seven infralabials; two postoculars; temporals enlarged; two primary temporals; three secondary temporals, uppermost in contact parietals; lower eyelids semitransparent, entirely scaled; external auditory meatus recessed, oval, its smallest diameter smaller than diameter of eye; mental wider than long, rounded posteriorly, as wide as rostral; single postmental in contact with first and second infralabial; three pairs of chinshields; first pair of chinshields enlarged in medial contact, laterally contacting second and third infralabial; second pair of chinshields enlarged, entirely separated by one gular scale, laterally contacting third and fourth infralabial; third pair of chinshields entirely separated by six gular scales, laterally in contact with fourth and fifth infralabials.

Body slender; dorsals smooth, cycloid, imbricate; pectoral scales slightly enlarged; two precloacal scales enlarged; subcaudals not enlarged; 32 scales around midbody; 73 paravetebral scale rows; 70 ventral scale rows; 20 scale around tail at level of 10th subcaudal; limbs well developed, pentadactyl, barely overlapping when adpressed; palmar and plantar scales raised (subtuberculate granular); digits short; subdigital lamellae keeled; five lamellae under first finger, eight under second finger, 11 under third finger, 11 under fourth finger, seven under fifth finger, five under first toe; eight under second toe; 14 under third toe; 17 under fourth toe; eight under fifth toe.

Measurements in mm: snout–vent length 54.26; tail length 10.43 (incomplete); axilliary–groin distance 26.49; head length 10.29; head width 7.08; snout–arm length 18.75; internarial distance 2.13; interoccular distance 3.83; rostral length 3.68; interoccipital distance 6.29; diameter of eye 3.48; arm length 12.52; leg length 18.98; length of 4th finger 3.03; length of 4th toe 6.34; tail width 5.33; width of external ear opening 1.03; high of external ear opening 1.52; body mass 2.6 g.

Coloration.—Dorsal ground color dark brown with small black dots forming 8 longitudinal lines, the lines end at proximal of tail; ventral color immaculate, yellowish on trunk, orange on throat and under tail; thick black dorsolateral stripe with serrate edge from posterior margin of eye to proximal tail around at 10th of subcaudal scale; lateral ground color light brown with dark brown spots fading towards venter; head scales dark brown; labials with dark bands crossing scale sutures; palmar and plantar surfaces darker brown than adjacent antebrachium and shank.

Variation.—The two paratypes are very similar to the holotype, except as noted here. ENS 14854 has the frontal in contact with the first, second, and third supraoculars and the frontoparietal laterally in contact with the third and fourth supraoculars. UTA-R 64204 (ENS

14699) has eight fade dark longitudinal lines and line 4th and line 5th from the left having prominent black dots in some part of trunk on the dorsum and pale pink throats and ventral tails.

We present mensural (in mm) and meristic data for UTA-R 64204 (ENS14699) follow by values of UTA-R 64205 (ENS14854): snout–vent length 56.32, 59.74; tail length 33.80, 6.45 (both incomplete); axilla–groin distance 31.25, 33.22 mm; head length 10.22, 10.26; head width 6.74,7.98; snout–arm length 17.66, 19.22; internarial distance 2.05, 1.63; interocular distance 4.21, 4.18; rostral length 3.91, 4.17; interoccipital distance 6.21, 6.10; diameter of eye 3.63, 3.06; arm length 13.23, 13.50; leg length 18.95, 19.58; length of 4th finger 3.03, 3.35; length of 4th toe 5.86, 6.13; tail width 5.11, 6.04; width of external ear opening 0.89, 1.31; height of external ear opening 1.24, 1.67; body mass 2.0, 3.2 g; 32, 34 midbody scale rows; 73, 74 paravetebral scale rows; five, six lamellae under first finger; eight, eight lamellae under second finger; 11, 11 lamellae under third finger; 11, 12 lamellae under fourth finger; six, seven lamellae under fifth finger; five, five lamellae under first toe; seven, eight lamellae under second toe; 15, 15 lamellae under third toe; 16, 17 lamellae under fourth toe; eight, nine lamellae under fifth toe.

Distribution and natural history.—*SphenomorphusIII sp. 1* occurs in montane forests of the Barisan Mountain Range in southern Sumatra between 1055 and 1558 m elevation. Though currently known from only three specimens from South Sumatra and Lampung, ecological niche modeling identified apparently suitable habitat in from southern Lampung to the mountain pass between Pagar Alam in South Sumatra and Kapahiang in Bengkulu.

We found the new species in leaf litter immediately after sunset at 6:30–7:45 pm.

SphenomorphusIII ***sp.2*** sp. nov.

(Fig. 7–8)

Holotype.—an adult female (MZB 14453, field number ENS 15514), from Kecematan Berastagi, Karo Regency, North Sumatra, Sumatra, 3.24521°N, 98.53438°E, 1,271 m elevation, collected 14 January 2014 by Efendi (Fig. 9).

Diagnosis.— *Sphenomorphus*III *sp.2* can be identified by having limbs barely overlap when addressed, no parietal eye-spots, enlarge temporal scales, a serrate dorsolateral stripe from posterior margin of the eye to anterior margin of the tail, the anterior loreal devided, dorsal black spots form eight longitudinal lines. 36 midbody scale rows, 73 paravertebral scale rows, 71 ventral scale rows, and 18 lamellae under fourth toe.

Comparisons.—*SphenomorphusIII sp.2* is most likely to be confused with its two congeners. Unlike *SphenomorphusIII sp.1* (characters in parentheses), the new species has 36 (32–34) midbody scale rows, 8 (9) supracillaries, 18 (16–17) lamellae under the fourth toe, and dorsal black spots arrayed in longitudinal lines (dorsal black spots forming an irregular pattern, Fig. 8, Table 3). Unlike *SIII. cameronicus,* the new species has a divided anterior loreal (entire) and 18 (20–21) lamellae under the fourth toe.

Unlike most Southeast Asia and Sunda Shelf *Sphenomorphus*, the new species has limbs that barely overlap when addressed (limb completely overlapping in *S. anomalopus*, *S. crassus*, *S. cyanolaemus*, *S. haasi*, *S. indicus*, *S. kinabaluensis*, *S. lineopunctulatus*, *S. maculatus*, *S. maculicollus*, *S. melanopogon*, *S. multisquamatus*, *S. murudensis*, *S. praesignis*, *S. puncticentralis*, *S. sabanus*, *S. sanctus*, *S. scotophilus*, *S. stellatus*, *S. sungaicolus*, *S. tanahtinggi*, *S. tonkienensis*, *S. tenuiculus*, *S. tersus*, *S. variegatus*; limbs not overlapping in *S. alfredi*, *S.*

cophias, *S. grandisonae*, *S. helenae*). Like the new species, limbs slightly overlap in *S. shelfordi,* however this species has 28–29 lamellae under the fourth toe, whereas *SIII. sp.2* has 18. The new species lacks a parietal eye spot and has a thick serrate dorsolateral stripe, whereas *S. modigliani* has a parietal eye spot and lacks a serrate dorsolateral stripe.

Description of Holotype.—Adult female, head longer than wide; dorsal head scales plate-like, smooth; snout pointed in dorsal aspect, rounded in profile; rostral wider than high, visible from above; rostral in broad contact with frontonasal, forming strait suture; supranasal absent; frontonasal wider than long, in contact with upper anterior loreal and prefrontals; prefrontals in contact; frontal elongate, narrow posteriorly; frontal in contact with prefrontals, first, second and third supraoculars, and frontoparietals; four supraoccular, third widest, followed by two small postsupraoculars; frontoparietal unequaly divided, anteriorly in contact with frontal, laterally in contact with third and fourth supraoculars, posteriorly in contact with interparietals and parietals; interparietal diamond-shaped, slightly projecting posteriorly between parietals; no parietal eye-spot; parietals in contact posteriorly, in contact with last supraoccular anteriorly; parietal laterally surrounded by five scales; nostril in center of single nasal; suture above nostril present; nasal in contact anteriorly with rostral, dorsally with frontonasal, posteriorly with anterior loreals, ventrally with first supralabial; three loreals; anterior loreal divided; upper anterior loreal in contact with nasal and posterior loreal; upper anterior loreal in contact with frontonasl, prefrontal; lower anterior loreal in contact with first supralabials; posterior loreal in contact with upper and lower anterior loreals, preocular scales, first supercilliary, and second and third supralabials; two preoculars; upper preocular smaller than lower preocular; three suboculars contacting supralabials; eight supraciliaries, first largest; one posterior supraciliaries elongate and projecting dorsomedially; seven supralabials; two post-supralabials; seven infralabials; two postoculars; temporals enlarged; two primary temporals; three secondary temporals, uppermost in contact parietals; lower eyelids semitransparent, entirely scaled; external auditory meatus recessed, circular, its smallest diameter smaller than diameter of eye; mental wider than long, rounded posteriorly, as wide as rostral; single postmental in contact with first and second infralabial; three pairs of chinshields; first pair of chinshields enlarged in medial contact, laterally contacting second and third infralabial; second pair of chinshields enlarged, entirely separated by one gular scale, laterally contacting third and fourth infralabial; third pair of chinshields entirely separated by six gular scales, laterally in contact with fourth and fifth infralabials.

Body slender; dorsals smooth, cycloid, imbricate; pectoral scales slightly enlarged; two precloacal scales enlarged; subcaudals not enlarged; 36 scales around midbody; 73 paravetebral scale rows; 71 ventral scale rows; 22 scale around tail at level of 10th subcaudal; limbs well developed, pentadactyl, barely overlapping when adpressed; palmar and plantar scales raised (subtuberculate granular); digits short; subdigital lamellae keeled; four lamellae under first finger, seven under second finger, 11 under third finger, 11 under fourth finger, five under fifth finger, five under first toe; eight under second toe; 15 under third toe; 18 under fourth toe; nine under fifth toe.

Measurements in mm: snout–vent length 54.26; tail length 21.24 (incomplete); axilliary–groin distance 26.71; head length 10.65; head width 7.10; snout–arm length 19.78; internarial distance 2.20; interoccular distance 4.55; rostral length 4.01; interoccipital distance 6.19;

diameter of eye 3.68; arm length 13.97; leg length 19.69; length of 4th finger 3.22; length of 4th toe 5.83; tail width 5.52; width of external ear opening 1.03; high of external ear opening 1.17; body mass 2.7 g.

Coloration.—Dorsal ground color dark brown with small black dots forming irregular pattern; ventral surfaces immaculate; ventrally, trunk pale yellow, throat and tail pale pink; thick black dorsolateral stripe with serrate edge from posterior margin of eye to to proximal tail around at 8th of subcaudal scale; lateral ground color light brown with dark brown spot fading towards venter; head scales dark brown; labial sutures with sharp dark bands.; palm and sole darker brown than ventral antebrachium and shank.

Distribution and natural history.—The only known specimen of this skink was collected during the 2014 eruption of Mount Sinabung in a forest covered with ash. Thus, we have no knowledge of the species natural history. Ecological niche modeling found habitat similar to the type locality from around the Lake Toba and Gunung Leuser National Park to a mountain pass between Padangsidempuan and Panyabungan, North Sumatra.

DISCUSSION

Ours is the first phylogenetic analysis to include all the species of Sumatran and Javan *Sphenomorphus.* The group presents difficult challenges, because many of the species remain rare in collections and tissue samples are available for only a few of them. Our combined analysis of morphological and molecular characters revealed at least four groups of

Sphenomorphus on Java and Sumatra. These skinks include species assignable to both the Oceanian and Sundanese clades of *Sphenomorphus, Tytthoscincus*, and *Sphenomorphus III.*

Ours is also the first analysis to use osteological characters to investigate relationships among species of sphenomorphine skinks from SE Asia. Greer and Parker (1979) used some osteological characters when revising *Sphenomorphus* before many genera were removed from it. In this study, the skull proved a useful source of characters to diagnose our new genus, and we were able to distinguish it from *Sphenomorphus* using characters of ectopterygoid shape, relative size of the braincase, and relative size of the orbits. These differences may be correlated with semi-fossorial habits, though this hypothesis cannot be investigated without a wider sampling of species. Nonetheless, Evans (2008) also suggested that borrowing skinks relatively small brain cases and compact skulls. Conservative external morphology has long complicated the systematics of these skinks and osteological study will likely reveal additional characters.

Many montane skinks are exceedingly rare, and this is certainly the case for the species in this study. Their rarity presents a challenge for understanding their distribution and conserving them in the face of rampant deforestation. Though known from only four specimens, ecological niche modeling of *SphenomorphusIII* identified apparently suitable habitat where these skinks may occur. Interestingly, the model did not identify habitat in the northernmost Sumatran province of Aceh, even though the region is mountainous and populated by other montane lizards widely distributed in the Barisan Range (Harvey et al. 2017). Though mountainous and still heavily forested, much of Aceh has a more seasonal climate that the rest of the island and this may explain the absence of suitable habitat. Our modeling identified three gaps in suitable habitat on Sumatra. We have discovered one species above the first break in North Sumatra and another species in South Sumatra and Lampung. However, we have not yet found any specimens from the central part of Sumatra, and this region likely contains one or more undescribed members of *SphenomorphusIII*.

Ecological niche modeling predicts suitable habitats of particular lineages and can be used as evidence for the ecological species concept (Wogan and Richmond 2015). Similar to our study Raxworthy et al. (2007) and Pearson et al. (2007) used ecological niche modeling to examine cryptic species of gecko. They argued that ecological niche modeling is powerful tool for studying species with poorly known distributions, low vagility, and a high potential for endemism. Wogan and Richmond (2015) used ecological niche modeling in their study of the *Plestiodon skiltonianus* species complex, a group of skinks presenting systematic challenges similar to the *Sphenomorphus* group. They proved that niche modeling is suitable for morphological-ecological associations that leading to ecological speciation in the skink.

The time caribrated phylogeny indicated *SphenomorphusIII* was spited from other genera of Sphenomorphinae about 35.28 Ma in late Eocene. This result similar to Karin et al. (2016b). they described a new genus of skink in Mabuyinae from mainland Southeast Asia and they found that their new genus (*Toenayar*) diverse from closely-related genus (*Dasia*) about 41.9 Ma. We also found that the intergeneric divergenc in Sphenomorphinae is younger that the divergence of those and *SphenomopusIII* Within the *SphenomorpusIII*, *S. sp.1* from southern Sumatra separated from *S. sp.2* from northern Sumatra about 13 MYA in middle Miocene. This result correlated with geologic event in Sumatra. The Barisan range of Sumatra was formed about 10-5 Ma in late Miocene. Before that 20-10 Ma the highlands of Sumatra were isolated (Sheldon et al. 2015). The intraspecific divergence of *S.sp.1* are about 1.46-2.20 Ma in early Pleistocene indicate that this seperations were shaped by Pleistocene glacier cycles in Sunda Land (Woodruff 2010). This finding also similar to separation patterns of *Tytthoscincus* skinks in Malay Pennisula. Grismer et al. 1017b suggested that intraspecific divergence and interspecific divergence of closly-related species of montane species of *Tytthoscincus* in Malay Peninsula occurred in early to late Plestocene.

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APPENDICES

Appendix I: Specimens Examined

Carlia nigrauris (n = 1).—INDONESIA: Banten: Palau Tinjil, SMF 53916 (male)–Holotype.

Dasia grisea (n = 1).—THE PHILIPPINES: BMNH 1946.8.20.51

Emoia atrocostata (n = 1).—THE PHILIPPINES: Luzon: Paracali, MSG 28080 (male; *Euprepes bitaeniatus*–Syntype).

Eutropis balinensis (n = 1).—INDONESIA: Bali: Gitgit, SMF 22087 (male)–Holotype.

E. multifasciata (n = 1).—INDONESIA: Banten: Pandeglang, 525 m, 6.32756 °S, 105.95988 °E, MZB 11912 (male)–Neotype.

E. sikkimensis (n = 1).—INDONESIA: Aceh: Gunung Putri Tidur, 467 m, 3.2921 °S, 97.19642 °E, UTA-R 64106 (female).

E. tjendikianensis (n = 1).—INDONESIA: Java Tengah: Wonosobo, UTA-R 64139 (male).

Eremiascincus emigrans (n = 1).—INDONESIA: Sumba: RMNH.RENA 30750–Syntype.

Lamprolepis leucosticta (n = 1).—INDONESIA: Malabar: Pengalengun, MZB 354.

Lipinia viggitera (n = 1).—INDONESIA: Sumatra: Mentawai: Sipura: Sereinu, MSG 55855–Holotype.

Lygosoma bowringii (n = 1).—INDONESIA: West Java: Borgor: Baranan Siang, near Botanical Garden, MZB 1587.

L. quadrupes (n = 1).—INDONESIA: West Java: Borgor: Kecamatan Dramaga, IPB campus, UTA-R 64185.

L. opisthorhodom (n = 1).—INDONESIA: Sumatra: ZMH R01850–paratype.

Sphenomorphus alfredi (n = 1).—MALAYSIA: North Borneo: BMNH 1898.7.20.2, 1946.8.19.40–type.

S. anomalopus (n = 1).—INDONESIA: Java: ZMB 12026 (*Lygosoma paradoxum*–Holotype).

S. buttikoferi (n = 3).—INDONESIA: Boreo: Liang Koeboeng, RMNH.RENA 4471–Syntype; RMNH.RENA 30753–Syntype; RMNH.RENA 30754–Syntype.

S. cameronicus (n = 1).—MALAYSIA: Pahang: Lipis, Cameron Highland (1,400 m): BMNH 1924.5.25.1, 1946.8.3.27–Type.

S. cophias (n = 2).—MALAYSIA: Pahang: Gunung Tahan (3,000 ft): BMNH 1906.2.28.17, 1946.8.3.15–Type.

S. cyanolaemus (n = 1).—INDONESIA: Aceh: Aceh Besar: Mt. Batee Meucica, UTA-R 63040 (male).

S. haasi (n = 1).—MALAYSIA: Borneo: Sarawak: Gunung Gading, ZRC 2.5307.

S. indicus (n = 1).—THAILAND: Chonburi: Kaokiew Waterfall, ZRC 2.5366.

S. kinabaluensis (n = 1).—MALAYSIA: Borneo: Sabah: Kinabalu, ZRC 2.1581

S. maculatus (n = 1).—INDIA: Andaman Island: Saddle Peak, ZRC 2.4691

S. maculicollus (n = 1).—MALAYSIA: Borneo: Sabah: Kinabalu, Kinokok, ZRC 2.1623

S. malayanum (n = 1).—INDONESIA: Sumatra: Sumatra Barat: Mt. Singalang, Alahan Panjang (1500 m), BMNH 1946.8.3.11–Type

S. melanopogon (n = 2).—INDONESIA: Florense, ZMA 11060 (*S. florense*–Syntype); Sumbawa: Mt. Tambora, MZB 13253 (male).

S. modigliani (n = 1).—INDONESIA: Sumatra: Mentawai Island: Sipora, BMNH 1894.12.18.10, 1946.8.16.98–Type.

S. multisquamatus (n = 2).—MALAYSIA: Borneo: Sabah: Kinabaluh, BMNH 1893.3.6.42–Paratype; BMNH 1893.3.6.43–Paratype.

S. murudensis (n = 1).—MALAYSIA: Sarawak: Mt. Murud: (7,000–7,200 ft.) BMNH 1925.9.1.11, 1946.8.15.6–Type, (5,500-6,300 ft.) BMNH 1927.3.16.1, 1946.8.15.7–Paratype.

S. necopinatus (n = 3).—INDONESIA: West Java: Borgor, RMNH.RNEA 7969-Holotype; BMNH 1948.1.8.17-Palatype; Gn. Halimun 950 m -6.7109 S, 106.5191667 E, MZB 7644.

S. praesignis (n = 1).—MALAYSIA: Perak: Larut Hill, (1,312 m) BMNH 1903.4.13.59, 1946.8.15.53–Holotype.

S. puncticentralis (n = 1).—INDONESIA: Cenral Java: Baturaden, MZB 7747, MZB 7748, MZB 7748.

S. sabanus (n = 1).—MALAYSIA: Sabah: Sandakan: Sapagaya Forest Reserve, BMNH 1954.1.9.13–Paratype.

S. sanctus (n = 1).—INDONESIA: Java: MNHN 0000.7116 (Female)–Holoype.

S. scotophilus (n = 1).—MALAYSIA: Selangor: Batu Caves, BMNH 1946.8.16.94-Type; INDONESIA: Sumatra: Sumatra Utara: Tanpanuli Selatan T. Anjing, MZB 14454 (male).

S. stellatus (n = 1).—MALAYSIA: Perak: Larut Hills, (4,400 ft.) BMNH 1898.9.22.217, 1946.8.3.26–Type; (3,500 ft.) BMNH 1898.9.22.217, 1946.8.3.26–Type.

S. sungaicolus (n = 1).—INDONESIA: Bengkulu: Bengkulu Tenggah, UTA-R 63035 (female).

S. vanheurni (n = 1).—INDONESIA: East Java: Mount of Argopuro (Ijang): Bremi: Taman Hidub, RMNH.RENA 7967-Holotype.

Tropidophorus beccarii (n = 1).—MALAYSIA: Borneo: Langanan, Kinabalu, ZFMK 52214 (*Sphenomorphus aquaticus*–Holotype).

T. brookii (n = 1).—MALAYSIA: Borneo, BMNH 1946.8.19.1–Type.

Tytthoscincus temmincki (n = 2).—INDONESIA: Wets Java: Bundung: Mount of Kencana, 1884 m, -7.29276 S, 107.63394 E, UTA-R 64192; Java, MHNP 1344-Holotype

Tytthoscincus sp. nov. 1 (n = 1).—INDONESIA: East Java: Bondowoso: Jampit: Mount of Ijen, 1591 m, -8.07724 S, 114.14472 E, MZB 14402 (female)–Paratype, *Tytthoscincus sp. nov. 2* (n = 1).—INDONESIA: Aceh: Aceh Besar: Mount of Batee Meucica, 502 m, 5.26157 N, 95.54176 E, MZB 14401 (male)-Holotype.

Appendix II: Morphological and Ecological Characters Used in Combined-data Phylogenetic Analysis

Binary-morphological characters (n = 106).— head longer than wide; upper head scales plate-like, smooth; snout pointed, rounded anteriorly in ventral view; rostral wider than high; rostral visible from above; rostral in broad contact with frontonasal with strait suture; supranasals absent; frontonasal wider than long; frontonasal in contact with anterior loreal; frontonasal in contact with frontal; frontonasal in contact with prefrontals; prefrontals in contact; frontal elongate narrow posteriorly; frontal in contact with frontonasal; frontal in contact with prefrontals; frontal in contact with frontoparietals; frontoparietal equaly divided; frontoparietals in contact; frontoparietal anteriory in contact with frontal anteriorly; frontoparietal posteriorly in contact with parietals; frontoparietal posteriorly in contact with interparietals; interparietal diamondshaped; interparietal slightly projecting posteriorly; parietal eyespot present; parietal eyespot in posterior projection; parietals in contact posteriorly; parietal in contact the last supraocular anteriorly; enlarge nuchal scale; post nasal present; nostril in center of single nasal post nasal fused; nasal in contact with rostral anteriorly; nasal in contact with frontonasal dorsally; nasal in contact with first loreal posteriorly; nasal in contact with first supralabial ventrally; anterior loreal devided; anterior loreal much wider than posterior loreal; anterior loreal in contact with nasal; anterior loreal in contact with prefrontal; anterior loreal in contact with frontonasal; anterior loreal in contact with first supralabial; anterior loreal in contact with second supralabial; posterior loreal in contact with anterior loreal; posterior loreal in contact with preocular scales; posterior loreal in contact with first supercilliary; posterior loreal in contact with second supralabial; posterior loreal in contact with third supralabial; upper preocular present smaller; lower preocular present larger; lower preocular followed by a couple of suboculars; first supraciliaries largest; temporals enlarged; uppermost secondary temporal in contact parietal; lower eyelids transparent; lower eyelids scaley; lower eyelids with enlarge disc; external ear opening recess; melanin pigment in tympanum; external ear opening in circular shape; tympanum diameter smaller than eyeball diameter; mental wider than long; mental rounded posteriorly; mental equal to rostral; single post mental; postmetal contact 1st infralabial; post mental contact 2nd inflalabial; 1st pair of chinshield enlarge; 1st pair of chinshield in contact; 2nd pair of chinshield enlarge; 2nd pair of chinshield seperated by one gular scale; 3rd pair of chinshield enlarge; 1st pair of chinshield in contact with first and second inflalabials; 2nd pair of chinshield in contact with second and third inflalabials; 3rd pair of chinshield in contact with third and fourth inflalabials; body scale smooth; body scale cycloid; body scale imblicate; dorsal scale larger than ventral scale; pectoral scale slightly enlarge; dorsal scale striate; median precloacal scales overlap outer precloacal scales; subcaudal enlarged; limb well develop; limb pentadactyl; palmer scale raised; plantar scale raised; digit short; digit scale at dorsal surface in a single row; subdigital lamellae keeled; subdigital lamellae bicarinate; smooth scale on palmar surface; smooth scale on plantar surface; overlap between dorsal and ventral scale planes; dorsal ground color dark brown; dorsal color uniform no dots no lines; dorsal with dark longitudinal lines; dorsal with light medial longitudinal line; body with cross bands; ventral color pale; ventral immaculate; lateral head speckled with light color marking; labials with dark distinct banded; dorsolateral stripe present; dorsolateral stripe with serrate edge; gular region stipped with dark brown; palmar darker than subforearemregion; plantar darker than subtibial region; subforearm region stripped with dark dots; subtibial region stripped with dark dots; subcaudal stipped with dark dots; epipterygoid make right angle with sagittal plane from dorsal view.

Multistate-morphological characters (n = 34).— number of supraoculars in contact with frontal (2–3); number of supraocular (4–7); the widest supraocular (1–3); number of small postsupraocular (0–2); number of supraoculars in contact with frontoparietal (2–4); number of scales surrounded laterally of parietal (3–6); number of loreal (1–3); number of supraciliaries (6–9); number of posterior supraciliary elongate and projecting dorsomedially (0–2); number of supralabials (6–8); number of infralabials (6–8); number of postsupralabials (1–3); number of primary temporals (1–3); number of secondary temporals (1–3); number of lobules at external ear opening (0–4); number of pair chinshields (2–3); 3rd pair of chinshield seperated by number of gular scale (4–6); number of mid body scale rows (rank: 0–9); number of paravertebral scale rows (rank: 0–9); number of ventral scale row (rank: 0–9); number of precloacal scale enlarge (0–4); number of 10th subcaudal row (rank: 0–9); limb overlap when adpressed (0: not overlap, 1 slightly overlap, 2 completely overlap); number of subdigital lamelae on 1st finger (rank: 0–9); number of subdigital lamelae on 2nd finger (rank: 0–9); number of subdigital lamelae on 3rd finger (rank: 0–9); number of subdigital lamelae on 4th finger (rank: 0–9); number of subdigital lamelae on 5th finger (rank: 0–9); number of subdigital lamelae on 1st toe (rank: 0–9); number of subdigital lamelae on 2nd toe (rank: 0–9); number of subdigital lamelae on 3rd toe (rank: 0–9); number of subdigital lamelae on 4th (rank: 0–9); number of subdigital lamelae on 5th toe (rank:

0–9); body slender (0: robust, 1: truncate, 2 slender); throat and neck with color (0: no color, 1: black, 2: blue, 3: orange);

Binary-ecological character (n = 2).— riparian species; climbing ability.

Multistate-ecological character (n = 2).—behavior (0: terrestrial, 1: semi-fossorial, 2: scansorial, 3: arboreal), habitat elevation (0: low elevation 0–500 m asl., 1: mid elevation 500–1,000 m asl., 2: high elevation above 1,000 m asl.)

LIST OF TABLE

Table 4.1 Summary of morphological comparison among Sunda Shelf *Sphenomorphus*. All measurements are in mm. The column number refer as following; 1 = snout vent length, 2 = midbody scale row, 3 = dorsal scale striated, 4 = paravertebral scale row, 5 = ventral scale row, 6 = supraoccular, 7 = parietal in contact with supra ocular, 8 = supracilliary projected dorsomedialy, 9 = prefrontals in contact, 10 = loreals, 11 = supralabial, 12 = infralabial, 13 = subdigital lamalae on the fourth toe, 14 = keeled lamellae texture , 15 = enlarge precloacal, 16 = body band, 17 = dark dorsolateral stripe,18 = light post-orbital stripe, 19 light dorsolateral stripe, 20 = limb overlapping, and (-) = data not available, data of obtained from original description and from gathered data by Grismer et al. 2009.

Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
S. alfredi	33	26	N/A	-	-	4	-	N/A	0
S. anomalopus	70	38–39	0	71	-	5	1	1pro	1
S. cameronicus	70	38	0	69	-	4	1	1 pro	0
S. cophias	37	24	0	56	-	4	1	-	0
S. crassus	82	32	0	-	72	4	1	-	0
S. cyanolaemus	60	40	0	67–75	78–93	6	1	2 pro	1
S. grandisonae	30	34	-	71	-	4	-	-	1
S. haasi	57	41–42	0	-	93–98	6	1	-	0,1
S. helenae	28	30	N/A	-	-	4	-	N/A	0

S. indicus	75–80	34–36	0	73	84–87	4	1	2 pro	0
S. kinabaluensis	45–58	32–38	0	80–89	73–91	5,6	1	1 pro	0,1
S. lineopunctulatus	84	38	N/A	76	-	4	-	-	0
S. maculatus	63	38–42	N/A	-		5	1		0
S. maculicollus	47	35–36	0	79	84	7	1	1 pro	0
S. melanopogon	71	40–50	1	-	-	6,7	-	-	1
S. mimicus	36	30	N/A	61	-	4	-	N/A	
S. modigliani	41	32	N/A	-	-	4	1	N/A	1
S. multisquamatus	69	42–49	1	74-78	83-101	6,7	1	2 pro	1
S. murudensis	50.4	34	0	71	74	6	1	2 pro	1
S. praesignis	109	28	N/A	-	N/A	4	-	-	-
S. puncticentralis	45	29	1	64	-	5	1	-	1
S. sabanus	58	38–42	1	84–95	71–91	6,7	1	1 pro	0,1
S. sanctus	40–45	32–34	1	71	-	5	1	2pro	1
S. scotophilus	50	28–31	0	67–74	-	5	1	2 pro	0,1
S. shelfordi	67	23–34	0	-	-	4	1	-	1
S. stellatus	80	24	0	60–63	-	4	1	1 pro	0,1
S. sungaicolus	66.89.6	39–44	0	72–81	74–86	4	0	-	0
S. tanahtinggi	48–64	40–42	0	76–79	-	5	1	0	0,1
S. tonkienensis	35.8–48.8	32–34	0	65–72	58–71	4	1	1 pro	0,1
S. tenuiculus	46	26	0	57	68	4	1	-	0

S. tersus	90–92	34–36	0	-	-	4	-	-	1
S. variegatus	49–63	38–44	N/A	66–76		6		1	0,1
S. sp. 1	54.26–59.74	32–34	0	73–74	69-70	4	1	2 pro	1
S. sp. 2	53.45	36	0	73	71	4	1	1pro	1

Table 4.1 (continue)

Species	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
S. alfredi	-	6	-	12	0	0	N/A	1	0	0	0
S. anomalopus	2	7	6,7	16–17	-	1	1	0	0	0	1
S. cameronicus	2	7	5	20–21	-	1	0	1	0	0	barely
S. cophias	2	7	7	9	-	1	0	1	0	0	0
S. crassus	2	7	7	18–19	-	1	0	1	0	0	1
S. cyanolaemus	3	7	6	18	1	1	0	1	0	0	1
S. grandisonae	2	6	5	12	-		-	1	1	-	0
S. haasi	2	7	6	16–18	0	1	0	0	0	0	1
S. helenae	1	-	-	17	0	1	N/A	1	0	1	0
S. indicus	2	7	7	17–19	1	1	0	1	0	0	1
S. kinabaluensis	1	7	7	15–17	0	1	0	1	0	-	1
S. lineopunctulatus	2	7	-	22	-	1	0	1	1	1	1
S. maculatus	1	-	-	16–22	1	1	N/A	N/A	N/A	N/A	1

S. maculicollus	1	6	6	18–23	0	1	0	0	0	0	1
S. melanopogon	2	-	-	27–29	0	1	0	1	0	0	1
S. mimicus	2	7	6	16	-	1	N/A	1	0	0	barely
S. modigliani	-	-	-	15	0	1	N/A	0	0	0	barely
S. multisquamatus	3	6,7,8	5	16–23	0	1	0	0	0	0	1
S. murudensis	2	6	7	17	0	1	0	1	0	0	1
S. praesignis	2	7	7	20	-	1	1	-	-	-	1
S. puncticentralis	2	7	7	25	0	1	0	1	0	0	1
S. sabanus	1	7	5,6,7	18–22	1	1	0	0	0	0	1
S. sanctus	2	7	6	26–27	-	1	0	0	0	0	1
S. scotophilus	2	7	6	22–23	-	1	0	1	0	0	1
S. shelfordi	-	-	-	28–29	0	1		0	1	0	sligtly
S. stellatus	2	7	7	18–23	-	1	0	0	0	0	1
S. sungaicolus	1-2	7	7	18–21	0	1	1	0	0	1	1
S. tanahtinggi	4	8,9	7	16–17	1	1	0	1	0	0	1
S. tonkienensis	2	7	6	15–19	0	1	0	1	0	0	1
S. tenuiculus	-	7	6	21–24	0	1	0	1	0	0	1
S. tersus	3	7	7	18–19	-	1	0	0	0	0	1
S. variegatus	2	7,8	6,7	19–25	1	1	-	-	-	-	1
S. sp. 1	3	7	7	16–17	1	1	0	1	1	0	barely
S. sp. 2	3	7	7	18	1	1	0	1	1	0	barely

Table 4.2 Specimens used in phylogenetic analysis with accession numbers from GenBank and locality (sequences in bold are generated from this study).

Species	Voucher No.	GenBank No.			
		16S	ND4	NGFB	R35
SphenomorphusIII sp.1	MZB 14452	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
SphenomorphusIII sp.1	UTA-R 64204	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
SphenomorphusIII sp.1	UTA-R 64205	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
SphenomorphusIII sp.2	MZB 14453	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
Insulasaurus traanorum	KU 311442	JF497987	JF498469	-	JF498343
Insulasaurus victoria	KU 309443	JF497989	-	-	JF498345
Insulasaurus wrighti	KU 311422	JF497990	JF498471	JF498227	JF498346
Lipinia noctua	CAS 236454	JF497992	JF498473	-	JF498348
Lipinia pulchella	TNHC 56378	JF497993	JF498474	JF498228	JF498349
Papuascincus sp.	ABTC 48281	DQ915323	DQ915347	-	-
Papuascincus stanleyanus	RNF 0065	-	JF498479	JF498234	JF498355
Papuascincus stanleyanus	RNF 0067	JF498000	JF498480	JF498235	JF498356

Scincella reevesii	FMNH 255540	JF498078	JF498515	-	HQ907634
Scincella rufocaudata	ZFMK76239	HM773217	-	-	-
Parvoscincus decipiens	KU 306558	JF498006	JF498486	JF498241	JF498362
Parvoscincus leucospilos	TNHC 62682	JF498027	JF498506	JF498258	JF498383
Pinoyscincus jagori	KU 307684	JF498066	-	JF498294	JF498422
Pinoyscincus llanosi	KU 306557	JF498068	JF498542	JF498296	JF498424
Tytthoscincus sp.1	MZB 14404	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
Tytthoscincus sp.2	MZB 14401	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
Sphenomorphus cyanolaemus	FMNH 239867	JF498084	JF498557	JF498311	JF498436
Sphenomorphus sabanus	FMNH 239881	JF498092	JF498565	JF498319	JF498444
Sphenomorphus multisquamatus	FMNH 243828	JF498091	JF498564	JF498318	JF498443
Sphenomorphus variegatus	KU 309900	JF498096	-	JF498323	JF498448
Sphenomorphus variegatus	KU 315087	JF498097	JF498569	JF498324	JF498449
Sphenomorphus indicus	CAS 214892	JF498089	JF498562	JF498316	JF498441

Sphenomorphus sungaicolus	LSUHC 11722	KX398013	-	-	-
Sphenomorphus tersus	LSUHC 9041	KX398015	-	-	-
Sphenomorphus maculatus	CES 09/895	KF514650	-	-	-
Sphenomorphus maculatus	FMNH 261863	JF498090	JF498563	JF498317	JF498442
Sphenomorphus sanctus	UTA-R 64206	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
Sphenomorphus scotophilus	MZB 14454	Pending acceptance	Pending acceptance	Pending acceptance	Pending acceptance
Sphenomorphus concinatus	KU 307213	JF498080	JF498553	JF498307	JF498432
Sphenomorphus melanopogon	-	AY308312	-	-	-
Sphenomorphus cranei	KU 307167	JF498082	JF498555	JF498309	JF498434
Sphenomorphus fasciatus	KU 310807	JF498087	JF498560	JF498314	JF498439
Sphenomorphus fasciatus	KU 315061	JF498088	JF498561	JF498315	JF498440
Sphenomorphus solomonis	KU 307173	JF498094	JF498567	JF498321	JF498446
Otosaurus cumingi	RMB 808	JF497997	JF498477	JF498232	JF498352
Otosaurus cumingi	RMB 985	JF497998	JF498478	-	JF498353
Eutropis multifasciata	KU 302890	JF497984	JF498466	JF498223	JF498340
Eutropis multifasciata	CES 09/925	JQ767964	-	-	-

Dasia grisea	KU 305574	JF497978	JF498460	JF498217	HQ907631
Lygosoma quadrupes	LSUHC 8403	-	-	-	HQ907639
Emoia atrocostata	KU 304896	JF497979	JF498461	JF498218	HQ907627
Plestiodon quadrilineatus	KU 311490	JF498073	JF498547	JF498301	HQ907628
Takydromus sexlineatus	KU 311512	JF498098	-	JF498325	HQ907624
Takydromus sexlineatus ocellatus	-	-	-	JF818318	-

Table 4.3 Different *Sphenomorphus* species groups in Java and Sumatra used in CT scanning and scanning parameters.

Species	Vouncher	Tube voltage (kV)	Tube amperage (mA)	Voxel size (mm3)	Region
SphenomorphusIII sp.1	MZB 14452	40	40	0.015	head
SphenomorphusIII sp.1	MZB 14452	55	40	0.037	whole body

SphenomorphusIII sp.2	MZB 14453	40	40	0.015	head
SphenomorphusIII sp.2	MZB 14453	55	40	0.037	whole body
Sphenomorphus scotophilus	MZB 14454	40	40	0.013	head
Sphenomorphus scotophilus	MZB 14454	35	40	0.029	whole body
Sphenomorphus sungaicolus	UTA-R-63035	40	40	0.017	head
Sphenomorphus sungaicolus	UTA-R-63035	40	40	0.028	whole body
Sphenomorphus cyanolaemus	UTA-R-63040	40	40	0.018	head
Sphenomorphus cyanolaemus	UTA-R-63040	70	40	0.033	whole body
Sphenomorphus melanopogon	MZB 13253	40	40	0.023	head
Sphenomorphus melanopogon	MZB 13253	70	40	0.043	whole body

Table 4.4 Geographic data used in ecological niche modeling of *Sphenomorphus* III in Sumatra and adjacent areas.

Species		Latitude	Longitude	Elevation
SphenomorphuIII sp.1	MZB 14452	-5.51563	105.07667	1055 m
SphenomorphusIII sp.1	UTA-R 64204	-4.90589	104.13232	1558 m
SphenomorphusIII sp.1	UTA-R 64205	-4.96599	103.84954	1087 m
SphenomorphusIII sp.2	MZB 14453	3.24521	98.53438	1271 m

Table 4.5 Summary of morphological characters among species of *Sphenomorphus* III and congruent *Sphenomorphus* in Sunda Shelf.

Characters	*S. sp.1* MZB 14452 Holotype	*S. sp.1* UTA-R 64204 Paratype	*S. sp.1* UTA-R 64205 Paratype	*S. sp.2* MZB 14453 Holotype	*cameronicus* n = 3 -	*modigliani* BMNH 1946.8.16.98
Sex	male	female	female	female	-	-
SVL	54.26	56.32	59.74	53.45	65.00	~37
MBSR	32	32	34	36	34–38	32

PVSR	73	73	74	73	69–74	~ 72
VSR	69	70	70	71	69–71	~ 66
PI	yes	yes	yes	yes	no	yes
ALD	yes	yes	yes	yes	no	no
SL	7	7	7	7	7–8	6
IL	7	7	7	7	5–6	5
PES	no	no	no	no	no	yes
SC	9	9	9	8	8–10	-
4th SDL	16	17	17	18	20–21	15
Ty	ovular	ovular	ovular	circular	circular	circular
DBD	lines	lines	lines	irregular	irregular	-
SDLS	yes	yes	yes	yes	yes	no
habitat	1055 m	1558 m	1087 m	1271 m	~ 1160 m	< 150 m.

FIGURE CAPTIONS

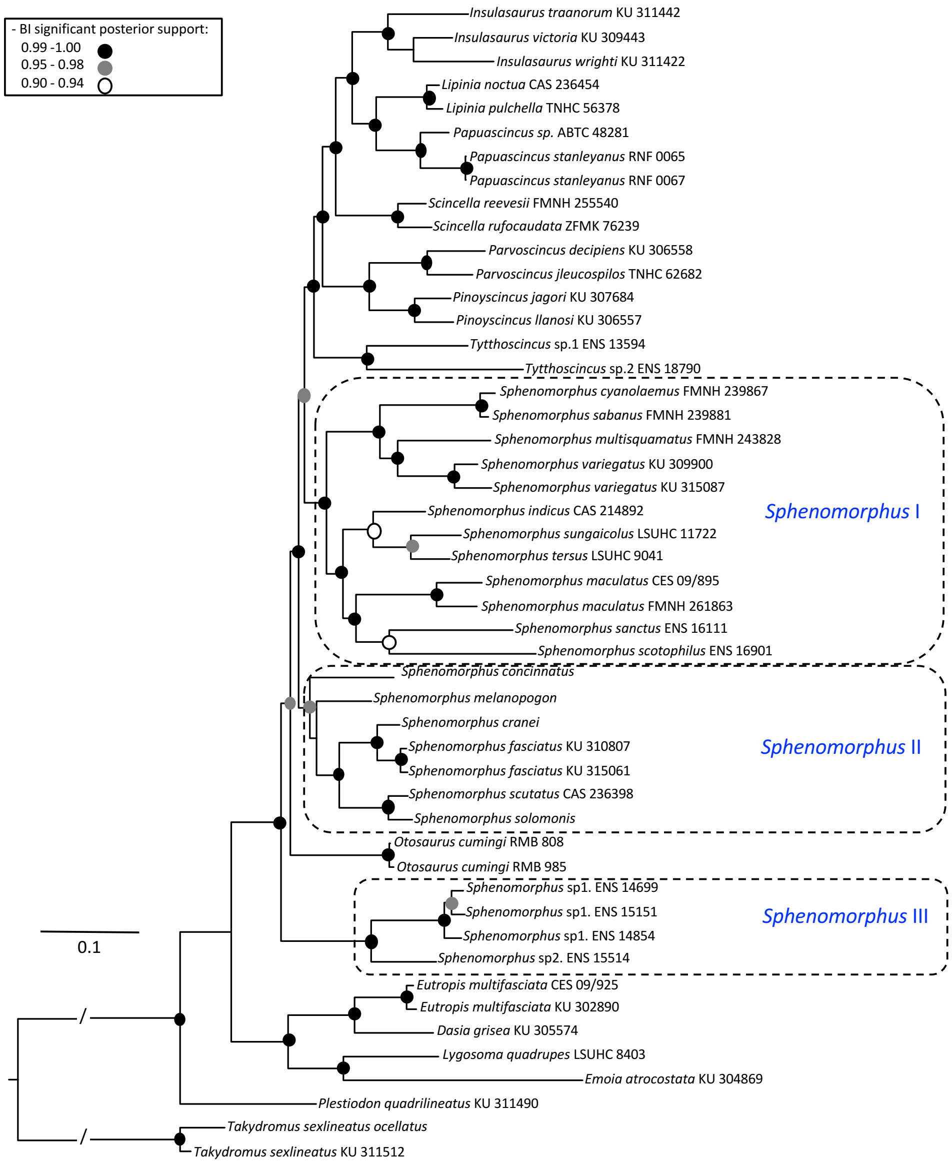


Figure 4.1 Partitioned model-based Bayesian phylogeny of *Sphenomorphus* from the Sunda Shelf and neighboring areas based on concatenated mitochondrial and nuclear data. Nodal support values are posterior probabilities from the Baysian analysis (BP ≥ 0.95) and bootstrap values from the maximum likelihood analysis (ML ≥ 70).

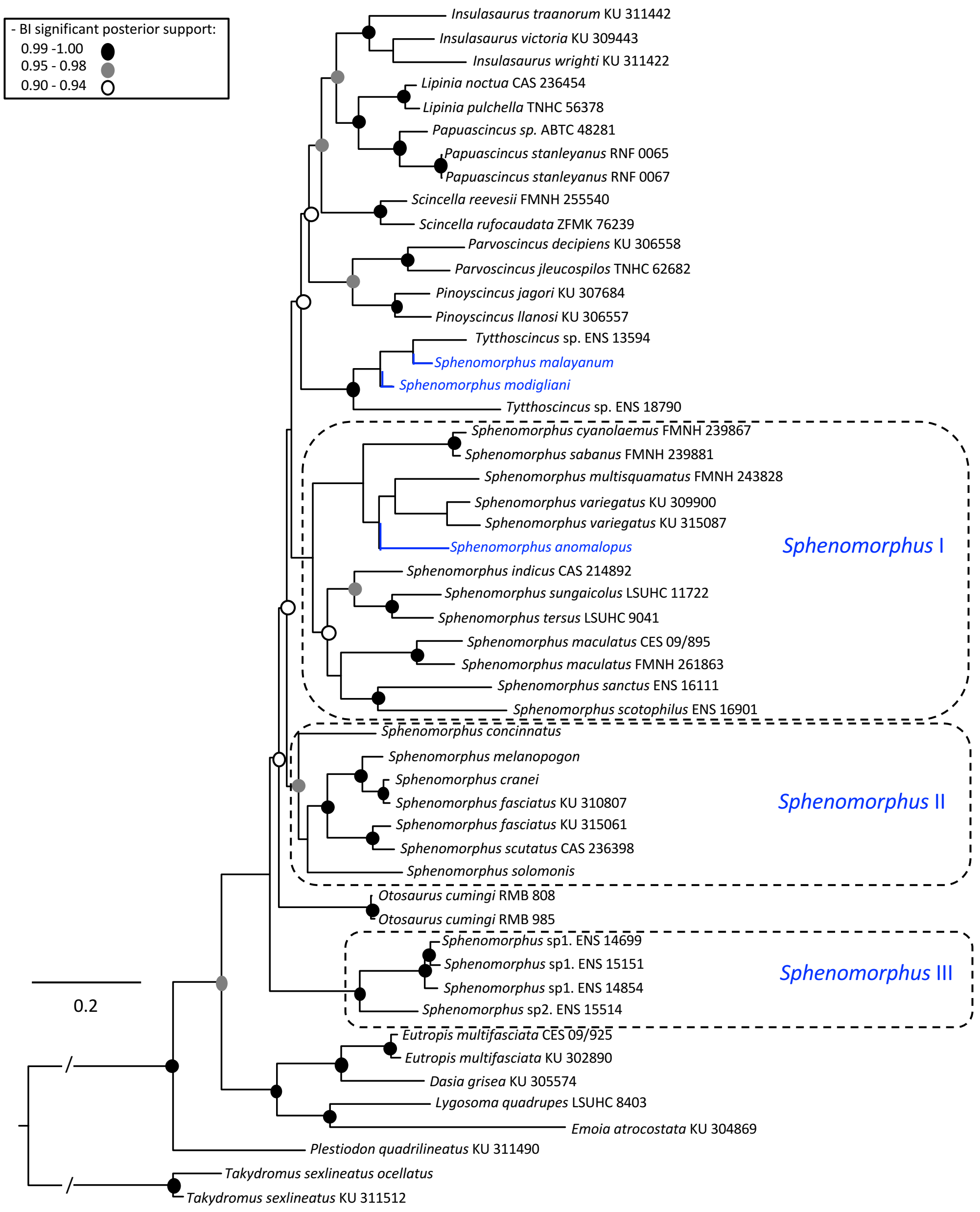


Figure 4.2 Bayesian phylogeny of *Sphenomorphus* from the Sunda Shelf and neighboring areas based on combined morphological, ecological, and molecular data. Nodal support values are posterior probabilities (BP ≥ 0.95).

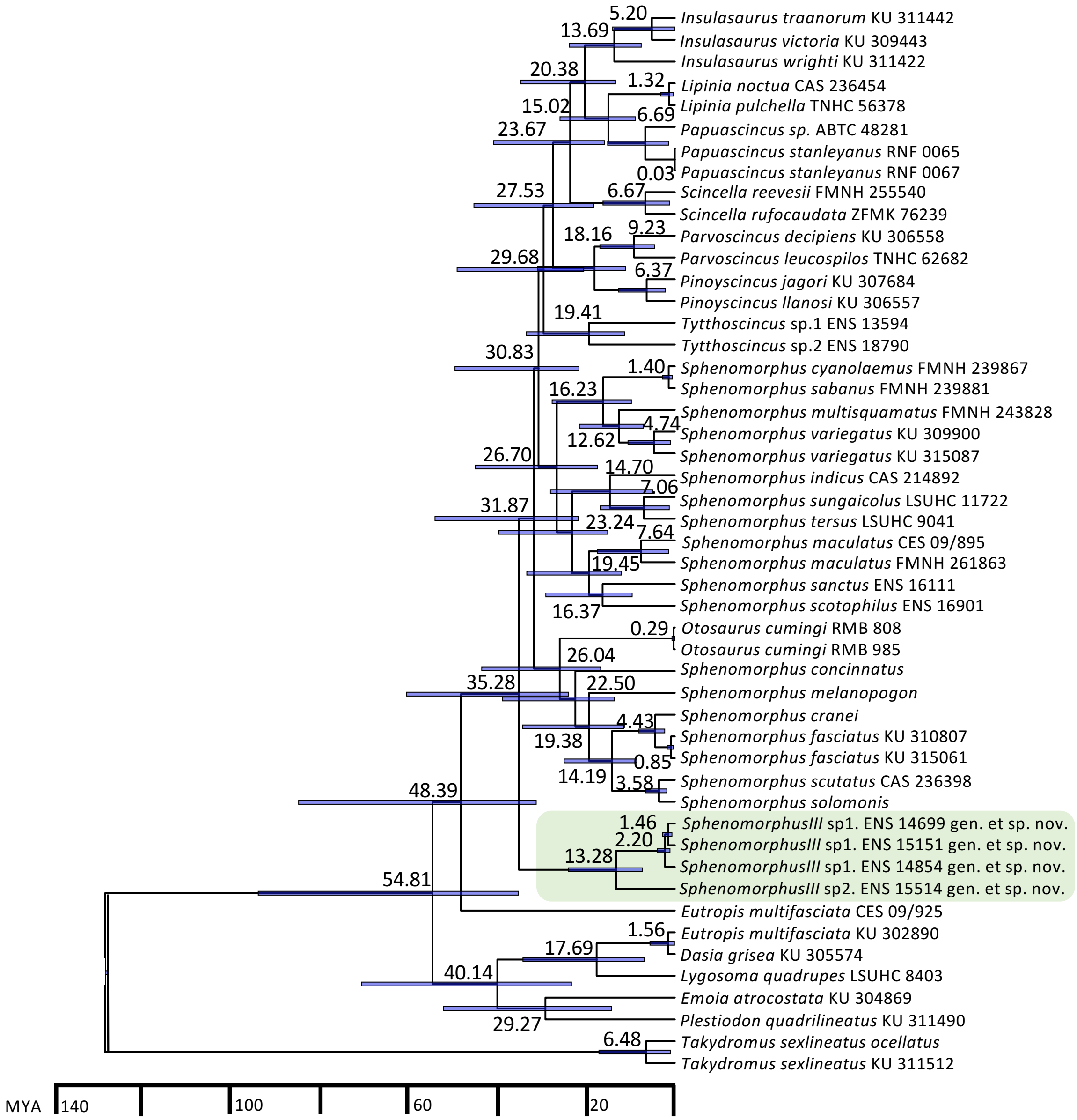
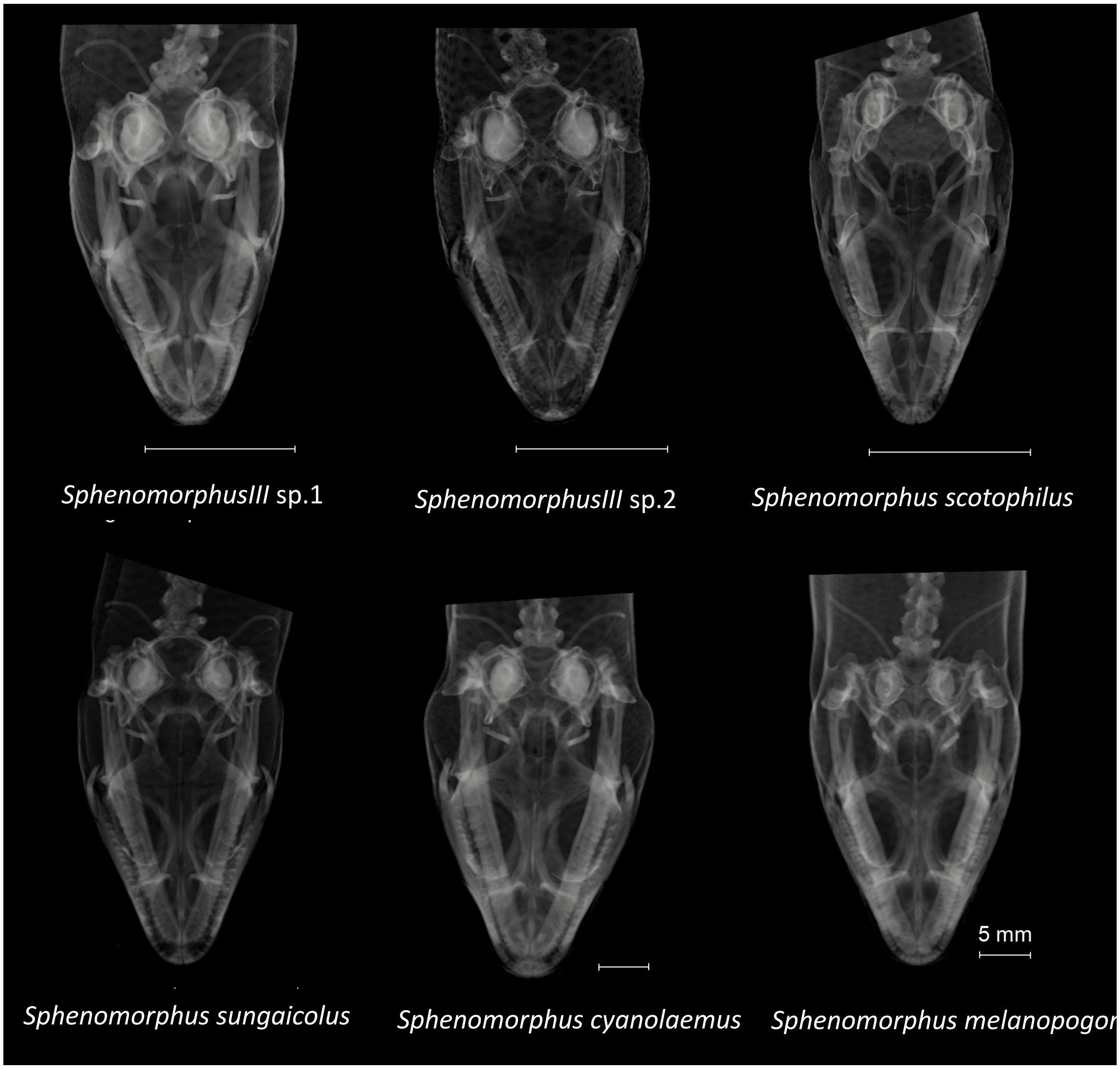


Figure 4.3 Time-calibrated Bayesian phylogeny of *Sphenomorphus* from the Sunda Shelf and neighboring areas. Nodal values are estimated divergence times.



SphenomorphusIII sp.1 *SphenomorphusIII* sp.2 *Sphenomorphus scotophilus*

Sphenomorphus sungaicolus *Sphenomorphus cyanolaemus* *Sphenomorphus melanopogo*

Figure 4.4 Dorsal aspect of the skull of *SphenomorphusIII* sp.1 (male holotype, MZB 14452; head length 10.29 mm), *S.III* sp.2 (male holotype, MZB 14453, head length 10.65 mm), *S. scotophilus* (male, MZB 14454; head length 8.64 mm), *S. sungaicolus* (female, UTA-R 63035, head length 11.20 mm), *S. cyanolaemus* (male, UTA-R 63040 head length 12.70 mm), and *S. melanopogon* (male, MZB 13253 head length 14.62 mm).

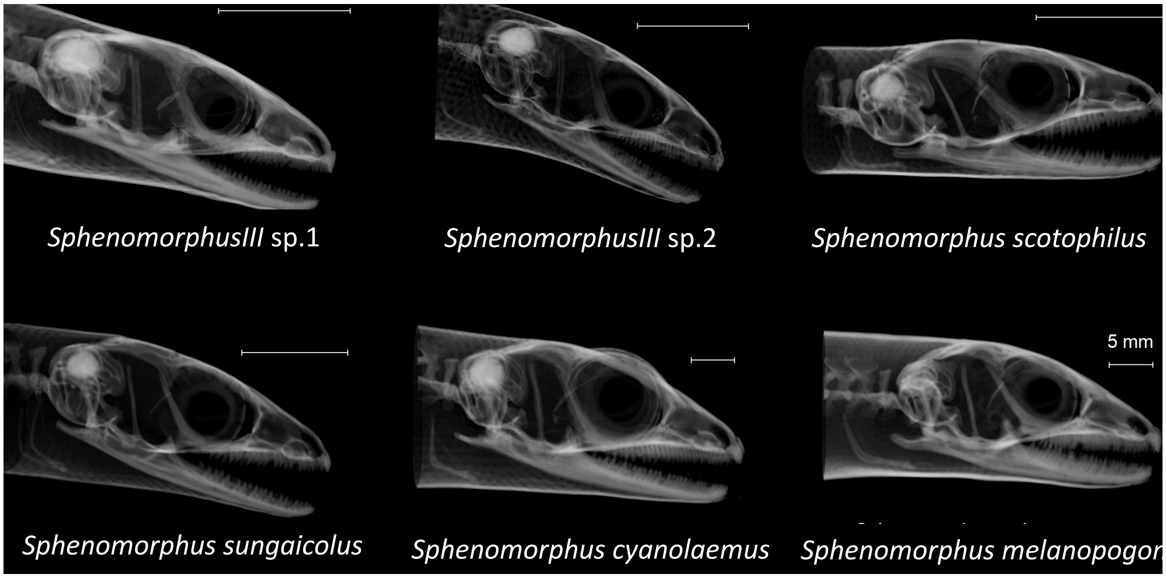


Figure 4.5 Lateral aspect of the skull of *SphenomorphusIII* sp.1 (male holotype, MZB 14452; head length 10.29 mm), *S.III* sp.2 (male holotype, MZB 14453, head length 10.65 mm), *S. scotophilus* (male, MZB 14454; head length 8.64 mm), *S. sungaicolus* (female, UTA-R 63035, head length 11.20 mm), *S. cyanolaemus* (male, UTA-R 63040, head length 12.70 mm), and *S. melanopogon* (male, MZB 13253, head length 14.62 mm).

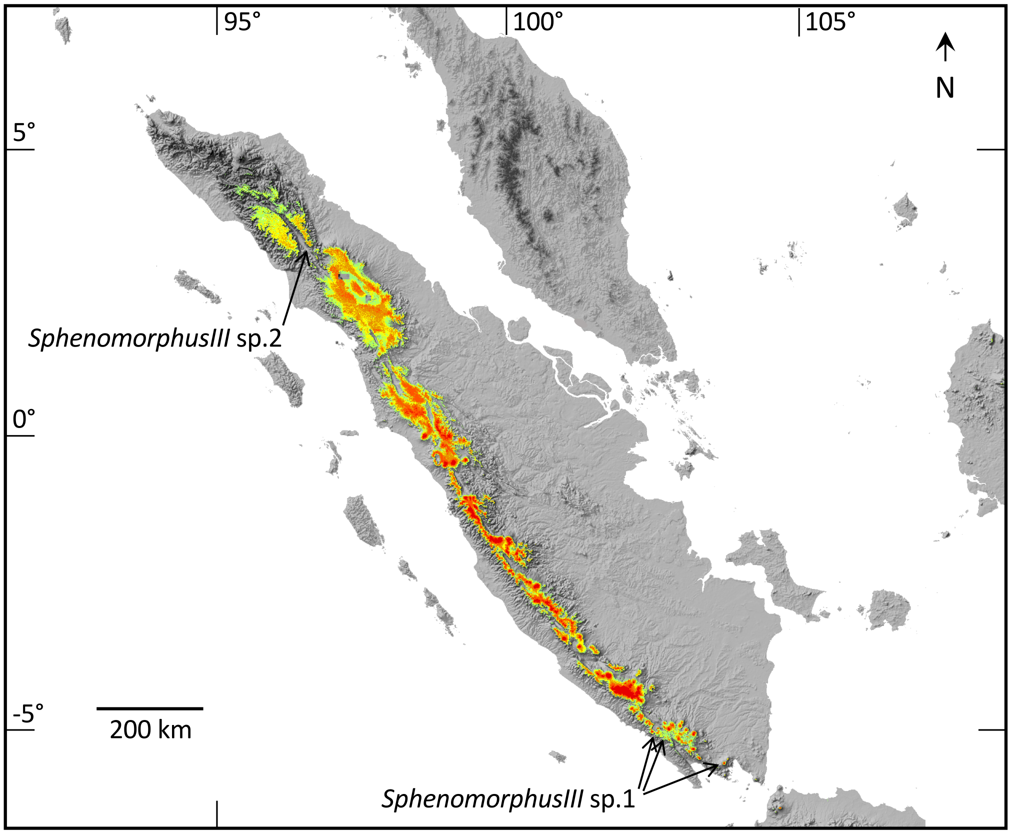


Figure 4.6 Suitable habitat for *SphenomorphusIII* identified by ecological niche modeling.

Figure 4.7 Adult male holotype of *SphenomorphusIII* sp. 1 (A, MZB 14452, SVL 54.26 mm from Mount of Pesawaran, Lampung Province, Lampung, Sumatra at 5.51563° S, 105.07667° E, 1055 m elevation; adult female paratype of *SphenomorphusIII* sp. 1 (B, UTA-R 64204, SVL 59.74 mm) from Maura Dua, Mount of Pesagi, South Sumatra, 4.90589° S, 104.13232° E, 1558 m; adult female paratype of *SphenomorphusIII* sp. 1 (C, UTA-R 64205, SVL 56.32 mm) from Ridge South of Lake Ranau, Lampung, Sumatra, 4.96599° S, 103.84954° E, 1087 m; female holotype of *SphenomorphusIII* sp. 2 (D, MZB 14453, SVL 53.45 mm) from highlands of Kecematan Berastagi, North Sumatra Province, Sumatra at 3.24521° N, 98.53438° E, 1271 m (photos by E. N. Smith).

Figure 4.8 Type series of the *SphenomorphusIII* from left to right: *S.* sp.1 holotype MZB 14452 (male, SVL 54.26 mm), paratype UTA-R 64204 (female), paratype UTA-R 64205 (female), and *S.* sp.2 holotype MZB 14453 (female).

Figure 4.9 Habitats of *SphenomorphusIII*: Mount of Pesawaran, Lampung, Sumatra, locality for MZB 14452 holotype (A), ridge of Lake Ranua, Lampung, Sumatra locality for UTA-R 64204 paratype (B), montane forest on Mount of Pesagi, South Sumatra for UTA-R 64205 paratype (C), forest near Brestagi covered by ash caused by the 2014 eruption of Mount Sinabung, North Sumatra for MZB 14453 holotype (D).

Chapter 5

General Conclusion

The Sunda Shelf has been considered a biological hotspot, however, the diversity of squamate reptiles in these area is still underestimated, especially regarding Scincid lizards—skinks. This study used integrated approaches to examine the systematics of skinks in Java and Sumatra, not only a classical taxonomy morphological approach but, also genetic and ecological approaches. Several groups of skinks in this area in need of taxonomic investigation but, each group faces singular taxonomic problems, so each group has been studied with different integrated methods. This study focused on three groups of skinks: first, the common sun skinks of the *Eutropis multifasciata* complex, which known as one of the largest distributed land-animals; second, the diminutive leaf-litter skinks in the genus *Tytthoscincus,* previously believed to be represented by a single species in this area; and third, the common forest skinks, *Sphenomorphus,* a genus known as a taxonomic waste bin for forest skinks in Java and Sumatra.

For the systematic revision of the common sun skinks *Eutropis multifasciata* complex I used several approaches including, phylogenetic analyses using single locus—gene trees, concatenated mitochondrial and nuclear loci, multi-locus coalescent species trees, genetic distance comparisons; morphometric-multivariate comparisons using discriminant functional analyses; and molecular species delimitation using mPTP and ABGD methods. The results indicated that the *E. multifasciata* complex can be divided into four valid full species, *E.*

balinensis, E. multifasciata, E. sikkimensis and *E. tjendikianensis*. However, limited sampling suggests the need for future genetic and morphological studies including more samples, from pertinent type localities and including a broader sampling of the geographic ranges of the species, particularly of *E. baliensis* and *E. tjendikianensis*. More sampling from mainland Southeast Asia, the Isthmus of Kra, Kalimantan (Borneo), Sulawesi, the Philippines, Wallacea, the Lesser Sundas, and Papua is necessary and might reveal cryptic species.

For the systematic revision of the diminutive Asian skinks in the genus *Tytthoscincus*, I also used multiple approaches including, external morphology compared across all *Tytthoscincus* and sympatric *Sphenomorphus* in the Sunda Shelf. Then I used a concatenated phylogenetic approach, genetic distances, and ecological niche modeling to examine species ranges and allopatry among populations. The results indicated that *S. necopinatus* and *S. vaheuni* belong in *Tytthoscincus* and considered their proposed subspecies of be species, *T. garutense* and *T. balicus,* base on distinctive morphological characters and also geographic separation. *Tytthoscincus temmincki* appears not to be composed of a single species, as considered today, as different populations are not resolved as monophyletic. In addition, I am also describing two new species of *Tytthoscincus* from Aceh, Sumatra and East Java. The new species from East Java is superficially similar to *T. vanheuni*, sister species, and niche modeling indicates geographic separation between the two. This work exemplifies the importance of using ecological data in conjunction with classical taxonomy, particularly when genetic material is not available. The new species from Aceh is superficially similar to *T. jaripendek* and *T. kakikercil* from the Malay Peninsula but, the phylogenetic results find these three species not to represent a monophyletic group. This results indicates possible convergent evolution of a trait, which might lead to a taxonomic misinterpretation of relatedness if using only external morphology. For futher study, I suggest to include more genetic material from pertinent type localities and to carefully interpret morphological characters.

For the systematic revision of the forest skinks in the genus *Sphenomorphus,* I used an integrative approach including, external morphology, concatenated mitochondrial and nuclear loci and genetic and morphology phylogenetics, and ecological niche modeling for species of *Sphenomorphus* in Java and Sumatra. The phylogenetic results indicate that *Sphenomophus* is paraphyletic, and that *S. malayanum* and *S. modigliani* need to be transferred to *Tytthoscincus*. From the three clades of *Sphenomorphus* depicted, one of them is morphologically and genetically distinct from typical *Sphenomorphus*. Therefore, I am describing this clade as a new genus with two new species from Sumatra. Although these two new species are superficially similar to *S. cameronicus* in the Malay Peninsula they differ in scalation. I also suggest to include *S. cameronicus* in the new genus. I examined the skull anatomy of the new species and *Sphenomorphus* to confirm the anatomical distinctiveness of the new genus. Also, a time calibrated phylogeny was used to examine the likelihood of divergece between the new genus and other *Sphenomorphus* in Java and Sumatra. Finally, I used ecological niche modeling to estimate the distribution of the new genus, and this indicated a possible highland range in Sumatra, along the Barisan mountain range. One species occurs in northern of Sumatra, the other, in southern of Sumatra. The niche modeling indicates the distribution of potential new species in most of Sumatra, particularly in the central region. For further study, I suggest to include more genetic material from pertinent type localities, including *S. cameronicus,* to confirm our generic placement. I also suggest to revisit taxonomically other species groups of

Sphenomorphus, since this genus appears to be paraphyletic and few species have been included in any analysis. Genetic material of *S. melanopogon,* the type species of the genus, is necessary from topotypic material, to confirm the identity of the clade belonging to true *Sphenomorphus,* the other clade necessitating a new generic dessignation.

In summary, using an integrated approach to study the systematics of Scincid lizards in Java and Sumatra will reduce overestimating or underestimating diversity, as compared to single approach techniques. This integrated approach study discovered more species diversity of Scincid lizards in the Sunda Shelf and adjacent areas. The taxonomic revision of Scincid lizards in this area still needs to continue, and I hope that this study can shed light on an impressive but hidden squamate diversity and can lead to more educated conservation efforts.

Biographical Information

Doctor Panupong Thammachoti was born in Bangkok Thailand. His parents are Mr. Pairat Thammachoti and Mrs. Sopit Thammachoti. He got a bachelor degree in Biology (2nd class honors) from Chulalongkorn University in 2009 and got a masters degree in Zoology from the same university in 2012. His projects were on Ecology and Morphology of amphibians. Both projects were supervised by Dr. Noppadon Kitana. In that time, he got a "Science Achievement of Thailand" scholarship from the Thai Ministry of Education. Accordingly, he is committed to be an academic in Thailand, after graduation.

Doctor Thammachoti started his doctoral degree in Quantitative Biology, Ecology and Evolution track, at the University of Texas at Arlington in 2013, supervised by Dr. Eric N. Smith. During his time as a Ph.D. student at UTA, he was interested in the systematics of reptiles and amphibians of Southeast Asia, particularly those of the Sunda Shelf. Consequently, he has been preparing chapters of his dissertation as manuscripts related to the systematics of skinks in the Sunda Shelf. He has also attended several international conferences and obtained awards for his presentations. Doctor Thammachoti also has participated in several herpetological expeditions with his advisor and colleagues, exploring Java and Sumatra. With his passion for herpetological research, he is an asset for the future of Herpetology in Thailand and Southeast Asia.