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A new *Liopeltis* Fitzinger, 1843 (Squamata: Colubridae) from Pulau Tioman, Peninsular Malaysia

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Abstract

Liopeltis is a genus of poorly known, infrequently sampled species of colubrid snakes in tropical Asia. We collected a specimen of *Liopeltis* from Pulau Tioman, Peninsular Malaysia, that superficially resembled *L. philippina*, a rare species that is endemic to the Palawan Pleistocene Aggregate Island Complex, western Philippines. We analyzed morphological and mitochondrial DNA sequence data from the Pulau Tioman specimen and found distinct differences to *L. philippina* and all other congeners. On the basis of these corroborated lines of evidence, the Pulau Tioman specimen is described as a new species, *L. tiomanica* sp. nov. The new species occurs in sympatry with *L. tricolor* on Pulau Tioman, and our description of *L. tiomanica* sp. nov. brings the number of endemic amphibians and reptiles on Pulau Tioman to 12.

Key words: *Liopeltis philippina*, *Liopeltis tricolor*, Palawan; taxonomy

Introduction

The genus *Liopeltis* Fitzinger, 1843 contains seven described species (Günther 1858, 1860; Boettger 1897; Sclater 1891; Schlegel 1837; Smith 1943; Poyarkov *et al.* 2019). These diurnal yet secretive colubrid snakes are distributed throughout South and Southeast Asia, ranging from northwestern India to Vietnam, and off the mainland into the Sundaic and Philippine archipelagos. Species of *Liopeltis* are generally characterized as having long, flattened heads in lateral profile and 15 rows of smooth dorsal scales at midbody (Leviton 1964). Although most species of *Liopeltis* are infrequently encountered by herpetologists (Wall 1910; Shaw *et al.* 1940; Leviton 1964; Smith 1943), recent fieldwork has resulted in new records of two species from Thailand (Hauser 2018, 2019) and the description of a new species from Vietnam (Poyarkov *et al.* 2019).

Pulau Tioman (=Tioman Island) is an island of approximately 114 km² in the Seribuat Archipelago approximately 38 km east of the mainland of Peninsular Malaysia (Bullock & Medway 1966; Fig. 1). Since 1972, approximately 60% of the island's forested interior (8,296 hectares) has been protected as the Pulau Tioman Wildlife Reserve by the Pahang State government (Abdul 1999). Pulau Tioman has been the focus of numerous herpetological surveys in recent years and shown to harbor high levels of species diversity and endemism (Hendrickson 1966a,b; J. Grismer *et al.* 2004; Grismer *et al.* 2002, 2006; Grismer 2011). To date, 25 species of amphibians and 73 species of

reptiles are known to occur on Pulau Tioman, of which 11 are considered to be endemic to the island (Badli-Sham *et al.* 2019; J. Grismer *et al.* 2004; Grismer *et al.* 2006; Grismer 2011). *Liopeltis tricolor* (Schlegel 1837), described from its type locality of Java Island, Indonesia, is the only species of *Liopeltis* previously reported from Pulau Tioman (Hendrickson 1966a; Lim & Lim 1999; Grismer 2011; J. Grismer *et al.* 2004; Grismer *et al.* 2002, 2006).

During the course of fieldwork on Pulau Tioman in August 2002, three of us (LLG, JLG, and PLW) collected a single specimen of *Liopeltis* that was originally reported as *L. tricolor* (J. Grismer *et al.* 2004). Our recent re-examination of that specimen revealed that it more closely resembles *L. philippina* (Boettger 1897), a species that is considered to be endemic to the Palawan Pleistocene Aggregate Island Complex (PAIC) of the Philippines (Taylor 1922; Leviton 1964; Gaulke 1999; Leviton *et al.* 2018) approximately 1,750 air-km east of Pulau Tioman (Fig. 1). Boettger (1897) originally described *L. philippina* based on two syntypes from Culion and Samar Islands, Philippines, as a species having four longitudinal stripes on the dorsum, a faint stripe separating the head and chin coloration, 144–146 ventral scales, and 118 subcaudal scales. Leviton (1964) deemed the Samar Island locality of one of the syntypes to be in error, and restricted the type locality to Culion Island in the Palawan PAIC, Philippines.

In this paper, we investigate the taxonomic status of the Pulau Tioman specimen that superficially resembles *L. philippina*. We compare morphological and mitochondrial DNA sequence data from the specimen to its congeners, and based on distinct, diagnosable differences in both datasets, we describe the Pulau Tioman specimen as a new species.

Materials and methods

Sampling. The Pulau Tioman specimen was collected in the field and fixed in 10% buffered formalin after preserving liver in 95% ethanol. The specimen was later transferred to 70% ethanol for permanent storage and deposited in the La Sierra University Herpetological Collection (LSUHC) in Riverside, California. Comparative material was examined from the holdings of the Field Museum of Natural History (FMNH), Biodiversity Institute, University of Kansas (KU), California Academy of Sciences (CAS), and the Bernice P. Bishop Museum (BPBM; Appendix I). Data were also taken from the original (Boettger 1897) and expanded (Taylor 1922) descriptions of *L. philippina*.

Morphology. Head and body scales were counted using an ocular microscope. Head scale counts included number of internasal, prefrontal, loreal, preocular, postocular, supralabial, infralabial, frontal, parietal, anterior and posterior temporal, dorsal, ventral and subcaudal scales. Ventral scales were counted from the first ventral scale bordered by the first row of dorsal scales and ending with the ventral scale immediately anterior to the cloacal plate (Dowling 1951). Dorsal scales were counted at one head length posterior to the neck, at the midpoint of snout-vent length, and at one head length anterior to the cloacal plate. Paired subcaudals were counted from immediately posterior to the cloacal plate to the tail tip, excluding the terminal scute. Snout-vent, tail and total lengths were taken to the nearest millimeter using a soft measuring tape. Color terminology and codes follow Köhler (2012).

Mitochondrial DNA analyses. Total genomic DNA was extracted from muscle or liver samples of five individuals of *Liopeltis* and one individual of the outgroup *Gongylosoma scriptum* (Table 1) using the DNeasy Blood and Tissue Kit (Qiagen). A 1,143–1,151 bp fragment of mitochondrial DNA that encodes the complete cytochrome *b* gene and parts of the flanking tRNAs Glu and Thr (hereafter as cyt *b*) was amplified using the primers L14910 and H16064 (Burbrink *et al.* 2000). PCR products were cleaned using ExoSAP-IT and sequenced in both directions by direct double strand cycle sequencing using the BigDye Terminator version 3.1 Cycle Sequencing Kit and the amplifying primers on a 3130 DNA Analyzer (all products by Applied Biosystems). The internal primers L-872Liopelt.cytb (5'-CAAGCTTGGAGGAACCATAGC-3') and H-220Liopelt.cytb (5'-GTGCRATGTGGGT-GTAGATGC-3') were also used to sequence the *Liopeltis* samples. The internal primers L-770Liopelt.cytb (5'-CCCAGAAAACCTCTAAAAGC-3') and H-350Liopelt.cytb (5'-GCTCAGAATGATATTGTCC-3') were also used to sequence the *Gongylosoma* sample. Sequences were edited using Sequencher version 5.4.6 (Gene Codes) and deposited in GenBank under accession numbers MT090058–MT090063 (Table 1).

Homologous sequences of all available species of *Liopeltis* and a second outgroup *Sibynophis collaris* were downloaded from GenBank (Table 1). The phylogenetic position of *Liopeltis* within the Colubridae remains untested, however, *Gongylosoma* has been hypothesized to be closely related to *Liopeltis* on the basis of morphology (Leviton, 1964; Grismer *et al.* 2003; Poyarkov *et al.* 2019). *Sibynophis* was selected as a more distant outgroup

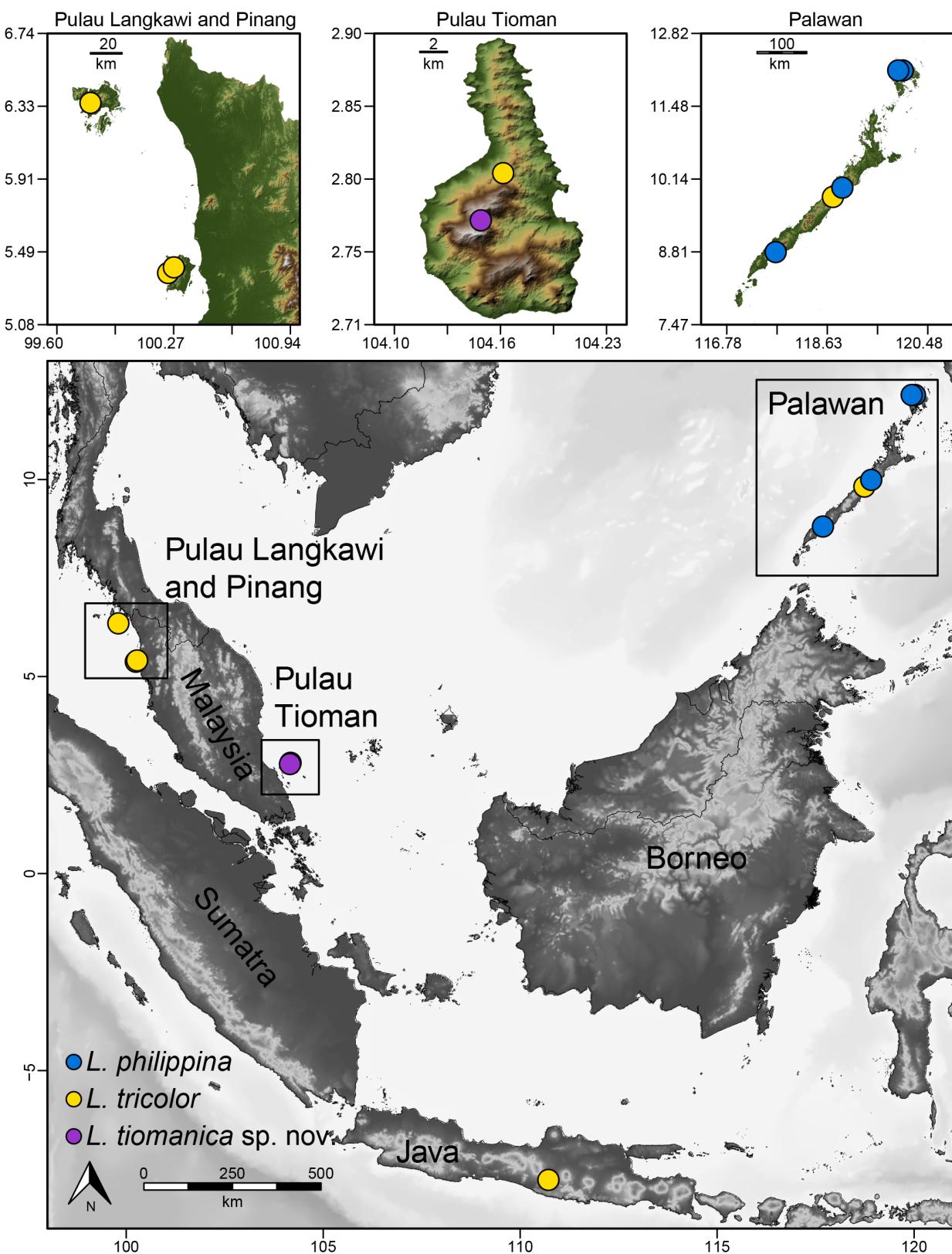


FIGURE 1. Map showing localities of material of *Liopeltis* examined in this study. The base map was generated using a global void filled grid obtained from the General Bathymetric Chart of the Oceans (GEBCO; <https://www.gebco.net>).

within the Colubridae. Newly generated and downloaded sequences were aligned using the default parameters in MAFFT version 7 (Katoh & Standley 2013) and then visually checked to ensure that insertion-deletions did not disrupt translation of the cyt b coding region. The alignment contained 1,152 characters, and was partitioned by cyt b codon position and tRNA (four partitions total). The best-fit partitioning scheme and models of sequence evolution were selected using PartitionFinder 2 (Lanfear *et al.* 2017). All four partitions were selected for use in the analysis, with the models TRN+G, TVM+G, GTR+I+G, and TIM+G selected for the tRNA, first, second, and third codon position partitions, respectively. Four independent Bayesian analyses were performed using MrBayes 3.2.6 (Ronquist *et al.* 2012) on the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway version 3.3 (Miller *et al.* 2010). In each analysis, four chains were run for 20 million generations using the default priors, the chain temperature was set to 0.1, trees were sampled every 4,000 generations, and the first 25% of trees were discarded as ‘burn-in.’ The resulting trace plots were viewed using Tracer v.1.7 (Rambaut *et al.* 2018). A 50% majority-rule consensus of the post burn-in trees was constructed to calculate the posterior probabilities of nodes. Nodes with posterior probabilities ≥ 0.95 were considered to be statistically supported. Uncorrected pairwise (*p*) distances were calculated using PAUP* version 4.0a165 (Swofford 2003).

TABLE 1. Mitochondrial cytochrome *b* (cyt *b*) gene sequences of *Gongylosoma*, *Liopeltis*, and *Sibynophis* used in this study. Museum abbreviations follow Sabaj (2016), with the addition of DTU = Duy Tan University, Da Nang, Vietnam and JK= Ke Jiang’s field number.

| Species | Voucher | Locality | GenBank | Source |
|------------------------------|--------------|---|----------|-----------------------------|
| <i>G. scriptum</i> | NCSM 99033 | Cambodia, Kampot Prov., Teuk Chou | MT090063 | This study |
| <i>L. frenata</i> | CAS 225548 | Myanmar, Kachin State, Putao | KX660457 | Figueroa <i>et al.</i> 2016 |
| <i>L. tiomanica</i> sp. nov. | LSUHC 5037 | Peninsular Malaysia, Pahang State, Pulau Tioman | MT090059 | This study |
| <i>L. pallidonuchalis</i> | ZMMU R-15682 | Vietnam, Gia Lai Prov., Kon Chu Rang | MK639008 | Poyarkov <i>et al.</i> 2019 |
| <i>L. pallidonuchalis</i> | DTU 307 | Vietnam, Thua Thien-Hue Prov., Bach Ma | MK639009 | Poyarkov <i>et al.</i> 2019 |
| <i>L. philippina</i> | KU 327731 | Philippines, Palawan Prov., Palawan Island | MT090058 | This study |
| <i>L. stoliczkae</i> | JK 201703 | China, Yunnan Prov., Xishuangbanna Dai | MK201562 | GenBank |
| <i>L. tricolor</i> | LSUHC 11579 | Peninsular Malaysia, Kedah State, Pulau Langkawi | MT090060 | This study |
| <i>L. tricolor</i> | LSUHC 14375 | Peninsular Malaysia, Penang State, Pulau Pinang | MT090061 | This study |
| <i>L. tricolor</i> | LSUHC 14383 | Peninsular Malaysia, Penang State, Pulau Pinang | MT090062 | This study |
| <i>S. collaris</i> | Not given | South Korea, Jeju Island, Hankyung- Myeon | JN211315 | Jang & Hwang 2011 |

Results

Liopeltis tiomanica sp. nov.

Liopeltis tricolor (part): J.L. Grismer *et al.* 2004: 275; Grismer 2011: 203.

Liopeltis tricolour [sic] (part): Grismer *et al.* 2006: 178.

Holotype. LSUHC 5037, adult female (Figs. 2–4), Peninsular Malaysia, Pahang State, Pulau Tioman (= Tioman Island), Gunung Kajang trail, 2.77900°N 104.15703°E (Datum WGS84), 618 m elev., coll. 11 August 2002 by Jesse L. Grismer, Perry L. Wood, Jr., and L. Lee Grismer.

Etymology. The specific epithet refers to the new species’ type and only known locality on the island of Pulau Tioman. The specific epithet is feminine, in agreement with the gender of the genus (Poyarkov *et al.* 2019).

Diagnosis. A species of *Liopeltis* having the combination of the nasal scale fused with the internasal scale; preoculars two; ventrals 161; distinct black lateral cephalic stripe extending from rostral through eye to approximately 30 mm behind neck before fading; four longitudinal stripes on dorsum; and venter immaculate, without stripes.

Description of holotype (Figs. 2–3). Adult female; head slightly distinct from neck, triangular in dorsal view; snout weakly pointed in lateral view, projecting beyond lower jaw; eye large, pupil round; body slender; tail thin. Rostral wide, clearly visible from above; nasal partially divided, portion anterior to nostril continuous with internasal, portion posterior to nostril with horizontal suture; loreal absent; two preoculars, upper rectangular, approximately 25% size of lower, trapezoidal preocular; two postoculars, squarish or rounded, upper scale slightly larger than lower scale; eight supralabials, 4th and 5th in contact with eye, 2nd–4th in contact with lower preocular, 5th (right side) and 5th–6th (left side) in contact with lower postocular, 7th largest; eight infralabials, 5th largest; one elongate anterior temporal; two subequal posterior temporals, shorter than anterior temporal; two internasals; two prefrontals; single frontal, approximately 63% length of parietals, with one supraocular on each side; two large, elongate parietals; anterior pair and posterior pairs of chin shields subequal in length, anterior pair broader; dorsal scales smooth, in rows 15:15:13, apical pits absent; 161 ventrals; cloacal plate divided; 119 paired subcaudals. Scale counts are summarized in Table 2.

TABLE 2. Morphological characters of *Liopeltis tiomanica* sp. nov. from Pulau Tioman, Peninsular Malaysia, and its sister taxon *L. philippina* from the Palawan Pleistocene Aggregate Island Complex (PAIC) of the western Philippines.

| | <i>tiomanica</i> sp. nov | <i>philippina</i> | <i>philippina</i> | <i>philippina</i> | <i>philippina</i> |
|--------------------|--|---|--|---|-------------------|
| | Holotype female | Male | Female | Male | Male |
| | LSUHC 5037 | FMNH 53372 | CAS 15284 | KU 327731 | BoS 940* |
| Internasals | 2, fused to nasal | 2, fused to nasal | 2, fused to nasal | 2, fused to nasal | 2, fused to nasal |
| Prefrontals | 2 | 2 | 2 | 2 | 2 |
| Frontal | 1 | 1 | 1 | 1 | 1 |
| Parietals | 2 | 2 | 2 | 2 | 2 |
| Temporals | 1+2 | 1+2 | 1+2 | 1+2 | 1+2 |
| Loreal | Absent, prefrontal in contact with supralabial 2 | Absent, prefrontal in contact with supralabials 2–3 | Absent, prefrontal in contact with supralabial 2 | Absent, prefrontal in contact with supralabials 2–3 | Absent |
| Preoculars | 2 | 1 | 1 | 1 | 1 |
| Postoculars | 2 | 2 | 2 | 2 | 2 |
| Supralabials | 8 (4,5) | 8 (4,5) | 8 (4,5) | 8 (4,5) | 8 (4,5) |
| Infralabials | 8 | 8 | 8 | 8 | 8 |
| Dorsals | 15:15:13 | 15:15:13 | 15:15:13 | 15:15:13 | 15 |
| Ventrals | 161 | 139 | 150 | 142 | 140 |
| Subcaudals | 119 | 115 | 110 | 116 | 119 |
| Snout-vent (mm) | 304 | 308 | 341 | 258 | 390 |
| Tail (mm) | 187 | 220 | 186 | 175 | 250 |
| Total (mm) | 491 | 528 | 527 | 433 | 640 |

*Data from Taylor (1922: 164, “No. 940, Bureau of Science Collection;” specimen destroyed during World War II).

Color of holotype in life (Fig. 2). Dorsal surface of head bronze-brown (Grayish Horn Color 268); chin, supralabials, and infralabials cream (Cream White 52); black stripe on lateral side of head and neck separates dorsal and ventral coloration, stripe slightly wider than one dorsal scale, extending from rostral through eye to approximately 30 mm posterior to neck, gradually fading; dorsum bronze (Grayish Horn Color 268) with four longitudinal brown (Olive-Brown 278) stripes, two dorsal stripes extending from neck to tail, two lateral stripes extending from area posterior of black head stripe to level of cloacal plate; venter uniform pale cream color (Cream White 52) with small dark spots on ventral scales.



FIGURE 2. Holotype (LSUHC 5037) of *Liopeltis tiomanica* sp. nov. in life. Photograph by LLG.

Color of holotype in preservative (Fig. 3). Dorsum faded to grayish green (Olive Horn Color 16); dorsal stripes faded to light brown (Clay Color 18).

Molecular data. The standard deviation of split frequencies among the four Bayesian runs was 0.003717 and the Estimated Sample Sizes (ESS) of parameters were $\geq 3,390$. The holotype of *Liopeltis tiomanica* sp. nov. was recovered with strong support (Bayesian posterior probability 1.00) to be the sister taxon of *L. philippina* (Fig. 4). The *L. tiomanica* sp. nov. + *L. philippina* clade was recovered with strong support (Bayesian posterior probability 1.00) to be nested within a clade containing *L. tricolor* and *L. stoliczkae*, although the relationships among *L. tricolor*, *L. stoliczkae*, and the *L. tiomanica* sp. nov. + *L. philippina* clade were not resolved (Fig. 4). *Liopeltis tiomanica* sp. nov. had uncorrected *p*-distances in *cyt b* of 9.6% from *L. philippina* and 12.9–13.3% from *L. tricolor*.

Distribution, natural history, and conservation. *Liopeltis tiomanica* sp. nov. is known only from the holotype specimen collected from Pulau Tioman (Fig. 1). The specimen was found in the afternoon while perched on a small tree branch 2 m above the ground in primary hill dipterocarp forest (J. Grismer *et al.* 2004, Fig. 5).

Comparisons. *Liopeltis tiomanica* sp. nov. differs from all other species of *Liopeltis*, except its sister taxon *L. philippina* (Fig. 4), by having the nasal fused with the internasal and four longitudinal stripes on the dorsum (Weinell *et al.* 2019). *Liopeltis tiomanica* sp. nov. differs from *L. philippina* by having 161 ventral scales (vs. 139–150 in *L. philippina*); two preocular scales (vs. one in *L. philippina*); and a distinct black lateral cephalic stripe (vs. indistinct in *L. philippina*; Fig. 5). *Liopeltis tiomanica* sp. nov. further differs from the sympatric (and possibly syntopic) *L. tricolor* by having the prefrontal in contact only with the second supralabial (vs. second and third supralabials in *L. tricolor*); and immaculate ventral scales (vs. three gray ventral stripes in most *L. tricolor*). Scalation differences among these three species are summarized in Tables 2 and 3.

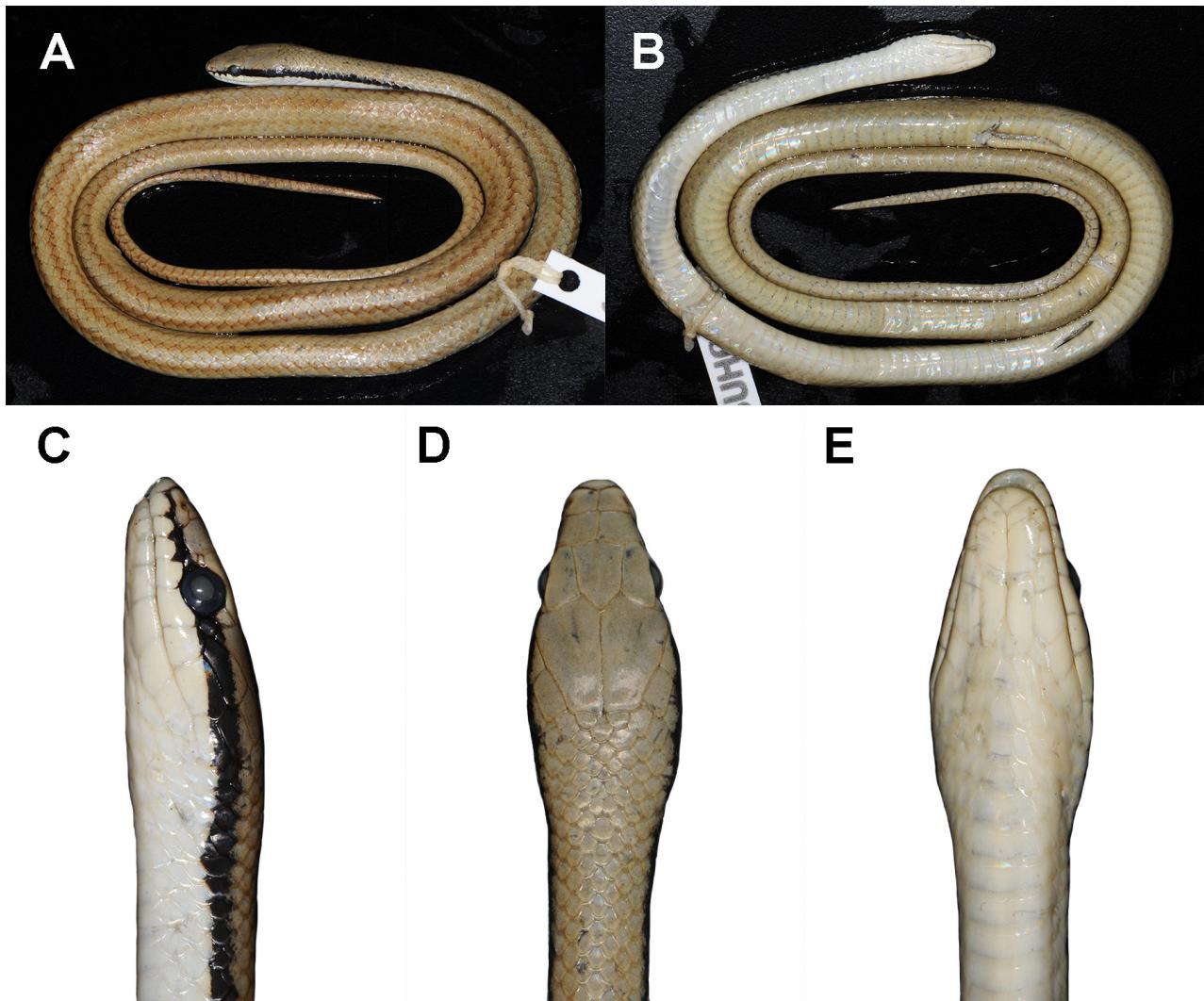


FIGURE 3. Holotype (LSUHC 5037) *Liopeltis tiomanica* sp. nov. in preservative. A. dorsal view of body. B. Ventral view of body. C. Lateral view of head. D. Dorsal view of head. E. Ventral view of head.

Discussion

Pulau Tioman is the largest, most ecologically diverse, and most thoroughly surveyed island for amphibians and reptiles in the Seribuat Archipelago of Peninsular Malaysia (Grismer 2011). The island supports surprisingly high herpetological diversity and endemism, in part due to its diversity in habitats (J. Grismer *et al.* 2004; Grismer *et al.* 2006; Grismer 2011) but also owing to its geographic position between the Peninsular Malaysia and Borneo; accordingly, the island supports populations of species with phylogenetic affinities to both regions (Grismer *et al.* 2006; Grismer 2011).

Two species of *Liopeltis* are now known to occur on Pulau Tioman. Hendrickson's (1966a) specimen of *L. tricolor* (now BPBM 7528; Appendix I) was collected at a lower (ca. 300 m) elevation approximately 3.8 air-km from the holotype of *L. tiomanica* sp. nov. As such, it is possible the two species occur in syntopy on Pulau Tioman. *Liopeltis tricolor* and *L. philippina* (the sister taxon of *L. tiomanica* sp. nov.; Fig. 4) do occur in syntopy on the islands of Calauit, Busuanga and Palawan in the Palawan PAIC, western Philippines (Leviton 1964; Leviton *et al.* 2018).

The description of *L. tiomanica* sp. nov. also brings the number of endemic amphibians and reptiles on Pulau Tioman to 12. These endemic species include three frogs, *Ansonia tiomanica* Hendrickson 1966b, *Kalophrynus tiomanensis* Chan, Grismer & Grismer 2011, and *Leptobrachella kajangensis* (L. Grismer, J. Grismer & Youmans 2004);

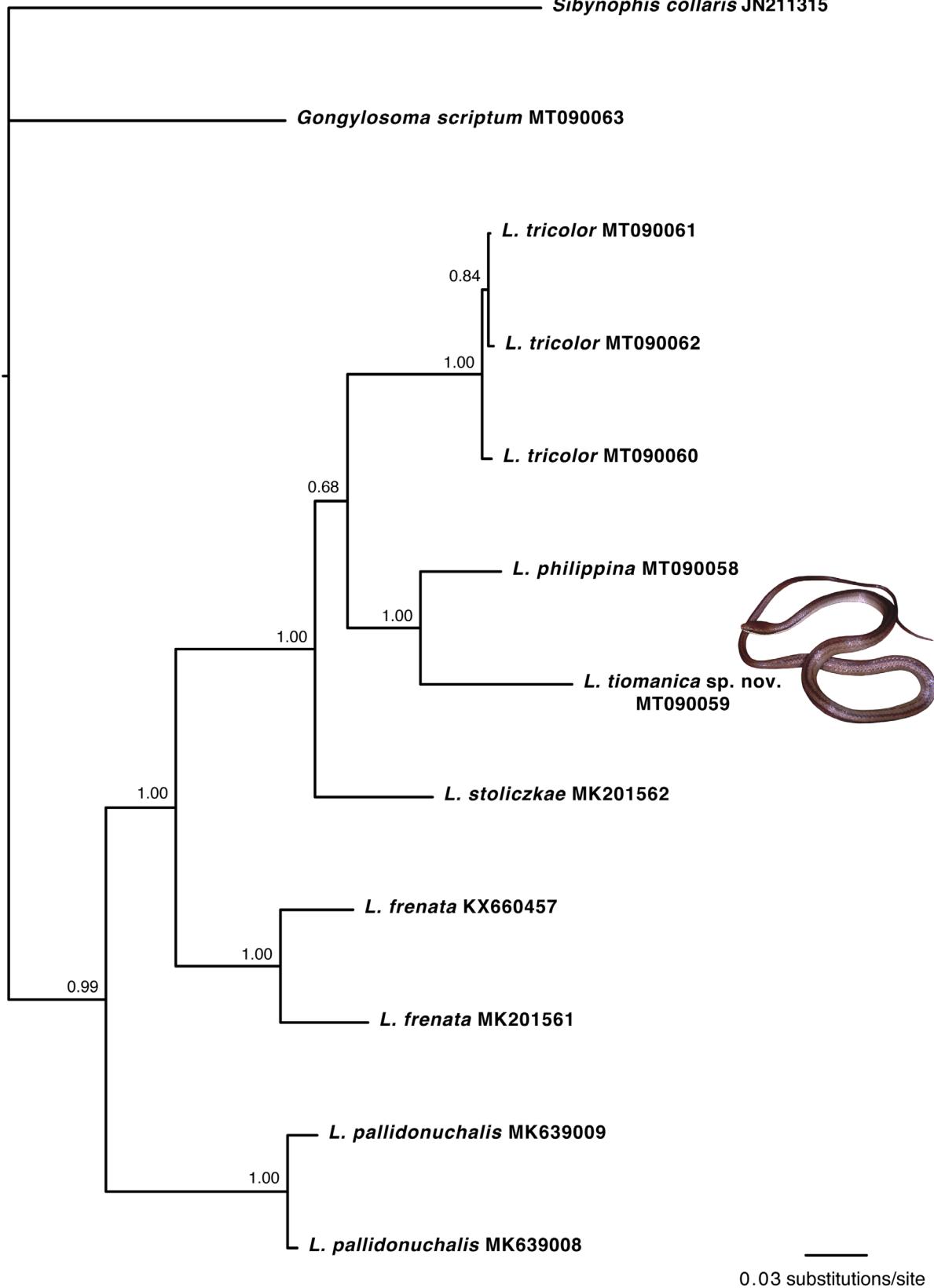


FIGURE 4. Fifty percent majority-rule consensus phylogram resulting from partitioned Bayesian analysis of 1,152 aligned characters of the complete mitochondrial cytochrome *b* gene and parts of its flanking tRNA genes from colubrid snakes of the genera *Liopeltis*, *Gongylotosoma* and *Sibynophis*. Numbers above nodes are Bayesian posterior probabilities. Numbers at terminal tips are GenBank accession numbers. Voucher and locality data for samples are provided in Table 2. The holotype of *Liopeltis tiomanica* sp. nov. in life is shown in the image.

TABLE 3. Morphological characters of *Liopeltis tricolor*, a species that occurs in sympatry with *L. tiomanica* sp. nov.

| | <i>tricolor</i> BPBM 7528 Male Pulau Tioman | <i>tricolor</i> FMNH 15054 Male Palawan | <i>tricolor</i> FMNH 72453 Male Java | <i>tricolor</i> LSUHC 14375 Male Pulau Pinang | <i>tricolor</i> LSUHC 14383 Female Pulau Pinang | <i>tricolor</i> LSUHC 11579 Female Pulau Langkawi |
|-----------------|---|---|---|---|---|--|
| Internasals | 2, separate from nasal |
| Prefrontals | 2 | 2 | 2 | 2 | 2 | 2 |
| Frontal | 1 | 1 | 1 | 1 | 1 | 1 |
| Parietals | 2 | 2 | 2 | 2 | 2 | 2 |
| Temporals | 1+2 | 1+2 | 1+2 | 1+2 | 1+2 | 1+2 |
| Loreal | Absent, prefrontal in contact with supralabials 2–3 |
| Preoculars | 1 | 1 | 1 | 1 | 1 | 1 |
| Postoculars | 2 | 2 | 2 | 2 | 2 | 2 |
| Supralabials | 8 (4,5) | 8 (4,5) | 8 (4,5) | 8 (4,5) | 8 (4,5) | 8 (4,5) |
| Infralabials | 7 | 8 | 8 | 7 | 7 | 7 |
| Dorsals | 15:15:13 | 15:15:13 | 15:15:13 | 15:15:13 | 15:15:13 | 15:15:13 |
| Ventrals | 157 | 148 | 149 | 152 | 159 | 154 |
| Subcaudals | 128 | 116 | 131 | 132 | 127 | 122 |
| Snout-vent (mm) | 328 | 301 | 275 | 239 | 312 | 280 |
| Tail (mm) | 207 | 174 | 172 | 161 | 189 | 164 |
| Total (mm) | 535 | 475 | 447 | 400 | 501 | 444 |

five lizards, *Dibamus tiomanensis* Diaz, Leong, Grismer & Yaakob 2004, *Cnemaspis limi* Das & Grismer 2003, *Cyrtodactylus tiomanensis* Das & Lim 2000, *Larutia seribuatensis* Grismer, Leong & Yaakob 2003, and *Tytthoscincus ishaki* Grismer 2006; and four colubrid snakes *Calamaria ingeri* Grismer, Kaiser & Yaakob 2004, *Gongylosoma mukutense* Grismer, Das & Leong 2003; *Oligodon booliati* Leong & Grismer 2004, and *L. tiomanica* sp. nov.

Unfortunately, Pulau Tioman is undergoing rapid economic development and increased levels of tourism that pose significant threats to wildlife on the island (Grismer *et al.* 2006; Grismer 2011). Despite comprehensive reviews by Grismer *et al.* (2006) and Grismer (2011), a more complete understanding of the species diversity of amphibians and reptiles, including population sizes and geographic distributions, is needed to generate informed management practices to mitigate loss of this biodiversity on Pulau Tioman (Grismer *et al.* 2006). Future field research on Pulau Tioman is likely to yield additional discoveries, potentially including more endemic species having unpredicted systematic and biogeographic affinities.

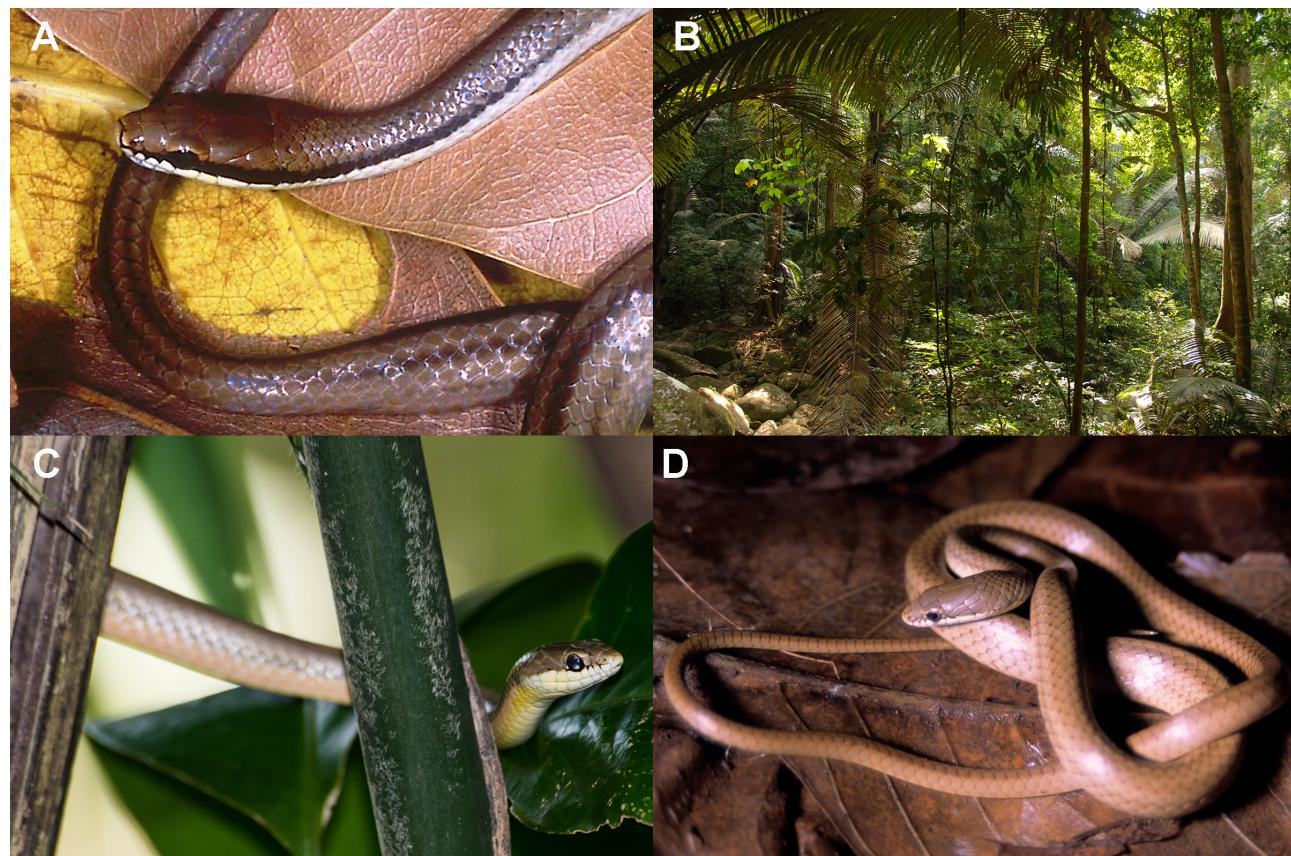


FIGURE 5. A. Holotype (LSUHC 5037) of *Liopeltis tiomanica* sp. nov. in life. Photograph by LLG. B. Primary hill dipterocarp forest near the type locality of *Liopeltis tiomanica* sp. nov. on Pulau Tioman, Pahang State, Peninsular Malaysia. Photograph by LLG. C. Unvouchered *L. philippina* from Salvacion, Busuanga Island, Calamianes Archipelago, Palawan Prov., Philippines (12.14378°N 119.93884°E), in life. Photograph by Shalom Pareja. D. Male *L. philippina* (KU 327731) from Mount Elyan in the Mantalingajan Mountain Range, Municipality of Brooke's Point, Palawan Island, Palawan Prov., Philippines, coll. 6 December 2001 by Arvin C. Diesmos, G. Gee, N. Antoque, M. L. Leonida, and J. C. Diesmos. Photograph by ACD. Note the distinct black lateral cephalic stripe in *L. tiomanica* sp. nov. that is absent in *L. philippina*.

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on *Liopeltis* taxonomy with Yodchaiy Chuaynkern, Nikolai Orlov, and Nikolay Poyarkov. This paper is contribution number 912 of the Auburn University Museum of Natural History.

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APPENDIX I. Comparative material examined. Localities are shown in Fig. 1.

Liopeltis tricolor—INDONESIA: FMNH 72453, Java, coll. March 1954 by R. Von Hentig. PENINSULAR MALAYSIA: Pahang State: BPBM 7528, Pulau Tioman [= Tioman Island], camp at Sungai Ayer Besar [= Ayer Besar Stream] on the trail between Tekek and Juara, ca. 300 m elev., fell from tree branch approximately 6 m above ground in tall primary forest, coll. 4 June 1958 by J.R. Hendrickson. Penang State, Pulau Pinang [= Penang Island]: LSUHC 14375, Bukit Ngoh Hean, coll. 28 April 2016 by Evan S.H. Quah; LSUHC 14383, Penang Hill, coll. 17 October 2017 by T.J. Low. Kedah State, Pulau Langkawi [=Langkawi Island]: LSUHC 11579, coll. 7 September 2013 by L.L. Grismer and Evan S.H. Quah. PHILIPPINES: Palawan Province: FMNH 15054, coll. March 1909 by W. Schultze.

Liopeltis philippina—PHILIPPINES: Palawan Province: CAS 15284, Busuanga Island, Calamianes Archipelago, coll. J.C. Thompson; FMNH 53372, Palawan Island, Puerto Princesa, Babuyan, ca. 0 m elev., coll. 21 March 1947; KU 327731, Municipality of Brooke's Point, Barangay Samariñana, Sitio Kamantian, Mount Elyan in the Mantalingajan Mountain Range, coll. 6 December 2001 by Arvin C. Diesmos, G. Gee, N. Antoque, M.L. Leonida, and J.C. Diesmos.