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A New Species of *Polypedates* from Sumatra, Indonesia (Amphibia: Anura)

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A rhacophorid tree frog from Sumatra that was once identified as *Polypedates otilophus* (Boulenger, 1893) is sufficiently divergent genetically and morphologically from topotypic specimens from Borneo as to be recognized as a distinct species. It is herein described as *P. pseudotilophus* sp. nov. The Sumatran frogs can be distinguished easily from the Bornean population by the possession of a much more weakly developed supratympanic bony crest, smoother dorsal skin, and a large, hourglass-shaped dark marking, instead of longitudinal stripes on the dorsum.

Key Words: Cryptic species, *Polypedates otilophus*, *Polypedates pseudotilophus* sp. nov., Sumatra, taxonomy, Indonesia.

Introduction

Sumatra is a large Indonesian island located in the Sunda region of Southeast Asia (Fig. 1). It is inhabited by quite a few endemic anuran species such as *Duttaphrynus totol* (Ohler in Teynié, David and Ohler, 2010); *Ansonia glandulosa* Iskandar and Mumpuni, 2004; *Huia modiglianii* (Doria, Salvidio and Tavano, 1999); *Hu. sumatrana* Yang, 1991; *Hylarana crassiovis* (Boulenger, 1920); *Hy. debussyi* (Van Kampen, 1910); *Hy. kampeni* (Boulenger, 1920); *Rhacophorus achantharrhena* Harvey, Pemberton and Smith, 2002; *R. barisani* Harvey, Pemberton and Smith, 2002; *R. bifasciatus* Van Kampen, 1923; *R. catamitus* Harvey, Pemberton and Smith, 2002; *R. modestus* Boulenger, 1920; and *R. poecilonotus* Boulenger, 1920. The distinct taxonomic status of some other endemic species was only recently elucidated through molecular phylogenetic analysis: *Hylarana rufipes* (Inger, Stuart and Iskandar, 2009); *Leptobrachium waysepuntiense* Hamidy and Matsui, 2010; *Limnonectes sisikdagu* McLeod, Horner, Husted, Barley and Iskandar, 2011; *Hylarana rawa* Matsui, Mumpuni and Hamidy, 2012.

One rhacophorid, *Polypedates otilophus* (Boulenger, 1893) was originally described from Borneo, another large island of the Sunda region, but was also recorded from part of Sumatra (Van Kampen 1905, 1923; Inger 1966). This species is thought to have been the first to diverge from its congeners in the course of *Polypedates* evolution (Kuraishi *et al.* 2013), but in Borneo it is not remarkably variable either morphologically or genetically (Inger 1966; Kuraishi *et al.* 2013). Riyanto *et al.* (2009) recently found this species in Java and compared it with populations from Sumatra and Borneo. They found that the Javanese and Sumatran populations are very similar to each other and show no significant morphometric differences from the Bornean population.

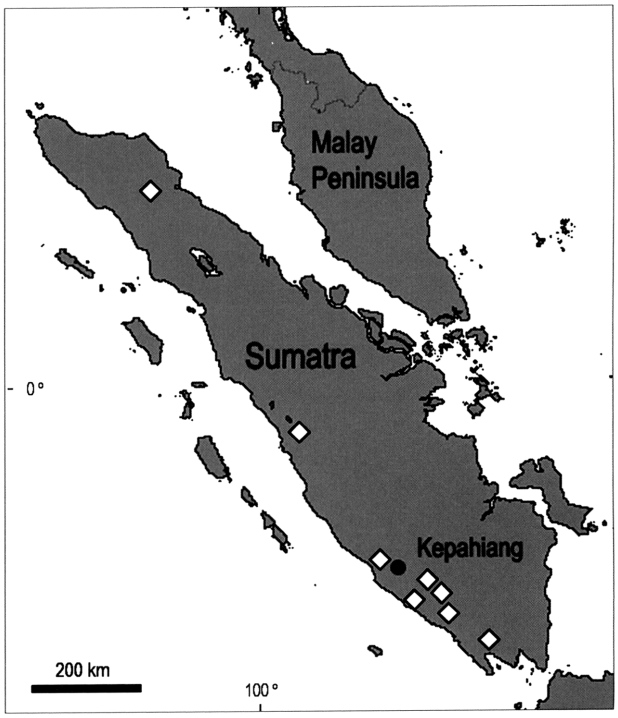

Fig. 1. Map of Sumatra, Indonesia, showing the known distribution (open diamonds) of *Polypedates pseudotilophus* sp. nov. The filled circle indicates the type locality.

Our own preliminary genetic analysis, however, showed a large genetic divergence between *P. otilophus* of Sumatra and Borneo. We therefore made a detailed morphological comparison of both populations and found characteristics that clearly distinguish them, in contrast to Riyanto *et al.*'s (2009) report. In this paper, we describe the Sumatran population as a new species distinct from *P. otilophus*.

Materials and Methods

Types and voucher specimens used in this study are in the collection of the Museum Zoologicum Bogoriense, Research Center for Biology, Indonesian Institute of Sciences, Cibinong, Indonesia (MZB), the Graduate School of Human and Environmental Studies, Kyoto University, Kyoto, Japan (KUHE), and the Institute for Tropical Biology and Conservation, University Malaysia Sabah (BORNEENSIS, hereafter abbreviated as BORN).

For genetic comparisons, first about 2.4 kbp of partial mtDNA genes from eight individuals of *P. otilophus* were analyzed: two adults (MZB Amp 16303 and 16304) and two larvae (MZB Amp unnumbered) from Sumatra and four individuals (BORN 08158, KUHE 17264, 39351, and 39268) from Borneo. In addition, analysis of about 4.7 kbp of partial nuclear DNA genes was carried out using two specimens from Sumatra (MZB Amp 16303 and 16304) and one from Borneo (BORN 08158). The resultant sequences were deposited in GenBank (AB 907710–907738). For comparison, GenBank data for *P. otilophus* from Borneo (KUHE 42555) and three outgroup species, *P. leucomystax* (Gravenhorst, 1829), *Rhacophorus norhayatii* Chan and Grismer, 2010, and *Buergeria buergeri* (Temminck and Schlegel, 1838), were used (details in Appendix). Methods for phylogenetic analysis are the same as those reported by Kuraishi *et al.* (2013). Briefly, total DNA was extracted and amplified by PCR with the primers shown in Kuraishi *et al.* (2013). Amplified fragments were sequenced using the amplification primers and 10 additional sequencing primers. An alignment matrix with 2402 mitochondrial nucleotide sites (909 bp for 12S rRNA; 71 bp for $tRNA^{val}$; 1422 bp for16S rRNA) and 4696 nuclear nucleotide sites (508 bp for brain-derived neurotrophic factor [BDNF]; 1000 bp for sodium–calcium exchanger 1 [NCX]; 571 bp for proopiomelanocortin [POMC]; 780 bp for recombination activating gene 1 [Rag1]; 316 bp for exon 1 of rhodopsin [Rhod]; 1076 bp for solute-carrier family 8 [SLC8A3]; 445 bp for exon 1 of tyrosinase [Tyr]) was used to estimate phylogenetic relationships by means of maximum likelihood (ML) and Bayesian inference. Pairwise comparisons of uncorrected sequence divergences (*p*-distance) for 16S rRNA were also calculated. Details for these procedures are given in Kuraishi *et al.* (2013).

For morphological comparison, we examined preserved specimens of *P. otilophus* from Sumatra (n=12) and Borneo (n=37, from Sabah, Sarawak, and Kalimantan). Body measurements were taken mostly following Matsui (1984): (1) snout–vent length (SVL), (2) head length (HL), (3) snout length (SL), (4) nostril–eyelid length (N-EL), (5) eye length (EL), (6) tympanum vertical diameter (TDV), (7) tympanum horizontal diameter (TDH), (8) tympanum–eye length (T-EL), (9) head width (HW), (10) internarial distance (IND), (11) intercanthal distance (ICD), (12) interorbital distance (IOD), (13) upper eyelid width (UEW), (14) forelimb length (FLL), (15) lower arm and hand length (LAL), (16) first finger length (1FL), (17) outer palmar tubercle length (OPTL), (18) inner palmar tubercle length (IPTL), (19) width of third finger disk (3FDW), (20) width of fourth finger disk (4FDW), (21) hindlimb length (HLL), (22) thigh length (THIGH), (23) tibia length (TL), (24) foot length (FL), (25) inner metatarsal tubercle length (IMTL), (26) first toe length (1TOEL), (27) width of fourth toe disk (4TDW), (28) bony ridge length (BRL), and (29) bony ridge width (BRW). All measurements were made to the nearest 0.1 mm with dial calipers and under a binocular dissecting microscope, when necessary. The system of description of toe-webbing states follows Savage (1975). In univariate comparisons, SVL was compared by the Tukey–Kramer test, while the percentage ratios (R) of the remaining characters to SVL were compared by Dunn's multiple comparisons test.

For preserved larvae, the following 14 measurements were taken to the nearest 0.01 mm using a binocular dissecting microscope equipped with a micrometer: (1) total length (TOTL), (2) head–body length (HBL), (3) maximum head–body width (HBW), (4) maximum head–body depth (HBD), (5) eyeball diameter, (6) internarial distance, (7) interorbital distance, (8) snout–spiracle-opening distance, (9) snout–eye distance, (10) oral disk width, (11) tail length, (12) maximum tail depth, (13) maximum tail width, and (14) muscle depth at middle of tail. We followed Gosner's (1960) table for staging.

Systematics

In the mtDNA phylogenetic trees constructed on the basis of our data (Fig. 2, left), all samples of *P. otilophus* formed a well-supported clade with respect to the other rhacophorids (bootstrap support for maximum likelihood [MLBS]=99%, for Bayesian posterior probability [BPP]=1.00). In the *P. otilophus* clade, the samples from Sumatra formed a clade (MLBS=99%, BPP=1.00) that is sister to the clade comprised of Bornean samples (MLBS=99%, BPP=1.00). Four sequences from Sumatra differed substantially from five sequences from Sabah and Sarawak in Borneo (uncorrected *p*-distance in 16S of 12.1–12.2%). Identical relationships were obtained in the nuDNA trees, where all clades were fully (MLBS=100%, BPP=1.00) supported (Fig. 2, right). The specimens from Sumatra are also morphologically distinct from the specimens of *P. otilophus* from Borneo, in accord with this genetic separation. Thus, we conclude that the supposed population of *P. otilophus* from Sumatra is a distinct species and describe it as follows.

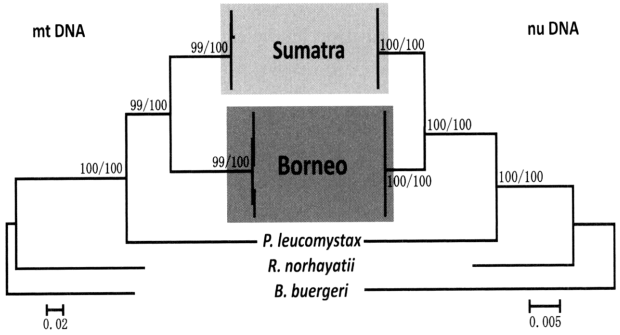

Fig. 2. ML tree from a 2402 bp sequence of mitochondrial 12S rRNA, $tRNA^{val}$, and 16S rRNA genes (left) and a 4696 bp sequence of nuclear BDNF, NCX, POMC, Rag1, Rhod, SLC8A, and Tyr genes (right) for samples of *Polypedates otilophus* from Sumatra and Borneo, and related species. Numbers above or below branches represent bootstrap supports for ML inferences and Bayesian posterior probabilities (MLBS/BPP).

Polypedates pseudotilophus sp. nov.
(Figs 3–6)

Rhacophorus otilophus: Van Kampen 1905: 705; 1923: 245 (part); Inger 1966: 329 (part).
Polypedates otilophus: Riyanto *et al.* 2009: 218 (part).

Etymology. The specific name is derived from the Greek prefix "*pseudo-*", meaning lying or false, and "*otilophus*", alluding to the fact that the new species has long been treated as though it were *Polypedates otilophus*.

Diagnosis. Large-sized species of *Polypedates,* with adult male SVL 60–70 mm and adult female SVL 90–93 mm, with sharp triangular bony process at commissure of jaws, and serrated bony crest projecting above tympanum. Very similar to *P. otilophus*, but with much lower supratympanic ridge; dorsum with solid, dark hourglass figure beginning at interorbital and ending at sacrum.

Holotype. MZB Amp 16304, male, from Bengkulu, Kepahiang, Merigi, Batu Ampar, southern Sumatra, Indonesia (03°30′46″S, 102°32′53″E, alt. 712 m asl), collected on 18 July 2010 by A. Hamidy and Nurrahim.

Paratype. Sumatra, Indonesia (Fig. 1): MZB Amp 3477 (male) from Rata Agung, Bukit Barisan Selatan National Park, Lampung, collected on 11 March 1998 by Andiek; MZB Amp 3457 (male) from Rata Agung, Bukit Barisan Selatan National Park, Lampung, collected on 11 March 1998 by Andiek; MZB Amp 3467 (female) from Dirgahayu Rimba, Bukit Barisan Selatan National Park, Bengkulu, collected in July to August 1997 by Andiek; MZB Amp 3819 (male) from Soraya, Gunung Leuser National Park, Aceh, collected on 20 April 1999 by D. T. Iskandar; MZB Amp 4221 (female) from Bintuhan, Bukit Barisan Selatan National Park, Bengkulu, collected on 26 August 1999 by Alfad; MZB Amp 4222 (male) from Bintuhan, Bukit Barisan Selatan National Park, Bengkulu, collected on 7 August 1999 by Alfad; MZB Amp 14609 (female) from Linau, Bukit Barisan Selatan National Park, Bengkulu, collected on 29 September 2005 by A. Ul Hasanah; MZB Amp 14857 (male) from Sipurak, Kerinci Seblat National Park, West Sumatra, collected on 6 March 2005 by H. Kurniati; MZB Amp 16303 (male) from Bengkulu, Bengkulu Tengah, collected on 19 July 2010 by A. Hamidy and Nurrahim; MZB Amp 22215 (male) from Gunung Tanggamus, Tanggamus, Lampung, collected in June 2013 by E. Wostl, W. Trilaksono, and G. Barranza; MZB Amp 22944 (female) from Rata Agung, Bukit Barisan Selatan National Park, Lampung, collected on 11 March 1998 by Andiek.

Referred Specimens. Three tadpoles, collection data same as for holotype.

Description of holotype. SVL 67.5 mm; body robust (Figs 3, 4A, B); head triangular, slightly broader (HW 25.9 mm, 38.4% SVL) than long (HL 24.9 mm. 36.7% SVL); snout (SL 12.3 mm, 18.2% SVL) longer than eye (EL 9.8 mm, 14.5% SVL), rounded in profile, slightly pointed at tip and projecting over lower jaw; canthus distinct; lore slightly oblique, slightly concave; nostril slightly protuberant, much nearer to tip of snout than to eye (N-EL 7.0 mm, 10.3% SVL); internarial distance (IND 5.3 mm, 7.9% SVL) much smaller than interorbital (IOD 8.2 mm, 12.2% SVL); latter slightly narrower than eyelid (UEW 8.6 mm, 12.7% SVL); pineal spot absent; eye large, protuberant, pupil horizontal; tympanum distinct, circular, diameter (TD 4.5 mm, 6.7% SVL) slightly smaller than half eye diameter and separated from eye (T-EL 1.9 mm, 2.8% SVL) by two-fifths of tympanum diameter; vomerine teeth in oblique groups between anterior halves of choanae, groups closer to choanae than to each other; bilateral round openings into median subgular vocal sac near jaw commissures; tongue deeply notched posteriorly.

Forelimb (Fig. 5A) slender, long (FLL 43.3 mm, 64.2% SVL); relative finger length I<II<IV<III; length of first finger (1FL 7.9 mm, 11.7% SVL) shorter than length of eye; tips of all fingers expanded into large disks with circummarginal and transverse ventral grooves; disk of third finger (3FDW 3.9 mm, 5.8% SVL) narrower than tympanum; rudimentary basal web between fingers (Fig. 5); subarticular tubercles rounded, formula 1, 1, 2, 2; other indistinct subarticular tubercles present; supernumerary tubercles absent on metacarpals; prepollex prominent, oval; flat, inner palmar tubercle (IPTL 4.4 mm, 6.5% SVL) and indistinct, round outer palmar tubercle (OPTL 3.3 mm, 4.8% SVL) present; grayish, velvety nuptial pad covering dorsal and medial surfaces of first finger from wrist to level of subarticular tubercle and also circular area on dorsal surface of second finger.

Hindlimb (Fig. 5B) slender, short (HLL 103.8 mm, 153.8%SVL), about 2.4 times length of forelimb; thigh (30.9 mm, 45.8% SVL) shorter than tibia (TL 34.2 mm, 50.7% SVL), heels overlapping when limbs held at right angles to body; tibiotarsal articulation of adpressed limb reaching point between eye and nostril; foot (27.2 mm, 40.3% SVL) shorter than tibia; relative length of toes I<II<III<V<IV; tips of toes expanded into round disks with distinct circummarginal grooves, smaller than those of outer fingers (4TDW 3.0 mm, 4.4% SVL); toes poorly webbed, toe webbing formula I 2-2¼ II 1½-3 III 1¾-3 IV 3-2 V (Fig. 5); subarticular tubercles distinct, rounded, formula 1, 1, 2, 3, 2; supernumerary tubercles absent; low, oval

inner metatarsal tubercle (IMTL 2.2 mm, 3.3% SVL) present, about one-fourth length of first toe (1TOEL 8.1 mm, 12.0% SVL), but no outer metatarsal tubercle evident.

Dorsum nearly smooth, with scattered non-spinose tubercles; skin of head co-ossified with roof of skull; a low, serrated bony ridge projecting from eye above tympanum, posteriorly running as dorsolateral fold and ending at anterior one-third of flank; blunt triangular bony process at commissure of jaws; flank wrinkled; underside of chin and chest smooth, abdomen and thigh coarsely granular; very narrow, smooth-edged fringe of skin along forearm ending as a small, triangular dermal appendage at elbow; triangular dermal appendage present at tibiotarsal articulation; two pairs of enlarged, white tubercles below vent.

Fig. 3. Dorsolateral view of male holotype of *Polypedates pseudotilophus* sp. nov. (MZB Amp 16304) from Kepahiang, southern Sumatra.

Color. Color in life pale brown above with large, brown hourglass marking between anterior part of each eye and sacral region (Figs 3, 4A); narrow brown dorsolateral streak continuing to bony ridge; forearm and tibia with three wide pale brown bars dorsally; thigh with seven narrow black bars dorsally; body dirty white below, dusted gray on chin and thigh (Fig. 4B). In alcohol dorsal color faded to gray brown.

Variation. Morphometric data are summarized in Table 1. Females are larger (90.9–93.3, mean±SD=91.9±1.1 mm in SVL) than males (60.7–69.9, 66.6±2.8 mm in SVL). Males have relatively larger eye (REL: 14.2–15.5, median=15.1% SVL in males *vs.* 12.3–15.6, median=12.8% SVL in females) but shorter first finger than females (R1FL: 11.2–12.7, median=11.9% SVL in males *vs.* 13.0–13.8, median=13.8% SVL in females). Specimens are fairly constant in coloration.

Eggs and larvae. A female collected in August had ovaries with fully developed ova of 0.80–0.90 mm in diameter, that were cream in color in both the animal and vegetal hemispheres.

Three tadpoles, stage 37 (TOTL=68.2 mm, HBL=23.0 mm), 41 (65.1 mm, 22.1 mm), and 41 (65.2 mm, 23.0 mm), collected from the type locality, were examined (Fig. 6). Head and body slightly flattened above, spheroidal below; HBW maximum posterior to level of spiracle 52–69% (median=61%) of HBL; HBD 40–58% (median=57%) of HBW; snout rounded; eyes dorsolateral, visible

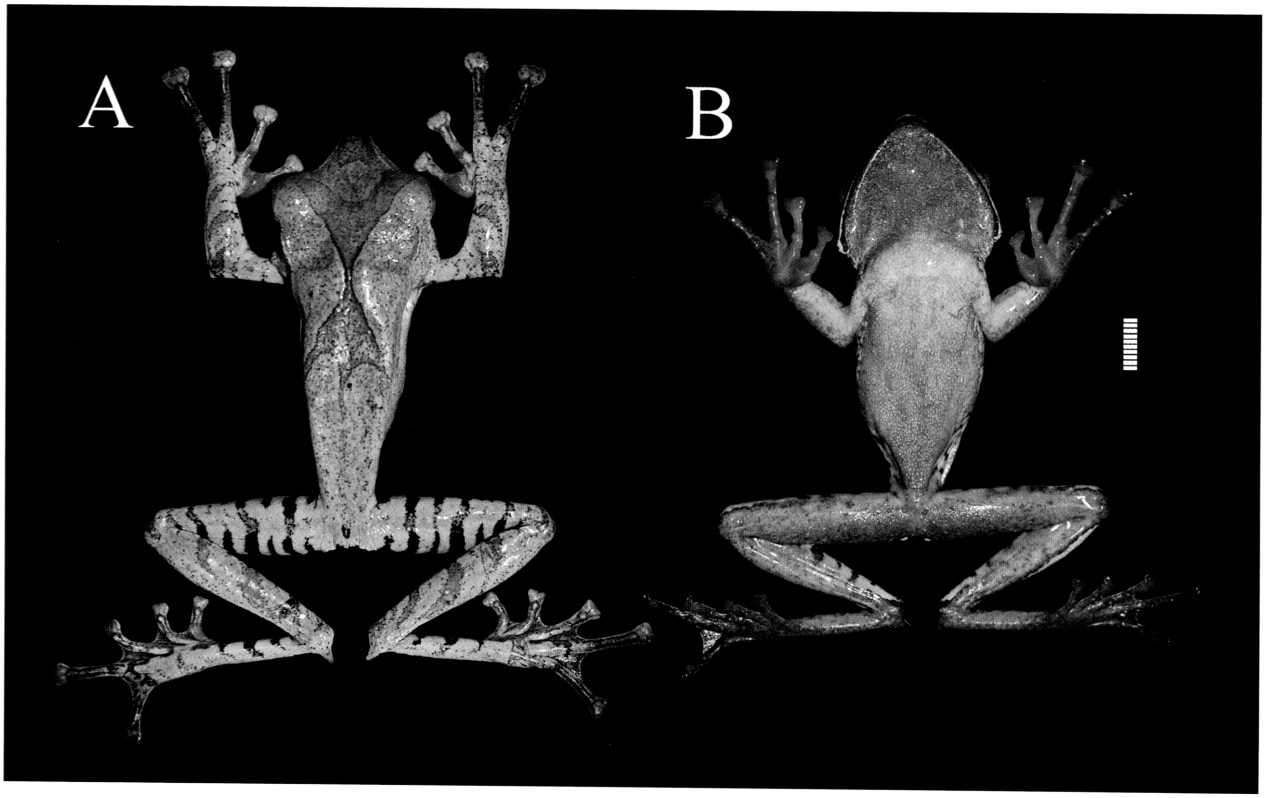

Fig. 4. Dorsal (A) and ventral (B) views of male holotype of *Polypedates pseudotilophus* sp. nov. (MZB Amp 16304) from Kepahiang, southern Sumatra. Scale bar=10 mm.

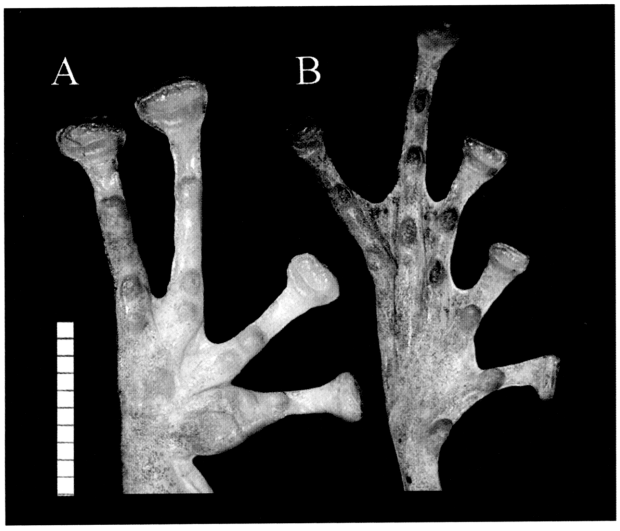

Fig. 5. Ventral views of hand (A) and foot (B) of male holotype of *Polypedates pseudotilophus* sp. nov. (MZB Amp 16304) from Kepahiang, southern Sumatra. Scale bar=10 mm.

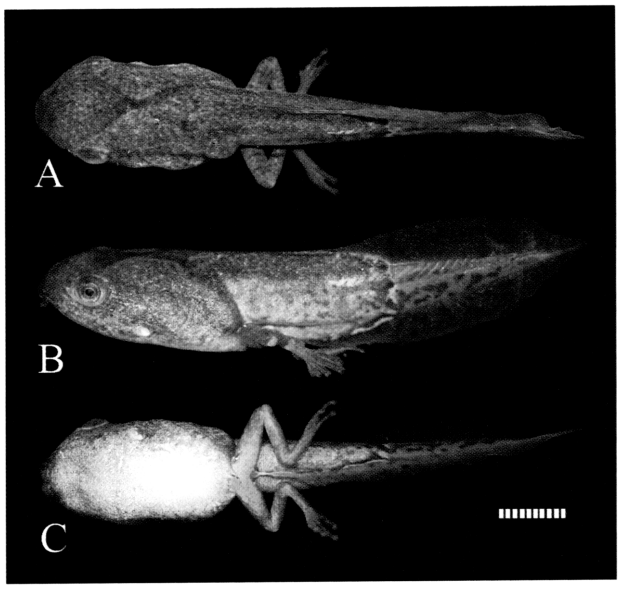

Fig. 6. Dorsal (A), lateral (B), and ventral (C) views of larval *Polypedates pseudotilophus* sp. nov. from Kepahiang, southern Sumatra (MZB Amp unnumbered, Stage 41, total length=65.1 mm). Scale bar=10 mm.

Table 1. Measurements of adult *Polypedates pseudotilophus* sp. nov. and *P. otilophus*. SVL (Mean±SD, in mm) and medians of pecentage ratios (R) of other characters to SVL, followed by ranges in parentheses. See text for character abbreviations.

	Male				Female			
	P. pseudotilophus (*n*=8)		*P. otilophus* (*n*=27)		*P. pseudotilophus* (*n*=4)		*P. otilophus* (*n*=10)	
SVL	66.6±2.8	(60.7–69.9)	75.0±4.0	(68.4–83.3)	91.9±1.1	(90.9–93.3)	93.3±4.5	(83.7–98.9)
RHL	39.1	(36.9–41.2)	37.7	(35.9–39.3)	37.6	(37.0–42.2)	36.7	(35.4–39.0)
RSL	19.4	(18.2–20.3)	18.1	(16.3–20.1)	19.1	(18.3–20.1)	18.0	(17.1–18.8)
RN-EL	12.2	(10.4–13.6)	11.7	(10.8–13.1)	12.8	(12.7–13.4)	12.1	(11.0–12.9)
REL	15.1	(14.2–15.5)	14.0	(12.9–14.8)	12.8	(12.3–15.6)	12.9	(11.5–13.7)
RTDV	7.4	(6.4–8.0)	8.1	(7.3–9.3)	7.2	(6.6–7.7)	8.1	(7.3–9.4)
RTDH	6.7	(6.2–7.4)	7.4	(6.6–9.1)	6.4	(5.5–7.8)	7.1	(6.4–7.6)
RT-EL	2.7	(2.3–3.0)	1.9	(0.8–2.8)	2.7	(2.4–3.0)	2.4	(1.0–2.6)
RHW	39.4	(37.7–40.9)	36.3	(34.4–43.1)	42.9	(40.1–44.4)	37.2	(34.1–42.8)
RIND	8.5	(7.9–9.4)	7.9	(7.4–8.7)	8.0	(7.4–8.2)	8.0	(7.5–8.4)
RICD	22.6	(18.2–23.5)	19.1	(17.1–21.6)	22.1	(21.2–22.2)	19.2	(17.7–22.4)
RIOD	13.1	(11.5–15.7)	12.3	(11.5–14.6)	13.0	(12.4–13.8)	12.4	(11.9–13.7)
RUEW	12.8	(11.9–13.4)	11.4	(10.4–13.1)	12.2	(11.8–12.7)	11.5	(9.9–13.5)
RFLL	60.8	(55.5–64.1)	63.9	(57.8–68.3)	57.6	(55.2–58.3)	62.7	(59.4–67.0)
RLAL	52.1	(49.8–54.0)	51.1	(46.4–54.4)	51.4	(49.2–52.2)	52.5	(48.1–56.8)
R1FL	11.9	(11.2–12.7)	11.9	(10.5–13.5)	13.8	(13.0–13.8)	12.7	(10.7–13.4)
ROPTL	5.1	(4.6–5.6)	4.8	(4.2–5.5)	5.0	(4.4–5.4)	5.1	(4.9–5.8)
RIPTL	6.9	(6.5–7.7)	6.1	(5.3–7.2)	7.5	(6.8–7.7)	6.7	(5.5–7.7)
R3FDW	6.2	(5.6–7.4)	6.1	(4.8–7.1)	6.7	(6.5–7.2)	6.8	(6.1–7.6)
R4FDW	6.5	(6.1–7.5)	5.9	(4.7–6.7)	7.2	(6.6–7.4)	6.6	(5.7–7.4)
RHLL	154.6	(151.8–160.4)	149.2	(140.7–157.8)	151.7	(150.1–153.5)	149.9	(143.9–161.8)
RTHIGH	48.8	(45.8–51.1)	47.9	(45.7–52.1)	49.3	(47.5–50.0)	50.1	(47.1–54.0)
RTL	50.6	(49.8–57.0)	48.7	(46.3–51.5)	51.4	(49.1–53.6)	50.3	(46.9–53.7)
RFL	40.8	(39.7–42.2)	38.8	(35.7–42.0)	39.5	(38.2–40.9)	39.4	(37.7–42.7)
RIMTL	3.7	(3.2–4.4)	3.3	(2.8–4.2)	3.7	(3.6–4.1)	3.4	(2.6–4.1)
R1TOEL	11.9	(11.1–12.9)	10.7	(8.6–12.1)	13.3	(11.4–14.2)	11.9	(10.4–13.1)
R4TDW	4.7	(4.4–5.3)	4.4	(3.4–4.7)	5.4	(4.8–5.6)	4.8	(4.3–5.6)
RBRL	9.9	(9.3–11.4)	13.3	(11.5–15.2)	9.6	(8.9–10.4)	12.3	(11.1–14.8)
RBRW	2.1	(1.5–2.4)	4.6	(3.1–5.6)	2.7	(2.4–3.1)	4.2	(3.6–5.3)

from below, eyeball 16–18% (median=18%) of HBL; interorbital wide, 185–208% (median=197%) of eyeball diameter; nostril open, dorsolateral, rim raised, much closer to tip of snout than to eye, internarial distance 51–59% (median=55%) of interorbital, equal to eye–nostril distance. Oral disk ventral, subterminal, emarginate, width 23–25% (median=24%) of HBW; papillae in double, staggered row along margin of lower, except for gap at center, also present at lip; denticles 5(2–5)/3; beaks strong, undivided, with black outer margins; outer surface smooth; margin of upper beak finely serrate, that of lower beak serrate; upper beak lacking pronounced medial convexity. Spiracle sinistral, non-tubular, not free of body wall; opening at 48–62% (median=57%) of HBL, closer to eye than to tail, below line between eye and insertion of hind limb, pointing upward and backward. Anal tube dextral, not reaching margin of ventral fin; loops of gut not visible in ventral view. Tail long and lanceolate, both margins convex, tapering abruptly to slightly rounded tip; tail length 184–197% (median=195%) of HBL; maximum depth at distal third of tail, 34–37% (median=34%) of tail length; dorsal fin origin at posterior end of body, as deep as ventral fin; ventral fin origin posterior to vent; caudal muscle moderate, maximum tail width 24–31% (median=27%) of HBW; muscle depth at middle of tail 31–41% (median=39%) of tail depth, steadily narrowing posteriorly from mid-length of tail, narrower than either fin in distal third of tail. Indistinct neuromasts of supranaso-orbital and oral lines discernible.

In formalin, head–body yellowish brown dorsally and laterally, densely covered with small, dark brown spots; dorsally with large, brown hourglass marking (Fig. 6); ventral surface white; proximal half of caudal muscle same as head–body dorsally, with scattered larger spots ventrally; distal half of caudal muscle grayish brown dorsally, yellowish brown with scattered large, dark spots ventrally; distal half of dorsal fin and ventral fin opaque with small, dark dots. Larvae acquire adult pattern on body and hindlimb before eruption of forelimb.

Comparisons. The presence of supratympanic bony ridge differentiates *P. pseudotilophus* sp. nov. from all known congeneric species except for *P. otilophus*. However, *P. pseudotilophus* has a much more weakly developed bony ridge than *P. otilophus*, and the large dorsal hourglass marking is quite unlike *P. otilophus*, in which the dorsum is marked by narrow longitudinal dark stripes. The two species are significantly different morphometrically in some characters: In males, *P. pseudotilophus* has larger RSL, REL, RT-EL, RHW, RIND, RICD, RUEW, RIPTL, RHLL, RTL, R1TOEL, and R4FDW, but smaller SVL, RTDV, RTDH, RBRL, and RBRW than *P. otilophus*. In females, *P. pseudotilophus* has smaller RFLL and RBRL than *P. otilophus*.

Range. Sumatra, Indonesia: Bengkulu (Kepahiang, Merigi, Batu Ampar; Bengkulu Tengah; Bukit Barisan Selatan National Park [Bintuhan, Linau, Dirgahayu Rimba]); West Sumatra (Sipurak, Kerinci Seblat National Park); Lampung (Rata Agung, Bukit Barisan Selatan National Park; Gunung Tanggamus, Tanggamus); Aceh (Soraya, Gunung Leuser National Park); Palembang district (Van Kampen 1905). Most probably also occurring in Java: Telaga Sunyi, Batur-Raden, Central Java; Salak mountain, West Java (Riyanto *et al.* 2009).

Natural History. Unknown, but supposed to be the same as that of *P. otilophus*, which spawns eggs in a foam nest on leaves. The larvae were collected together with the holotype in the secondary forest. They were found in a small pond with a diameter of about 1 m and depth of 50–70 cm.

Discussion

Polypedates pseudotilophus was first recorded from the Palembang district of Sumatra as *Rhacophorus otilophus*. Van Kampen (1905) noted that the Sumatran specimen he examined was similar to the Bornean one, differing only in having somewhat larger adhesive pads, and having a small dermal appendage not only on the ankle, but also on the elbow ("nur sind die Haftscheiben etwas größer und hat nicht nur die Ferse, sondern auch der Ellenbogen einen kleinen Hautanhang"). The first trait was confirmed in our study (significantly larger R4FDW in the Sumatran population), but the second one, presence of dermal appendage both on the ankle and on the elbow, actually also occurs in Bornean population. No detailed studies have ever been made since then, although there have been unpublished records from Sumatra. Recently, Riyanto *et al.* (2009) discovered *P. otilophus* in Java and compared it with Sumatran and Bornean *P. otilophus*. They could not find any statistically significant difference in body proportions between the Javanese and Sumatran specimens, and also found the Javanese specimens to be more similar to Sumatran than Bornean specimens in the color pattern and skin texture.

Our preliminary observations (Hamidy unpublished data) completely confirmed Riyanto *et al.*'s (2009) report. The Javanese frogs have the morphological characteristics typical of Sumatran ones, and are likely identical with *P. pseudotilophus* sp. nov., although we have no DNA data to confirm this. Because some frogs in different lineages, such as *Ingerophrynus biporcatus* (Gravenhorst, 1829) and *Leptobrachium hasselti* Tschudi, 1838, occur exclusively on Sumatra and Java (Iskandar 1998; Matsui *et al.* 2010), our tentative assessment of Sumatran and Javanese *Polypedates* as conspecific is plausible. Each of these two islands has its endemic elements (see Introduction for Sumatran taxa), but there are also elements common to both islands (and also to Bali), and elements occurring more widely on the islands nearby and the Malay Peninsula. These three categories of faunal elements may represent the approximate order of their historical invasions into the islands, and future studies of the divergence time in each taxon would greatly contribute in understanding the formation of the amphibian fauna of the Sunda region.

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Appendix

GenBank accession numbers of mtDNA (12S rRNA–16S rRNA) used for comparison. *Polypedates otilophus* from Borneo (KUHE 42555): AB728190. *Polypedates leucomystax* from Java (MZB Amp 12864): AB728137. *Rhacophorus norhayatii* (KUHE unnumbered larva): AB728191. *Buergeria buergeri*: AB127977.

GenBank accession numbers of nuDNA used for comparison, in the order BDNF, NCX, POMC, Rag1, Rhod, SLC8A3, and Tyr. *Polypedates otilophus* from Borneo (KUHE 42555): AB728213, 728230, 728247, 728269, 728286, 728303, 728320. *Polypedates leucomystax* from Java (MZB Amp 12864): AB728205, 728223, 728240, 728262, 728279, 728296, 728313. *Rhacophorus norhayati* (KUHE unnumbered larva): AB728214, 728231, 728248, 728270, 728287, 728304, 728321. *Buergeria buergeri* (KUHE13260): AB728215, 728232, 728249, 728271, 728288, 728305, 728322.