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A new species of *Tropidophorus* Duméril & Bibron, 1839 (Squamata: Sauria: Scincidae) from Sarawak, East Malaysia (Borneo)

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Abstract

A new species of the genus *Tropidophorus* is described from Putai, upper Baleh, Kapit districts, Sarawak, East Malaysia (Borneo). *Tropidophorus sebi* **sp. nov**. is diagnosable from congeners from Borneo by the combination of the following characters: head shields present, dorsal and lateral scales smooth; parietal scales in two pairs; supraciliaries eight; supraoculars four; supralabials seven; infralabials four; postmental undivided; longitudinal scale rows 58; ventrals 53; transverse scale rows at midbody 34; subcaudals 98; preanals enlarged, single; and subdigital lamellae of Toe IV 19. In addition, we determine the phylogenetic position of this species within the *Tropidophorus* group based on mitochondrial markers, and present a key to identification of the known Bornean species in the genus.

Key words: Borneo, new species, Scincidae, *Tropidophorus sebi* **sp. nov**.

Introduction

The water skink genus *Tropidophorus* Duméril & Bibron, 1839 (type species: *T. cocincinensis* Duméril & Bibron, 1839) is diagnosed by the exposure of the tympanum and presence of a single scale at the anterior and posterior corners of the eyelid (see Hikida *et al*. 2002; Greer & Biswas 2004). Remarkable amongst members of its family, these lizards are predominantly aquatic (Barbour 1921a; Bauer & Jackman 2008) and obligates of lowland forests. Currently, the genus comprises 28 nominal species that range from Bangladesh and north-eastern India, through mainland south-east Asia and southern China, southwards to Indo-China, the Malay Peninsula and Borneo, as well as the southern Philippines and Sulawesi (Brown & Alcala 1980; Honda *et al.* 2006; Ziegler *et al.* 2005; Nguyen *et al.* 2010a). On Borneo, six species of *Tropidophorus* have been recorded—*T. beccarii* Peters, 1871, *T. brookei* (Gray, 1845), *T. iniquus* van Lidth de Jeude, 1905, *T. micropus* van Lidth de Jeude, 1905, *T. mocquardii* Boulenger, 1894 and *T. perplexus* Barbour, 1921 (de Rooij 1915; Das 2004).

In this communication, we describe a new species of *Tropidophorus* from a previously unsurveyed site in central Sarawak, East Malaysia, in northern Borneo. We allocate this species to this nominal genus for showing the following characters that are currently associated with the genus (see Smith 1923, Mittleman 1952; Taylor 1963; Manthey & Grossmann 1997; Hikida *et al.* 2002; Greer & Biswas 2004), in addition to genetic data provided herein: lack of palatine teeth; limbs and eyelids well developed and moveable; lower eyelid scaly; supranasals absent; prefrontals well developed; frontoparietal distinct from interparietal; tympanum large and superficial; and 2–3 large preanals. The new *Tropidophorus* differs from congeners in a combination of size, colour pattern, body proportion and squamation characters. We define a species using the General Lineage Concept of de Queiroz (1998, 1999) as an extension of the Evolutionary Species Concept of Wiley (1978), in which phenotypically divergent populations represent distinct and separately evolving lineages. For the new *Tropidophorus*, we consider the possession of non-overlapping and diagnostic morphological characters relative to its Sundaic congeners to be indicative of speciation.

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Materials and methods

The type specimens were collected between 19–20 May 2015. Specimens were photographed in life, euthanized, fixed in formalin, and subsequently washed in water and transferred to 70% ethanol about a week after collection. Specimens were deposited at the Museum of the Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak. Sexes of the type specimens were determined through dissection. The following measurements were taken with Mitutoyo™ dial vernier callipers (to the nearest 0.1 mm) approximately two months after collection: snout–vent length (SVL, from snout tip to cloaca); tail length (TaL, from cloaca to tail tip); total length (TL, from snout tip to tail tip); head length (HL, distance between angle of jaws and snout-tip); head width (HW), measured across retroarticular process of the mandible; head depth (HD), greatest transverse depth of head, taken posterior of the orbital region; tibia length (TBL), distance between surface of knee to surface of heel, with the knee flexed; eye diameter (ED), horizontal diameter of the eyes-measured across the anterior and posterior margins of the palpebral margin; internarial distance (IN), distance between nostrils; eye–snout distance (E–S), distance between anteriormost point of eyes and tip of snout; eye–nostril distance (E–N), distance between anteriormost point of eyes and posterior-edge of nostrils; nostril–snout distance (N–S), distance between anteriormost point of nostril and tip of snout; axilla–groin distance (A–G), distance between posterior edge of forelimb at its insertion to body to anterior edge of hind limb at its insertion to body and body width (BW), greatest width of body. Scalation: nuchals (enlarged scales behind parietals); paravertebral scales (number of dorsal scales from posterior edge of parietals to a point above vent); ventrals in transverse rows (number of scales from first gular to precloacal scales), and scale rows at position of 10th subcaudal on tail including subcaudal.

Sources of data on character states and distribution include material in Appendix I as well as the following works: Barbour (1921b); Boulenger (1894); Bourret (2009); Bacon in Brown & Alcala (1980); Chuaynkern *et al.* (2005); Das (2004, 2010); de Rooij (1915); Fei *et al*. (2010); Guo *et al*. (2010); Hartmann *et al.* (2009); Hikida & Ota (1994); Hikida *et al.* (2002); Malkmus *et al.* (2002); Manthey & Grossmann (1997); Ngo *et al*. (2000); Nguyen *et al.* (2010a; 2010b); Rao *et al*. (2011); Smith (1919; 1923); Taylor (1963); van Lidth de Jeude (1905); Waiprom *et al.* (2013); Wen (1992); and Ziegler *et al.* (2005; 2007).

Museum abbreviations follow Sabaj (2016), except for the Lee Kong Chian Museum of Natural History (formerly, the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore) for which we use the acronym ZRC, following widespread usage; BM = Brunei Museum, Bandar Seri Begawan, Brunei Darussalam; BMNH = The Natural History Museum London; FMNH = Field Museum of Natural History, Chicago, U.S.A.; MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.; RMNH = Naturalis, the Nationaal Natuurhistorisch Museum, Leiden, the Netherlands; SBC = Sarawak Biodiversity Centre Museum, Jalan Semenggoh, Malaysia; SM = Sarawak Museum, Kuching, Malaysia; UBD = Museum of Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam; USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Genomic DNA was extracted as described in Aljanabi & Martinez (1997). Polymerase chain reactions (PCR) was performed on a Eppendorf Mastercycler nexus gradient thermocycler and PCR product was cleaned using a home-made magnetic bead solution (Rohland & Reich 2012). All PCR reactions began with an initial 2 min denaturation at 95°C, followed by 95°C for 35 s, annealing for 35 s at 50°C and extension at 72°C for 1 min 35 s for 34 cycles. Cycle sequencing was performed using Big Dye v3.1 chemistry, followed by an additional magnetic bead cleanup and analysis on an ABI3730xl. We sequenced the mitochondrial ribosomal 12s (395 bp) and ribosomal 16s (537 bp) genes for comparison with previously sequenced *Tropidophorus*. For amplifications of 12s, we used the primers L1019 (5'-AAAAAGCTTCAAACTGGGATTAGATACCCCACTAT-3') and H1478 (5'-TGACTGCAGAGGGTGACGGGCGGTGTGT-3') of Kocher *et al.* (1989) and for 16s we used the primers 16sbr-L (5'- CGCCTGTTTATCAAAAACAT-3') and 16sbr-H (5'- CCGGTCTGAACTCAGATCACGT-3') of Palumbi *et al.* (1991). All newly generated sequences are available on GenBank (GB Accession Numbers KY488450, KY488451, KY488452, KY488453, KY488454, KY488455, KY488456 and KY488457). DNA reads were manually checked and corrected for errors. Consensus sequences were aligned by eye to all *Tropidophorus* sequences available on GenBank: for 12s (AB028811, AB222933, AB222934, AB222935, AB222936, AB222937, AB222938, AB222939, AB222940, AB222941, AB222942, AB222943, AB222944, AB222945, AB222946, AB222947, AB222948, AY308473, AY308474) and for 16s (AB028823, AB222949, AB222950, AB222951, AB222952, AB222953, AB222954, AB222955, AB222956, AB222957, AB222958, AB222959, AB222960,

AB222961, AB222962, AB222963, AB222964, AY308322, AY308323, EF611186, GU550104, GU550105). These data were further aligned to the 12s and 16s genes from the existing dataset of *Sphenomorphus* group skinks of Linkem *et al.* (2011) downloaded from Dryad (http://datadryad.org/resource/doi:10.5061/dryad.30064) and trimmed to include a single specimen from each species. Pairwise sequence divergences were assessed using Geneious v9.0.4 (http://www.geneious.com, Kearse *et al.* 2012).

We concatenated the two genes and performed maximum likelihood (ML) and Bayesian inference (BI) phylogenetic analyses using RAxML v8.1.15 (Stamatakis 2006) and MrBayes v3.2.1 (Ronquist *et al*. 2012). For each analysis, we determined the optimal partitioning scheme using PartitionFinder v.1.1.1 (Lanfear *et al*. 2012), with the BIC and greedy algorithm supporting separate partitions for each mitochondrial gene and the GTR+I+G evolutionary model in both partitions. For the maximum likelihood analysis, we ran RAxML with both partitions under the GTRCAT model of evolution with 1000 rapid bootstrap replicates. For Bayesian inference, we ran the Markov Chain Monte Carlo in MrBayes for 20 million generations for two runs with four chains each, specifying the GTR+I+G model for both gene partitions. We assessed adequate burn-in of the Markov Chains in Tracer v1.6 (Rambaut & Drummond 2013) by eye and by ensuring all ESS values were greater than 200.

Systematics

Tropidophorus sebi sp. nov.

(Figs. 1–2)

Holotype. Museum of the Institute of Biodiversity and Environmental Conservation, UNIMAS P1167, from a small stream located at the First Count Logging Camp (01.35.644°N; 113.47.377°E; datum WGS84), Putai, upper Baleh, Kapit district, Sarawak, East Malaysia (Borneo), altitude 117 m ASL, coll. Pui Yong Min and Mohamad Paisal bin Wahab, 19 May 2015. Adult female. The type locality is shown in Fig. 3.

Paratype. UNIMAS P1166, same locality as holotype. Collected 20 May 2015. Adult female.

Diagnosis. A large-sized (SVL 83.8 mm and 85.9 mm in the two specimens known, both adult females); upper head shields, dorsal and lateral scales smooth; parietal scales in two pairs; presuboculars three; supraciliaries eight, first largest; supraoculars four, fourth contacting orbit; supralabials seven (supralabial five contacting orbit); infralabials four, second longest; postmental undivided; longitudinal scale rows 58; ventrals 53; transverse scale rows at midbody 34; subcaudals 98; preanals enlarged, single; and subdigital lamellae on Toe IV 19.

Etymology. The species name, *sebi* derives from the acronym 'SEB', for Sarawak Energy Berhad, with a genitive ending. We are pleased to name the new species after this organisation in acknowledgement of support received for our long-term research of the herpetofauna of the Upper Baleh region. Suggested common name: Baleh Water Skink.

Description of holotype. Adult female. Large size, SVL 83.8 mm, TL 121.4 mm; snout acute (IN:IO ratio 0.37), projecting beyond lower jaws; nostril laterally oriented; oval, situated closer to snout-tip than to orbit; eye–nostril distance 4.83 mm, eye–snout distance 6.58 mm (E-N:E-S ratio 0.73); head long, much longer than wide, HL 13.60 mm, HW 12.48 mm (HL:HW ratio 1.09); head shape slightly flattened, HD 8.91 mm (HL:HD ratio 1.53); upper head shields smooth; supranasals absent; frontonasal trapezoidal, as long as wide; prefrontals trapezoidal, in narrow contact medially; frontal elongated, trapezoidal, wider anteriorly; frontoparietals joined; interparietal single, with small transparent spot; parietal scales in two pairs; large posterior parietals, in contact posteriorly; small anterior parietal, in contact with frontoparietal and supraocular IV; nuchal scales in two pairs; nostrils on nasal located closer to anterior loreal; postnasal absent; supranasals absent; loreals two, anterior lower than posterior; preoculars two; presuboculars three, anterior large, second in contact with third and fourth supralabials, and third in contact with fourth and fifth supralabials; supraciliaries eight, first largest; supraoculars four, fourth contacting orbit; postsupraocular present; two postocular; pretemporal single; six postsuboculars, lower one contact with fifth and sixth supralabials; six primary temporals, lower one in contact with sixth and seventh supralabials; five secondary temporals; seven supralabials (supralabial five contacting orbit); four infralabials, second longest; mental smaller than rostral; rostral broad, projecting onto snout; posterior border of rostral straight; postmental undivided; genials in three pairs, first and second pair in broad contact, and third pair separated by three scales; auricular opening scaleless, ovoid and smaller than orbit of eye, its location indicated by a shallow

depression; eyes relatively small; pupil discernable in preserved specimen; moveable eyelids; upper palpebrals 14; lower palpebrals 14; tongue short; undivided anteriorly, tip obtuse, not pointed; teeth relatively small and somewhat pointed.

Body slender, BW 12.52 mm (BW:SVL ratio 0.15); head distinct from neck and body; 58 longitudinal scale rows from parietal to above level of anterior margin of hind limb; dorsal and lateral scales smooth; ventrals 53, counted from first postgular to last scale before preanals; transverse scale rows at midbody 34; subcaudals 98; preanals enlarged, single; tail laterally compressed, relatively long, longer than snout-vent length (TL:SVL ratio 1.45); tail tip acute; tail base wider than rest of tail; tail gradually tapering to a point; median row of subcaudals enlarged. Visceral fat bodies absent in abdomen.

Limbs short and pentadactyl, digits short and clawed; lamellae smooth, enlarged; adpressed limbs touching; lamellae under Finger I-8; II-12; III-11; IV-9; V-5 and lamellae under Toe I-7; II-11; III-15; IV-19; V-12.

FIGURE 1. Female holotype of *Tropidophorus sebi* **sp. nov**. (UNIMAS P1167) in life. (SVL = 83.8 mm).

Colouration in life. Dorsum chocolate brown, with dark greyish-brown transverse bars on trunk and tail; bars on nape fused to form collar-like pattern; blackish-grey postocular band, starting from posterior corner of orbit and broadening to axillary region, and narrowing thereafter along the flanks of torsi; forehead unpatterned chocolate brown; temporal region grey with cream-coloured flecks; axilla and lower flanks with scattered yellow flecks; labials brown with greyish-black bars; dorsal surface of tail greyish-brown with darker areas forming incomplete bands; dorsal surface of fore- and hindlimbs chocolate brown with darker variegation; digits brown with darker bands; gular region pale grey, the chin with dark grey variegation, forming about 10 lines that extend to the pectoral region; upper two-thirds of pectoral region pale yellow with indistinct grey stripes; lower third orange, each scale edged with yellow; cloacal region deep orange; lowest edge of anal scale dark grey; tail base grey with large, orange-coloured scales; rest of tail dark grey; lower parts of forearm unpatterned pale grey; hindlimbs unpatterned pale orange; manus and pes dark grey; pupil rounded, black, with a narrow, orange ring; iris grey with an orange cast; oral cavity pale cream-coloured; tongue dark grey, not pale apically.

Measurements (in millimeters; holotype with paratype, in parentheses). SVL 83.8 (85.9); HL 13.6 (14.7); HW 12.5 (13.6); HD 8.9 (9.8); BW 12.5 (13.5); TBL 11.3 (11.9); ED 4.1 (4.3); IN 3.1 (3.2); E–S 6.9 (6.9); E–N 4.8 (5.3); N–S 1.7 (1.7); A–G 36.7 (41.5) and TL 121.4 (87.2).

Squamation (holotype with paratype in parentheses). Transverse scale rows at midbody 34 (33); longitudinal scale rows 58 (57); ventral scale rows 53 (53); supralabials 7 (7); infralabials 4 (4); subcaudals 98 (22 +; regenerated tail) and lamellae under toe IV 19 (19).

FIGURE 2. Female holotype of *Tropidophorus sebi* **sp. nov**. (UNIMAS P1167), showing head in a. lateral; b. ventral; and c. dorsal views (scale markers = 10 mm); and d. pes and e. manus. (scale markers = 1 mm).

Ecological Notes and Distribution. The type series was collected from narrow crevices of rocky banks of small streams at the headwaters of Sungei Baleh. Currently, the new species is only known from its type locality, Putai, Upper Baleh, central Sarawak (Fig. 4).

Phylogenetic relationships. The ML and BI topologies were identical with respect to relationships within *Tropidophorus*. Phylogenetic analysis of mitochondrial l2s and 16s provide strong support for *Tropidophorus beccarii* as the closest relative of the new species (see Fig. 5). This sister relationship suggests a single origin of smooth dorsal scales among *Tropidophorus* on Borneo (see Comparison), assuming an ancestral state of keeled dorsal scales for the genus. The phylogenetic results presented here are generally concordant with results of Honda *et al.* (2006), though we recover much weaker support for the paraphyly of *Tropidophorus* with respect to the *Sphenomorphus* group (ML bootstrap 36 vs. 73). The ML and BI topologies were identical with respect to relationships within *Tropidophorus.*

Raw pairwise sequence divergence between *T. beccarii* and the new species is 6.8–7.0% for 12s and 5.4–5.6% for 16s. Genetic divergence between the two type specimens of the new species is low, with raw distances of 0.2% and 0.3% for 12s and 16s, respectively. However, this measure of genetic diversity within the new species may be an underestimate as the two type specimens were collected from the same locality, and increased genetic divergence would likely exist across a larger spatial area.

Comparison. We initially compare the new species with Bornean congeners here. *Tropidophorus sebi* **sp. nov**. differs from *T. brookei* (distribution: widespread on Borneo), *T. iniquus* (distribution: upper Sungei Kajan, central Kalimantan, Indonesia), *T. micropus* (distribution: Long Bloe in upper Sungei Mahakkam, Kalimantan, Indonesia and Putai, Sarawak, Malaysia) and *T. perplexus* (distribution: Sungei Tinjar, Sarawak, Malaysia) in having smooth dorsal scales (versus keeled in these four species). The new species is further distinguished from another two smooth dorsal scales congeners, *T. beccarii* (widespread on Borneo) and *T. mocquardii* (distribution: northern Sabah, Malaysia; treated as a synonym of *T. beccarii* by some authors but considered valid here; see below) from Borneo, in showing a higher count of midbody scale rows (33–34) versus lower in *T. beccarii* (28–30), in having

four supraoculars versus five supraoculars, and in lacking a thick, dark, dorsolateral stripe along flanks, that are with light transverse bands in *T. mocquardii*.

FIGURE 3. Map showing type locality of *Tropidophorus sebi* **sp. nov**., at Putai, Upper Sungei Baleh, Kapit District, Sarawak, Malaysia (Borneo). Inset: Map of the Indo-Pacific, showing the location of Borneo.

The presence of smooth dorsal scales distinguishes the new species from the following extra-Bornean congeners that possess keeled dorsal scales: *T. assamensis* Annandale, 1912 (distribution: north-eastern Bangladesh and north-eastern India, including Mizoram and Assam states); *T. baconi* Hikida, Riyanto & Ota, 2003 (distribution: Patunuang Natural Reserve, southern Sulawesi, Indonesia); *T. baviensis* Bourret, 1939 (distribution: Mount Ba Vi, Ha Tay Province, northern Vietnam and possibly, adjacent Thailand); *T. berdmorei* (Blyth, 1853) (distribution: Yunnan in southern China, Myanmar, Thailand and Vietnam); *T. cocincinensis* Duméril & Bibron, 1839 (distribution: Thailand, southern Vietnam and Cambodia); *T. davaoensis* Bacon, 1980 (distribution: south-central Mindanao, Philippines); *T. grayi* Günther, 1861 (distribution: Panay, Luzon, Polillo, Leyte, Negros, Mastabe, Cebu, Philippines); *T. guangxiensis* Wen, 1992 (distribution: Guangxi and Hunan, China); *T. hainanus* Smith, 1923 (distribution: Hainan, Guangxi, Jiangxi, Hunan, Guangdong and Guizhou in China, and Bac Kan, Cao Bang, Dak Lak, Ha tay, Hai Duong, Hoa Binh, Kon Tum, Lai chau, Ninh binh, Phu Tho, Quang Ninh, Vinh Phuc and Nam Dinh in Vietnam); *T. hangnam* Chuaynkern, Nabhitabhata, Inthara, Kamsook & Somsri, 2005 (distribution: Chaiyaphum Province, north-easten Thailand), *T. latiscutatus* Hikida, Orlov, Nabhitabhata & Ota, 2002 (distribution: Phu Wua Wildlife Sanctuary, Nong Kai Province, eastern Thailand); *T. matsuii* Hikida, Orlov, Nabhitabhata & Ota, 2002 (distribution: Phu Pa Namtip, Roi Et Province, eastern Thailand); *T. microlepis* Günther, 1861 (distribution: southern Thailand, Vietnam, Laos and Cambodia); *T. misaminius* Stejneger, 1908 (distribution:

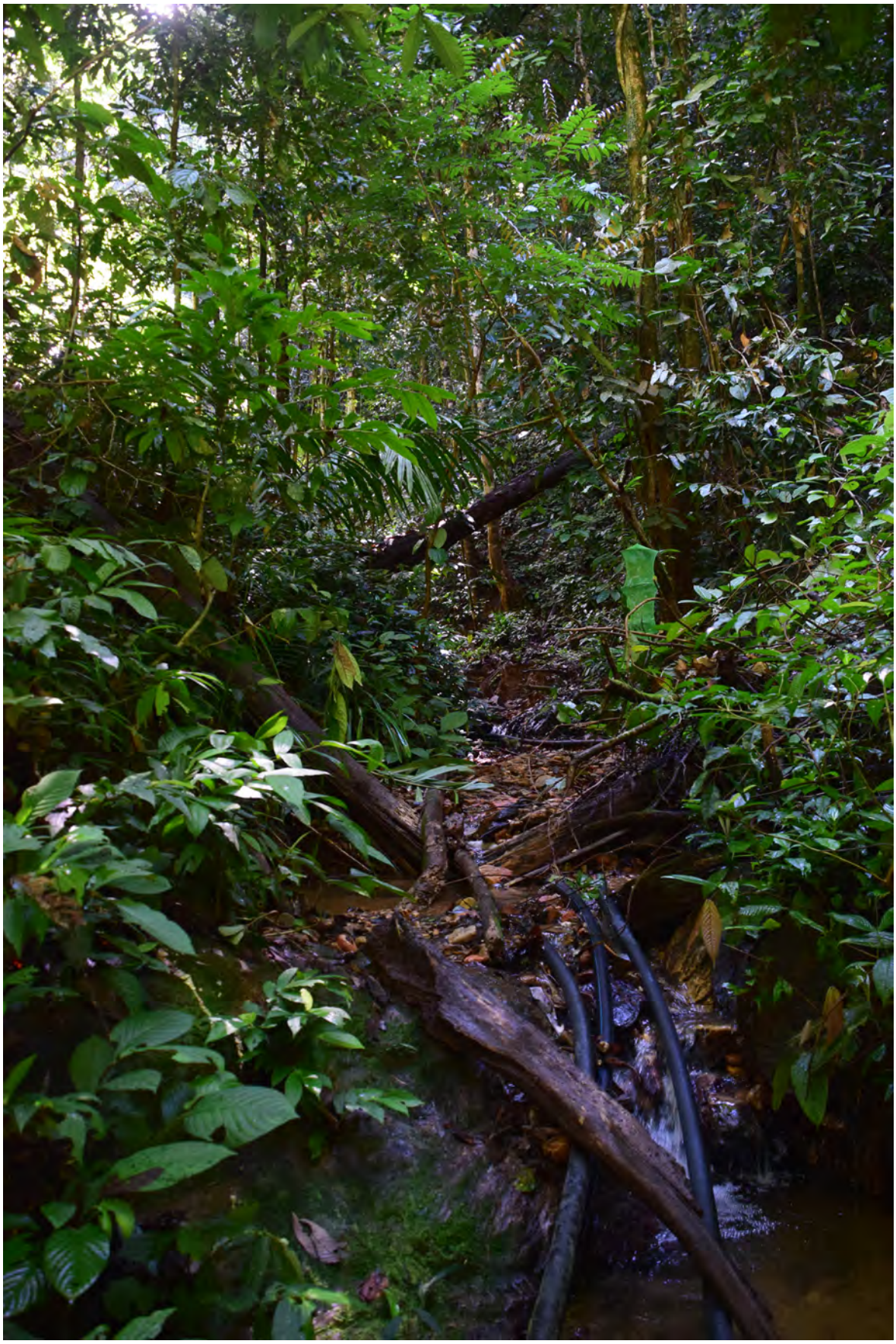

FIGURE 4. Habitat of *Tropidophorus sebi* **sp. nov**. at Putai, Upper Sungei Baleh, Sarawak, Malaysia (Borneo).

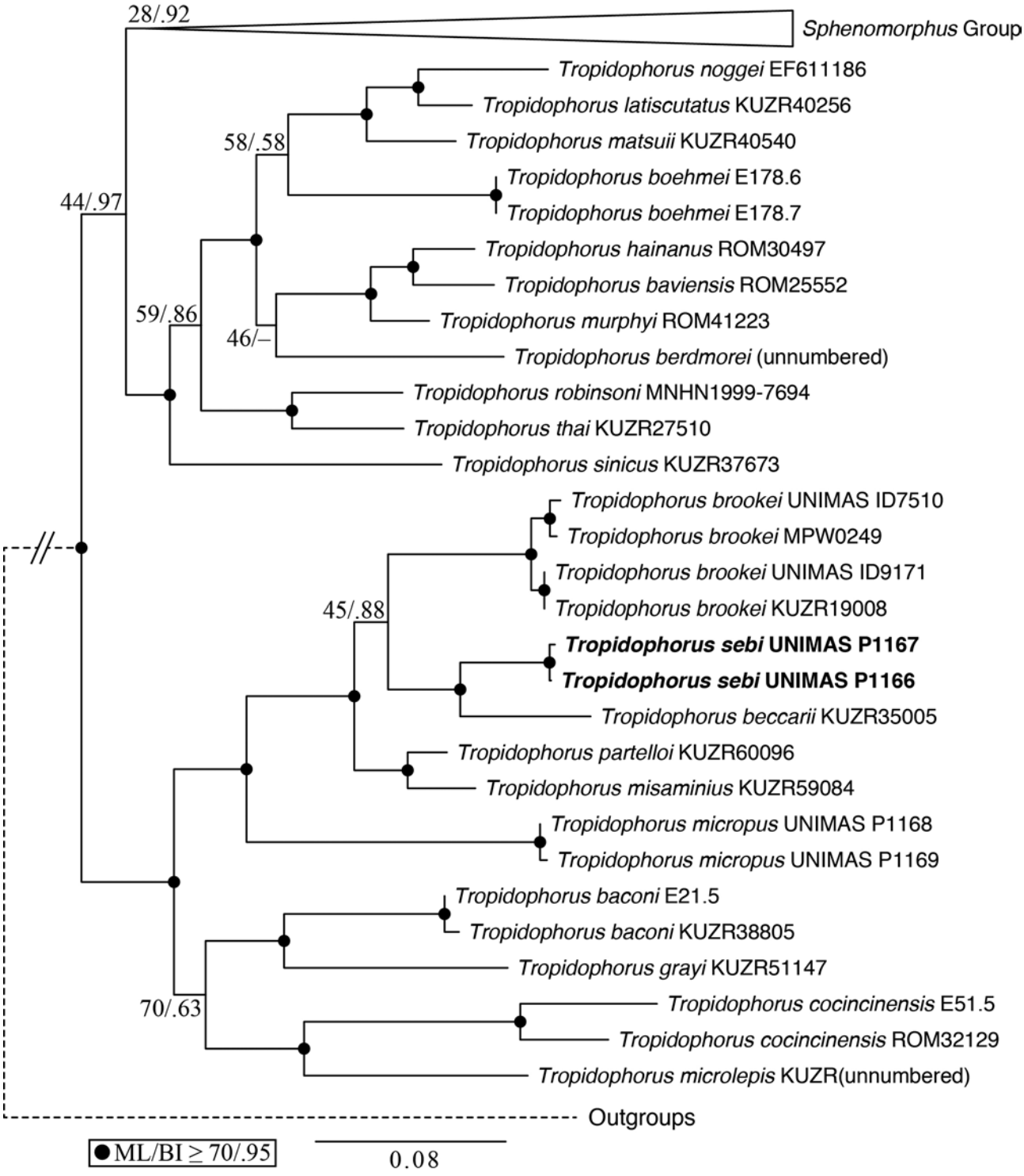

FIGURE 5. Concatenated ML phylogram of the mitochondrial 12s and 16s genes for *Tropidophorus* and close relatives with ML bootstraps (left number) and BI posterior probabilities (right number) shown at the nodes. Nodes with ML bootstrap ≥ 70 and BI posterior probability ≥ 0.95 are denoted with a black dot. The new species is indicated in bold.

Basilan, Camiguin and Mindanao, Philippines); *T. murphyi* Hikida, Orlov, Nabhitabhata & Ota, 2002 (distribution: Cao Bang Province, northern Vietnam); *T. noggei* Ziegler, Thanh & Thanh, 2005 (distribution: Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam); *T. partelloi* Stejneger, 1910 (distribution: Mataling River Falls, Cotabato Province, Mindanao, Philippines); *T. robinsoni* Smith, 1919 (distribution: Myanmar and Thailand); *T. sinicus* Boettger, 1886 (distribution: Guangxi, Guangdong, Hong Kong in China and Vietnam) and *T. thai* Smith, 1919 (distribution: Myanmar and northern and north-eastern Thailand).

Two extra-Bornean congeners possess smooth scales: *T. boehmei* Nguyen, Nguyen, Schmitz, Orlov & Ziegler, 2010 (distribution: Hoang Lien Mountain, Lao Cai Province, northern Vietnam) and *T. laotus* Smith 1923 (distribution: Pak Lai district in Laos and Thailand). *Tropidophorus boehmei* differs from the new species in showing tiny, reduced prefrontals vs. trapezoidal prefrontals that are in contact, supralabials six vs. seven, longitudinal scale rows 60–69 vs. 58, and transverse scale rows at midbody 30–32 vs. 34 in the new Bornean species. *Tropidophorus laotus* differs from the new species in showing a frontonasal that is divided vs. fused, supralabials six vs. seven, and anterior loreal divided vs. undivided in the new species.

Finally, to aid field identification, we present below a dichotomous identification key to the Bornean species of the genus *Tropidophorus*.

Key to Bornean species of *Tropidophorus*

1. Dorsal scales smooth . . . 2
- Dorsal scales keeled . . . 3
2. Midbody scale rows 28–30; thick dark dorsolateral stripe along flanks with light transverse bands. . . . *beccarii*
- Midbody scale rows 33–34; no dark dorsolateral stripe along flanks. . . . 6
3. Four supraoculars . . . *micropus*
- Five supraoculars . . . 4
4. Dorsal scales bicarinate, grooved . . . *iniquus*
- Dorsal scales unicarinate; not grooved . . . 5
5. Supraciliaries 14; midbody scale rows 32 . . . *brookei*
- Supraciliaries 5–6; midbody scale rows 30. . . . *perplexus*
6. Four supraoculars. . . . *sebi* **sp. nov.**
- Five supraoculars. . . . *mocquardii*

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APPENDIX I. Comparative material examined.

Tropidophorus assamensis Annandale, 1912: ZSI 17029 (holotype), 'Haraigaj range, 550 ft., Sylhet hills, Assam' (at present Sylhet District, north-eastern Bangladesh).

Tropidophorus beccarii Peters, 1871: AMNH 111914. Tubau Camp on Sungei Pesu, Miri Division, Sarawak, Malaysia; ZRC 2.1848. Sungei Baram, Sarawak, Malaysia; SBC R.30. Bukit Meraja, Bau, Sarawak, Malaysia; BMNH 72.2.19.15–16.

Gunung Matang, Sarawak, Malaysia; SM c.c.6.3.1 [two specimens]. Gunung Penrissen, Sarawak, Malaysia; FMNH 221481. Gunung Sungei Segaham, Kapit, Sarawak, Malaysia; USNM 197818. Labang Camp at Sungei Pesu, Sarawak, Malaysia; FMNH 248113; 248525. Tawau Hills Park, Tawau District, Sabah, Malaysia; FMNH 248526. Maliau Basin, Kinabatangan/Pensiangan Districts, Sabah, Malaysia; BM 1992.90. Sungei Ingei, Belait District, Brunei; UBD 84, 235, 295, 313, 538. Batu Apoi, Temburong District; Brunei; ZRC 2.4572. Sintang, along road at km 463 to Pontianak, Kalimantan Barat, Indonesia; ZRC 2.5801. Sungei Moleng at Baloi, Kalimantan Tengah, Indonesia; ZRC 2.5802. Mahakam basin, Kalimantan Tengah, Indonesia; MZB 2941–43; 18081; 18185; 18217. Maruwai, Kalimantan Tengah Propinsi, Indonesia.

Tropidophorus berdmorei (Blyth, 1853): ZRC 2.4618. Nam Tok Natee Rachan, Mae Hong Son Province, Thailand; ZSI 2270–72 (syntypes of *Aspris Berdmorei* Blyth, 1853), 'Mergui' (Myeik or Beik), Myanmar.

Tropidophorus brookei (Gray, 1845): AMNH 111915–18. Nanga Tekalit on Sungei Mengiong, Kapit Division, Sarawak, Malaysia; MZB 2391. Sungei Ulu Matai, Taman Nasional Bentuang Karimun, Kalimantan Barat Propinsi, Indonesia; MZB 3740–42. Sungei Menggulang, Taman Nasional Bentuang Karimun, Kalimantan Barat Propinsi, Indonesia; ZRC 2.1850. Sungei Baram, Sarawak, Malaysia; ZRC 2.3395, 2.4663. Bako National Park, Sarawak, Malaysia; ZRC 2.3447. Sarikei, Sarawak, Malaysia; ZRC 2.3522. Sungai Stum Muda near Lundu, Sarawak, Malaysia; ZRC 2.5739. waterfall at base of Gunung Pueh, Sarawak, Malaysia; ZRC 2.1852–58. Lawas, Sarawak, Malaysia; ZRC 2.4943. Nanga Ulai near Betong, Sarawak, Malaysia; ZRC 2.5749–51; 2.5845–46. Kapit, Sungai Belajau, Kapit, Sarawak, Malaysia; ZRC 2.4937, ZRC 2.4943. Ranchan Pool, Serian, Sarawak, Malaysia; ZRC 2.4617. Rajang basin near Kapit, Sarawak, Malaysia; ZRC 2.5337. Long Asap, Sarawak, Malaysia; ZRC 2.5338. Lambir Hills National Park, Miri, Sarawak; ZRC 2.3710. Danum Valley, Sungai Taliwas, Danum Valley, Sabah, Malaysia; ZRC 2.1850. Kabayo near Gunung Kinabalu, Sabah, Malaysia; ZRC 2.5805. Sungai Sepan, Sungei Sepan, Brunei Darussalam; ZRC 2.5266–67. Kuala Belalong Field Studies Centre, Temburong District, Brunei Darussalam; ZRC 2.5803. Sanggau, Kalimantan Barat, Indonesia.

Tropidophorus micropus van Lidth de Jeude, 1905: UNIMAS P1168. First Count Logging Camp, Putai, upper Sungei Baleh, Kapit District, Sarawak, Malaysia; RMNH 4452 (holotype of *Tropidophorus micropus*; digital image). "Long Bloe Upper Mahakkam River" (= Long Blu, also spelt Long Bloéoe, upper reaches of Sungei Mahakam, Kalimantan Timur Propinsi, Indonesia).

Tropidophorus perplexus Barbour, 1921: MCZ 14632 (holotype) "..near the Fort at Long Loba, Tinjar River, Sarawak" (= vicinity of Fort Hose, Marudi, Miri Division, Malaysia); FMNH 138551–56. Nanga Tekalit Camp on Sungei Mengiong, Kapit, Sarawak, Malaysia; FMNH 235156. Mendolong, Sipitang District, Sabah, Malaysia.

Tropidophorus sinicus Boettger, 1886: ZRC 2.4814. Lam Tseun, Pak Ngau Shek, New Territories, Hong Kong, China; ZRC 2.3478. Tai Po Kau Forest Reserve, New Territories, Hong Kong, China.