

Taxonomic Reassessment of the Arboreal Toad Genus *Pedostibes* Günther 1876 (Anura: Bufonidae) and Some Allied Oriental Bufonid Genera

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ABSTRACT: We reassessed the taxonomic status of an Asian genus of arboreal bufonids, *Pedostibes*, based on examination of preserved material of the two species currently attributed to this genus. Analysis of their morphological, morphometric, and geographic distribution data revealed that *Pedostibes tuberculosus*, the type species of this genus from the Western Ghats, southwestern India, is morphologically distinct from the geographically separated member, *P. kempfi*, which is distributed in northeastern India. Hence, the generic nomen *Pedostibes* is restricted to the type species, rendering it a monotypic genus from the Western Ghats of peninsular India. A re-examination and detailed comparisons of the types of *P. kempfi* with other bufonid genera revealed morphological similarities with another geographically proximate toad, *Bufoides meghalayanus*, from northeastern India. Hence, this taxon is formally transferred herein to *Bufoides* with a redescription. The composition of the recently described Southeast Asian toad genus *Rentapia* is reevaluated and the name-bearing type specimens of the currently ascribed taxa are redescribed. A detailed examination of the types of *Rentapia everetti* and *R. rugosa* revealed morphological congruence coupled with geographic sympatry. Hence, the latter nomen is synonymized with *R. everetti* in accordance with the International Code of Zoological Nomenclature principle of priority.

Key words: Arboreal anuran; Morphometric analyses; Northeastern India; Western Ghats

THE ASIAN genus of arboreal bufonids, *Pedostibes* Günther 1876, previously shown to be polyphyletic (Boclaer et al. 2009; Pyron and Wiens 2011; Ron et al. 2015), has recently been revised by Chan et al. (2016) with the recognition of a new Sundaic genus, *Rentapia* Chan, Grismer, Zachariah et al. 2016. Although this step has contributed toward providing a taxonomic solution to the problem of polyphyly in *Pedostibes* to a certain extent, the classification and rearrangement therein has not provided complete taxonomic clarity to *Pedostibes*. Not having examined any specimens of the taxa *Pedostibes kempfi* and *P. everetti*, which were ascribed to *Pedostibes* earlier, Chan et al. (2016) made an explicit remark on their uncertain generic status, and provisionally allocated them to the genera *Pedostibes* and *Rentapia* respectively. Although Chan et al. (2016) provided evidence for differentiation of the “Indian” and Sundaic lineages, they did not provide a comprehensive description of the included taxa. Thus, even after the rearrangement by Chan et al. (2016), the genus *Pedostibes* still shows a disjunct pattern in geographic distribution with two representative species, *P. tuberculosus* Günther 1876 and *P. kempfi* (Boulenger 1919) occurring in different biogeographic regions—the Western Ghats and the Garo Hills in the eastern Himalayas (both within the political boundary of India). In order to improve the taxonomic resolution of this group, we present results based on morphological examination of the name-bearing type specimens for all of the relevant taxa from these regions and provide detailed redescriptions of the species along with some justified taxonomic rearrangements. In addition, we provide revised diagnoses to the relevant genera based on (1) osteological characters, (2) refining of species content, and (3) comparison with another recently described Southeast Asian arboreal toad (see Chandramouli et al. 2016) that was not available to Chan et al. (2016).

MATERIALS AND METHODS

Specimens (including types) of the taxa *Pedostibes tuberculosus*, *P. kempfi*, *Rentapia hosii*, *R. everetti*, *R. rugosa*, and *Bufoides meghalayanus* were examined in collections (see Appendix). Museum acronyms follow Sabaj Pérez (2014). We obtained comparable morphometric data and distribution records from examined specimens, as well as available literature (Dinesh and Radhakrishnan 2008; Frost 2015). With a dial caliper (± 0.1 mm) and a Leica Wild M3Z dissecting microscope, we measured the following characters (on the left side of the body for symmetric characters): snout–vent length (SVL, from the tip of the snout to the anterior margin of the cloaca), axilla–groin length (from the posterior margin of the forelimb at its insertion point on the body to the anterior margin of the hind limb at its insertion point on the body), head length (HL, from the posterior edge of the mandible to the tip of the snout), head width (HW, the maximum width of the head at the angle of the jaws), head depth (HD, the maximum depth of the head at the region between the eye and the parotoid gland), body width (the maximum width of the body at the trunk), eye diameter (ED, the greatest horizontal diameter of the orbit), eye–nostril length (EN, from the anterior border of the orbit to the middle of the nostril), eye–snout length (ES, from the anterior border of the orbit to the tip of the snout), snout–nostril length (NS, from the tip of the snout to the middle of the nostril), tympanum–eye length (TYE, from the posterior border of the orbit to the anterior border of the tympanum), upper eyelid width (UEW, the maximum width of the upper eyelid), interorbital distance (IO, the shortest distance between the dorso-medial margins of the orbits), internarial distance (IN, the shortest distance between the dorsal margins of the nostrils), tympanum diameter (TYD, the greatest horizontal diameter of the tympanum), upper arm length (on the dorsal surface, from the axilla to the inflection of the flexed elbow), lower arm length (LAL, on the dorsal surface, from the posterior margin of the elbow while flexed

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to the base of the outer metacarpal tubercle), palm length (PAL, from the posterior border of the outer metacarpal tubercle to tip of the longest finger), femur length (FEL, from the anterior margin of the hind limb at its insertion point on the body to the knee while flexed), tibia length (TBL, from the posterior surface of the knee while flexed to the base of the heel), foot length (FOL, from the base of the inner metatarsal tubercle to the tip of the longest toe), parotoid gland length (PL, the maximum length of the parotoid gland), parotoid gland width (PW, the maximum width of the parotoid gland), and finger and toe lengths (from the tip of the disc to the nearest fork).

A subset of the above measurements (SVL, HL, HW, HD, ED, EN, ES, IO, IN, TYD) was log transformed and subjected to principal components analysis (PCA). Juvenile specimens were excluded from the analysis. Statistically informative tests were not performed on the holotype specimen of *Rentapia everetti* because it is a subadult specimen. However, extensive comparisons of its morphological characters were made. The data from the *R. rugosa* holotype were used. The resulting component scores were plotted to examine the distribution of the specimens in multivariate morphological space. A distribution map of these taxa was prepared based on relevant published literature, type localities, and additional collection localities of specimens examined and those of the corresponding species listed in the VertNet database (available at <http://portal.vertnet.org/>).

One specimen each of *Pedostibes tuberculosus* and *Bufoides meghalayanus* was cleared and stained for studying osteological features (following Hanken and Wassersug 1981). The clear-stained specimens were then examined under an illuminated microscope in order to describe the skeletal traits.

RESULTS

The PCA of the morphometric data extracted factors that, taken together, explained 97.55% of the variance observed between the samples and separated them into three discrete clusters (Table 1; Fig. 1), each pertaining to a particular genus from separate geographic regions. The first cluster comprises the taxa *Bufoides* Pillai and Yazdani 1973 and *Pedostibes kempfi* from northeastern India. The second cluster consists of only the type species, *P. tuberculosus*, from the Western Ghats. The third cluster includes the specimens of *Rentapia hosii* from different parts of Southeast Asia (see Appendix) and the holotype of *R. rugosa*. Our analysis of morphological data (Table 2) reveals that the specimens allocated to the taxon *P. tuberculosus* show a distinct morphological separation from *P. kempfi* which, in turn, clusters together with a morphologically similar and geographically proximate taxon, *Bufoides meghalayanus* (Yazdani and Chanda 1971) from Khasi Hills in the eastern Himalayas. *Rentapia hosii* and *R. rugosa* collectively show a morphological separation from the above two clusters (*P. tuberculosus* and *Bufoides* + *P. kempfi*).

In addition to the morphometric differences detailed above, *Pedostibes tuberculosus* is distinguished from *P. kempfi* in having an exposed tympanum (vs. concealed in *P. kempfi* and *Bufoides*) and from both *Rentapia hosii* and *R. rugosa* by the absence of a sharp tarsal fold (vs. present

and well-defined). Moreover, we observed the following differences in osteological characters (Fig. 2). *Pedostibes tuberculosus* and *R. hosii* have eight presacral vertebrae while *Bufoides meghalayanus* has seven; sternum is bony in *P. tuberculosus* while cartilaginous in *R. hosii* and *B. meghalayanus*. Terminal phalanges in both fingers and toes are widely expanded to truncate discs in *P. tuberculosus*, relatively narrower in *R. hosii*, and with rudimentary expansions in *B. meghalayanus*. Frontoparietal elements of the skull are long and narrow in *P. tuberculosus*, trapezoidal with a much broader posterior than anterior end in *Rentapia*, and ovoid in *Bufoides*.

Based on our results and the above criteria, we hereby restrict the genus *Pedostibes* to its type species, *P. tuberculosus*, from the Western Ghats, southern India. Our results show that the eastern Himalayan taxon, *P. kempfi*, exhibits morphological characters similar to, and diagnostic of, the genus *Bufoides* Pillai and Yazdani 1973. Based on our examination of the type specimens, we transfer *P. kempfi* to *Bufoides*. An examination of the types of the geographically sympatric taxa *Rentapia everetti* and *R. rugosa* did not reveal any morphological characters that serve to separate these two nominal species. Therefore, we synonymize *Rentapia rugosa* with *R. everetti* in accordance with the principle of priority (ICZN 1999: Article 23).

SYSTEMATICS

Bufonidae Gray 1825

Pedostibes Günther 1876

(Tables 2, 3; Figs. 2–4)

Type species.—*Pedostibes tuberculosus* Günther 1876 (by monotypy).

Diagnosis (redefined herein).—The genus *Pedostibes* is diagnosed by having small to moderate adult body size of SVL 35.0–47.2 mm; absence of cephalic ridges; presence of short, rounded parotoid glands; presence of an externally visible tympanum; presence of eight presacral vertebrae; a bony sternum; digit tips widely expanded to spatulate discs with truncate anterior ends; short and broadly expanded sacral diapophysis; absence of tarsal folds; glandular texture of the dorsal skin; presence of partial webbing on fingers and complete webbing on toes (Table 2).

Comparison.—The genus, *Pedostibes*, a member of the largely South Asian Adenominae clade (Bocxlaer et al. 2009), is distinguished from *Rentapia* and other Asian bufonid genera (comparative traits in parentheses) by having smaller adult body size of SVL 35.0–47.2 mm (52.3–99.5 mm in *Rentapia*; up to 215 mm in *Phrynooidis* [fide Malkmus et al. 2002]); absence of cephalic ridges (present in some species of *Duttaphrynus*, *Adenomus*, and *Xanthophryne*); presence of short, rounded parotoid glands (absent in *Sabahphrynus*); presence of an externally visible tympanum (concealed in *Sabahphrynus* and *Bufoides*); presence of partial webbing on fingers (absent in *Duttaphrynus*, *Xanthophryne*, *Adenomus*, *Ghatophryne*, and *Phrynooidis*) and complete webbing on toes (incomplete webbing in *Sabahphrynus*); absence of a tarsal ridge (present in *Rentapia*); presence of eight presacral vertebrae (vs. seven in *Bufoides*); and glandular texture of the dorsal skin (smooth or granular in *Rentapia*, *Xanthophryne*, *Adenomus*, *Ghatophryne*, *Bufoides*, and *Phrynooidis*).

TABLE 1.—Factor loadings and the percentage of variance explained by a principal components analysis of morphometric values from five species of arboreal toads in Southeast Asia.

Trait ^a	Principal component				
	1	2	3	4	5
SVL	0.33	0.00	-0.01	0.02	0.09
HL	0.33	-0.02	-0.20	-0.41	-0.06
HW	0.33	0.06	-0.19	-0.43	0.08
HD	0.32	-0.29	-0.25	0.13	-0.33
ED	0.32	-0.19	-0.39	-0.02	0.38
EN	0.31	0.12	0.58	-0.06	-0.44
ES	0.33	0.10	0.21	-0.32	-0.14
IO	0.31	-0.12	0.52	0.18	0.67
IN	0.29	0.82	-0.23	0.42	0.02
TYD	0.31	-0.41	-0.04	0.56	-0.26
Eigenvalue	8.88	0.35	0.22	0.17	0.15
% variance	88.77	3.47	2.18	1.66	1.47

^a SVL = snout-vent length, HL = head length, HW = head width, HD = head depth, ED = eye diameter, EN = eye-nostril length, ES = eye-snout length, IO = interorbital distance, IN = internarial distance, TYD = tympanum diameter.

Redescription based on a voucher specimen (Wildlife Institute of India, Dehradun, India [WII] 38.6.91 from Tamil Nadu, India).—An unsexed adult, SVL 47.2 mm. Head slightly convex, smooth, and wider than long (HL 84.0% of HW, 25.0% of SVL), lacking cranial ridges. Nostril oval in shape, laterally oriented, with a slender inner margin. Internarial area smooth and concave. Canthal ridges weakly defined and rounded in dorsal aspect. Snout smooth, flat in lateral aspect and pointed in dorsal aspect (ES 35.8% of HL, 9.0% of SVL). Nostril to snout distance less than distance between eye and nostril (NS 3.0% of EN). Loreal region oblique and smooth. Large distinctly visible tympanum, vertically oval. Parotoid glands weakly distinct, rounded, small, smooth and undivided (unlobulated). Interorbital area flat, broad and smooth, IN less than interorbital width (IN 52.8% of IO). Upper eyelids concave, their outer edges rounded, width less than interorbital width.

Lower arm shorter than head (LAL 112.0% of HL, 28.0% of SVL). Fingers with basal webbing and tips of fingers sharp and smooth, Finger III the longest. Finger I slightly shorter than II. Relative length of fingers I < II < IV < III. Terminals with widely expanded discs; base of the Finger IV with a large, flat, oval outer metacarpal tubercle.

Femur and tibia equal in length (FEL 46.0% of SVL). Foot length shorter than TBL (FOL 104.5% of TBL, 47.0% of SVL). Two metatarsal tubercles present, a larger lateral tubercle and a smaller medial tubercle; tarsal ridge absent. Toe IV the longest. Toes completely webbed; the dorsal and ventral surfaces of all toes smooth, their tips rounded.

Skin structures.—Dorsal skin glandular in texture; not warty. Small globular glandules present on the dorsal and dorso-lateral regions, more intensely on posterior than on anterior part. Ventral surface with small warts, less dense on anterior and posterior ends but intense on the belly. Groin and undersurfaces of the thigh smooth.

Coloration (in preservative).—Pale brown above with dark and white marbled pattern along the flanks; ventral surfaces with marbled pattern.

Distribution.—*Pedostibes* is endemic to the Western Ghats of Peninsular India and has been recorded from localities between the Agasthyamalai Hills (8.50°N, 77.47°E, 1000 m elevation; in all cases, datum = WGS84) in the south, northward to Amboli (15.96°N, 73.99°E, 744 m elevation) in the northern portion of the Western Ghats (Fig. 4; Dinesh and Radhakrishnan 2008).

Included species.—*Pedostibes tuberculosus* Günther 1876 (with the genus *Pedostibes* being monotypic).

Rentapia Chan, Grismer, Zacharia, Brown, and Abraham 2016

(Tables 2, 3; Figs. 2–4)

Type species.—*Nectophryne hosii* Boulenger 1892.

Diagnosis.—*Rentapia* is characterized by having large adult body size of SVL 52.3–99.5 mm, long and relatively narrow sacral diapophyses, and presence of a cartilaginous sternum (Table 2). In addition to the traits described by Chan et al. (2016), this genus is characterized by the presence of tarsal folds and smooth or granular texture of the dorsal skin.

Comparison.—Phylogenetically, the genus *Rentapia* is not a member of the Adenominae clade and can be defined as the member of a clade including *Phrynoidis* as its closest taxon (Matsui et al. 2007, 2015; Bocxlaer et al. 2009; Pyron and Wiens 2011; Ron et al. 2015; Chan et al. 2016), but not *Pedostibes tuberculosus*. *Rentapia* is distinguished from *Pedostibes*, *Phrynoidis*, and other Asian bufonid genera (characters in parentheses) by having larger adult body size of SVL 52.3–99.5 mm (21.8–27.4 mm in *Blythophryne* Chandramouli, Vasudevan, Harikriahnan et al. 2016; 35.0–47.2 mm in *Pedostibes*; 215 mm in *Phrynoidis* [fide Malkmus et al. 2002]); absence of cephalic ridges (present in some species of *Duttaphrynus*, *Adenomus*, and *Xanthophryne*); presence of short, rounded or triangular parotoid glands (absent in *Sabahphrynus*, slender and elongated in *Blythophryne*); presence of an externally visible tympanum (hidden in *Sabahphrynus* and *Bufoides*); presence of expanded discs in finger and toe tips (absent in *Phrynoidis*); presence of

TABLE 2.—Comparison of the characters of the morphologically similar species of arboreal toads formerly assigned to the genus *Pedostibes*.

Character	<i>Pedostibes tuberculosus</i> (n = 3)	<i>Rentapia hosii</i> (n = 43)	<i>Rentapia everetti</i> (n = 2)	<i>Bufoides kempi</i> (n = 2)
Type locality	“Malabar,” South India	Mt. Dulit, Borneo	Mt. Kinabalu, Borneo	Tura, Garo Hills, Northeast India
Adult snout-vent length (mm)	35.0–47.2	52.3–99.5	74.3 (n = 1)	17.3–29.8
Cephalic ridges	Absent	Absent	Absent	Present
Parotoid glands	Short and round	Elongated	Oval	Elliptical
Tympanum	Distinct	Distinct	Moderately distinct	Hidden
Tarsal folds	Absent	Present	Present	Absent
Dorsal skin	Glandular	Smooth	Granular	Granular
Webbing on fingers	Partial	Basal	Basal	Basal
Webbing on toes	Fully	Fully	Fully	3/4
Throat	Granular	Granular	Smooth	Granular

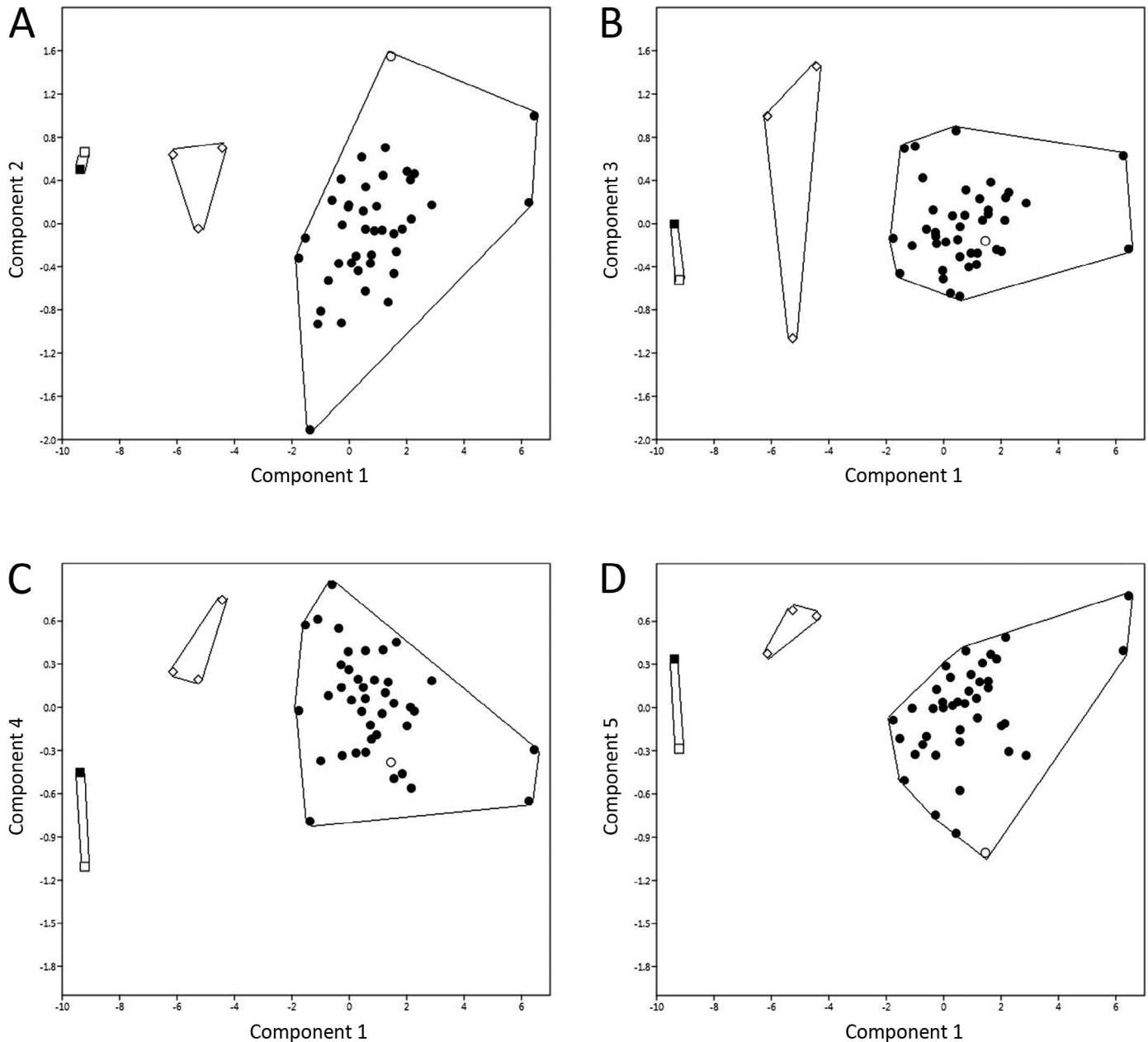


FIG. 1.—Plotted results of principal component (PC) analyses showing morphometric separation between five species of arboreal toads: *Pedostibes tuberculosus* (open diamonds), *Rentapia hosii* (filled circles), *R. everetti* (open circles), *Bufoides meghalayanus* (open squares), and *B. kempii* (filled squares). (A) PC1 vs. PC2; (B) PC1 vs. PC3; (C) PC1 vs. PC4; (D) PC1 vs. PC5.

partial webbing on fingers (absent in *Phrynoidis*) and complete webbing on toes (incomplete webbing in *Sabahphrynus*); presence of eight presacral vertebrae (vs. seven in *Bufoides* and six in *Blythophryne*); presence of a tarsal ridge (absent in *Pedostibes* and *Bufoides*); and smooth or rugose texture of the dorsal skin (granular in *Phrynoidis*; glandular in *Pedostibes*).

Distribution.—*Rentapia* occurs in Peninsular Thailand, Malaysia, Borneo, and Sumatra (Fig. 4; Frost 2015; Chan et al. 2016).

Included species.—*Rentapia hosii* (Boulenger 1892) and *R. everetti* (Boulenger 1896).

Rentapia hosii (Boulenger 1892)

Nectophryne hosii Boulenger 1892:508.

Pedostibes hosii—Barbour (1938:192).

Pedostibes hosi—Inger (1958:478).

Pedostibes hosei—Inger (1966:93).

Rentapia hosii—Chan et al. 2016:9.

Holotype of *Nectophryne hosii*.—Adult male (Natural History Museum, London, UK [BMNH] 1947.2.19.29; formerly 92.6.3.19), “Mt. Dulit, Sarawak,” East Malaysia (Borneo).

Diagnosis.—*Rentapia hosii* is distinguished by having large adult body size of SVL 52.3–99.5 mm, absence of cephalic ridges, presence of elongated parotoid glands, presence of an externally visible tympanum, presence of tarsal folds, smooth texture of the dorsal skin, presence of basal webbing on fingers and complete webbing on toes, and granular texture of the throat skin (Table 2).

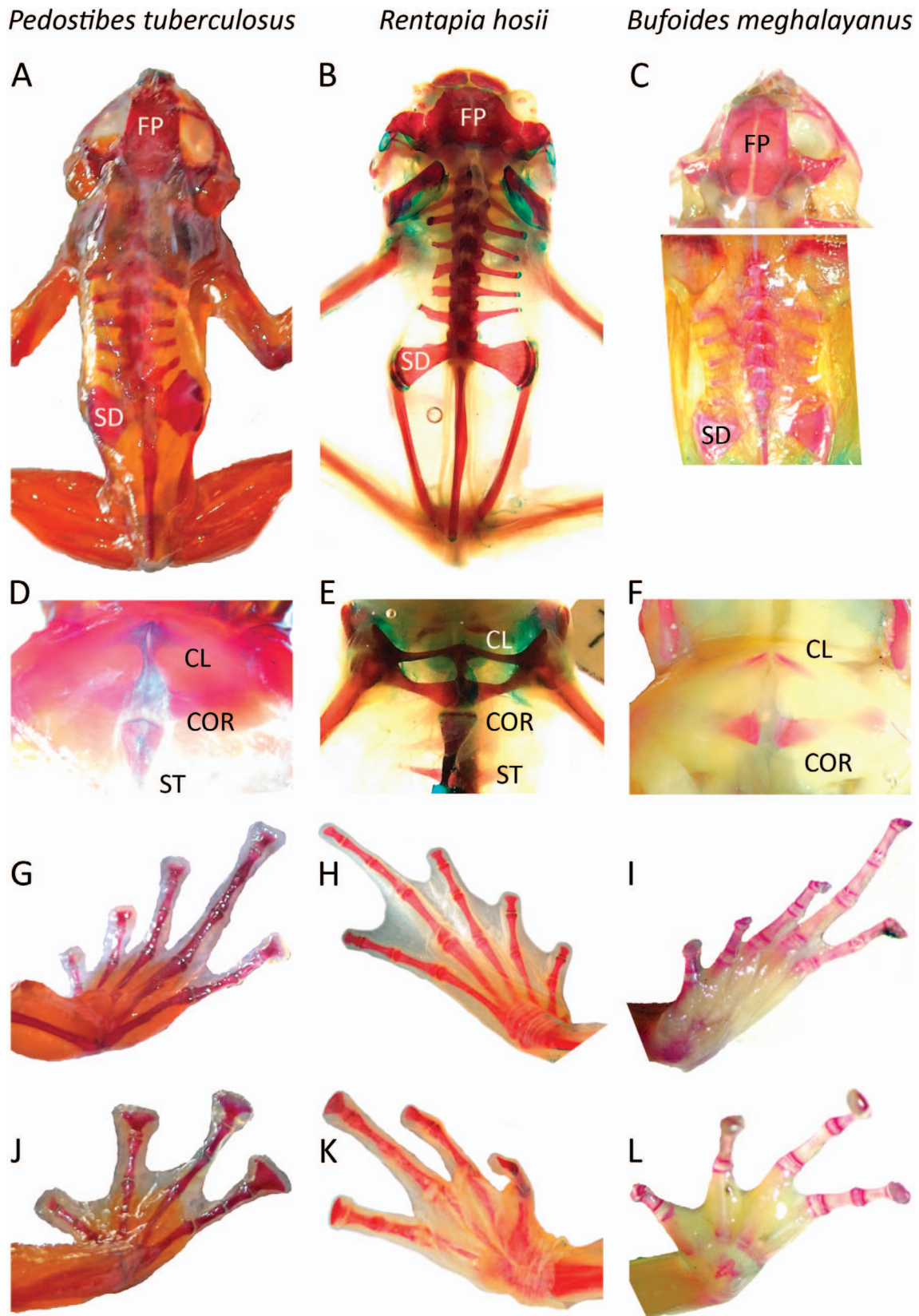


FIG. 2.—Cleared and stained specimens of *Pedostibes tuberculosis* (first column), *Rentapia hosii* (second column), and *Bufooides meghalayanus* (third column) showing dorsal views of the following skeletal characters: skull and vertebral column (A–C), pectoral girdle (D–F), feet (G–I), and hand (J–L). FP = frontoparietal; SD = sacral diapophysis; CL = clavicle; COR = coracoid; ST = sternum. A color version of this figure is available online.

TABLE 3.—Comparison of the morphometric measurements (mm) of the holotypes of *Rentapia hosii*, *R. everetti* and its junior synonym, *Rentapia rugosa*.

Character	<i>Rentapia hosii</i>		<i>Rentapia everetti</i>	
	<i>Nectophryne hosii</i> (adult male; BMNH 1947.2.19.29)	<i>Nectophryne everetti</i> (subadult male; BMNH 1947.2.18.27)	<i>Nectophryne everetti</i> (adult male; FMNH 81297)	<i>Pedostibes rugosus</i> (adult male; FMNH 81297)
Snout–vent length	59.8	33.0	74.3	
Axilla–groin length	29.8	14.7	24.5	
Head length	17.9	11.5	22.7	
Head width	18.5	9.7	24.8	
Head depth	10.3	5.6	11.0	
Body width	13.5	7.9	17.5	
Eye diameter	6.9	4.3	6.5	
Eye–nostril length	5.2	2.5	6.3	
Snout–nostril length	1.8	1.1	2.5	
Eye–snout length	7.0	4.0	9.7	
Tympanum–eye length	0.8	0.8	1.1	
Upper eyelid width	4.6	2.7	8.5	
Interorbital distance	7.8	3.7	7.6	
Internarial distance	3.5	1.5	4.5	
Tympanum diameter	3.5	1.3	3.2	
Upper arm length	11.3	7.0	19.8	
Lower arm length	17.3	8.2	21.4	
Palm length	15.4	10.6	24.6	
Femur length	28.8	11.5	30.4	
Tibia length	28.8	15.4	33.5	
Foot length	25.4	12.9	34.2	
Parotoid gland length	6.9	4.3	10.1	
Parotoid gland width	3.2	1.7	7.4	
Finger I length	4.8	1.5	5.0	
Finger II length	6.6	3.7	11.9	
Finger III length	10.3	5.5	16.2	
Finger IV length	9.5	2.6	10.7	
Toe I length	3.8	2.1	5.7	
Toe II length	5.5	2.5	8.6	
Toe III length	8.4	3.7	11.4	
Toe IV length	14.1	6.1	18.9	
Toe V length	9.5	4.3	11.7	

Redescription of holotype.—An adult male SVL of 59.8 mm. Head slightly concave, smooth and wider than long (HL 96.7% of HW, 29.9 of SVL). Nostril oval in shape, laterally oriented, with a slender inner margin. Internarial area smooth and concave. Canthal ridges prominently defined and rounded in dorsal aspect. Snout smooth, rounded in lateral aspect and pointed in dorsal aspect (ES 39.1% of HL, 11.7% of SVL), NS less than distance between eye and nostril (NS 34.6% of EN). Loreal region oblique and smooth. Large distinctly visible tympanum, vertically oval (TYE 4.5% of HL). Parotoid glands elongated, narrow (posteriorly wider), smooth, and undivided (unlobulated; PW 46.4% of PL; PL 38.5% of HL). Interorbital area concave and smooth, IN less than interorbital width (IN 44.8% of IO). Upper eyelids concave, their outer edges rounded, width less than interorbital width (UEW 58.9% of IO).

Lower arm slightly shorter than head (LAL 96.6% of HL, 28.9% of SVL). Fingers with basal webbing and tips of fingers sharp and smooth, Finger III the longest (FL3 66.8% of PAL, 59.5% of LAL, 147.1% of ES). Finger I slightly shorter than II (FL1 72.7% of FL2). Relative length of fingers I < II < IV < III, a nuptial pad on dorsal side of Finger I. Subarticular tubercles on fingers rounded, two palmar tubercles, the lateral one larger than the medial.

Femur and tibia equal in length (FEL 48.1% of SVL). Foot length shorter than TBL (FOL 88.2% of TBL, 42.5% of SVL). Two metatarsal tubercles present, the medial one oval,

the lateral one rounded; tarsal ridge present. Toe IV the longest (TL4 55.5% of FOL, 78.7% of HL, 201.4% of ES, 167.8% of TL3). Toes completely webbed, the dorsal and ventral surfaces of all toes smooth, their tips rounded. Relative surface of toes I < II < III < V < IV.

Skin structures.—Throat rough and granulated, but belly smooth. Both sides of the gape without warts, and distal edges of lower and upper jaws are smooth. Anterior end of mandible with symphyseal knob. Axilla-to-groin area smooth. Middorsal area smooth and larger warts present on lateral and posterior parts of the body. Both dorsal and ventral surfaces of arms covered with sharp and rough small warts on dorsal aspect. Thigh relatively smooth on both anterior and posterior surfaces.

Coloration (in preservative).—Dorsum uniform with olive brown; dorsal surfaces of limbs without any bars; all ventral surfaces similar to dorsal coloration, except for a darker throat.

Variation.—In some live specimens from East Kalimantan, we observed a dark variegated skin color pattern in *Rentapia hosii*.

Distribution.—*Rentapia hosii* occurs in peninsular Thailand, Malaysia, Borneo, and Sumatra (Fig. 4; Frost 2015).

Rentapia everetti (Boulenger 1896)

Nectophryne everetti Boulenger 1896:450.

Pedostibes everetti—(Barbour 1938:192).

Pedostibes rugosus Inger 1958:476–478 syn. nov.

Rentapia rugosus—Chan et al. 2016:9,11.

Rentapia rugosa—Chandramouli and Amarasinghe (2016) [this work].

Holotype of *Nectophryne everetti*.—A subadult male (BMNH 1947.2.18.27; formerly 96.4.29.13), “Mount Kina Balu, North Borneo,” Sabah, East Malaysia (Borneo).

Nomenclatural note.—When transferring the taxon *Pedostibes rugosus* Inger 1958 to the genus *Rentapia*, Chan et al. (2016) used the combination *Rentapia rugosus* (sic.). According to the International Code of Zoological Nomenclature (ICZN 1999) Articles 30 and 31, the generic name *Rentapia* erected by these authors is feminine in gender. Because the specific epithet, *rugosus*, is an adjective in masculine gender, referring to the rugose texture of its skin, we amend it here as *Rentapia rugosa*, in accordance with the Article 31.2 (Agreement in Gender).

Diagnosis.—*Rentapia everetti* is distinguished by having large adult body size of SVL 74.3 mm, absence of cephalic ridges, presence of oval parotoid glands, presence of an externally visible tympanum, presence of tarsal folds, granular texture of the dorsal skin, presence of basal webbing on fingers and complete webbing on toes, and smooth texture of the throat skin (Table 2).

Redescription of the holotype of *Nectophryne everetti*.—A subadult male SVL of 33.0 mm. Head slightly concave, wider than long (HW 118.5% of HL, 34.8% of SVL) and with numerous tiny round warts. Nostril round in shape, laterally oriented, with a slender inner margin, Internarial area concave with tiny warts. Canthal ridges prominently defined and sharp in dorsal aspect. Snout with tiny warts, flat in both lateral and dorsal aspects (ES 34.8% of HL, 12.1% of SVL), Nostril to snout distance less than distance between eye and nostril (NS 44.0% of EN). Loreal region oblique and



FIG. 3.—Dorsal aspect of the bodies of five species of arboreal toads collected from southern and Southeast Asia: (A) holotype of *Rentapia hosii* BMNH 1947.2.19.29; (B) holotype of *R. everetti* BMNH 1947.2.18.27; (C) holotype of *Rentapia rugosa* (junior synonym of *R. everetti*) FMNH 81297; (D) a syntype of *Pedostibes tuberculosus* BMNH 1947.2.22.70; (E) a voucher specimen of *Bufoides meghalayanus* (WII uncatalogued); and (F) a syntype of *Nectophryne kempfi* (ZSI 18481A). In each panel, bar = 5 mm. A color version of this figure is available online.

smooth. Small distinctly visible tympanum, vertically oval (TYE 6.9% of HL). Parotoid glands elongated, narrow (posteriorly wider), rough and undivided (unlobulated; PW 39.5% of PL; PL 37.4% of HL). Interorbital area flat and with tiny warts, internarial distance less than interorbital width (IN 40.5% of IO). Upper eyelids concave, their outer edges sharp, width less than interorbital width (UEW 72.9% of IO).

Lower arm shorter than head (LAL 71.3% of HL, 24.8% of SVL). Fingers with basal webbing, web reaching subarticular tubercle of Finger I, beyond basal subarticular tubercle on lateral edge of II. Tips of fingers sharp and smooth, with Finger III being the longest (FL3 51.8% of PAL, 67.1% of LAL, 137.5% of ES). Finger I shorter than II (FL1 40.5% of FL2). Relative length of fingers I < II < IV < III, a nuptial pad on dorsal side of Finger I. Subarticular tubercles on fingers rounded; two palmar tubercles, the lateral one larger than the medial.

Femur shorter than tibia in length (FEL 34.8% of SVL). Foot length shorter than TBL (FOL 83.7% of TBL, 39.1% of SVL). Two metatarsal tubercles present, the medial one oval,

the lateral one rounded; tarsal ridge present. Toe IV the longest (TL4 47.3% of FOL, 53.0% of HL, 174.3% of ES, 164.8% of TL3). Toes completely webbed, the dorsal and ventral surfaces of all toes smooth, their tips rounded. Relative length of Toes I < II < III < V < IV.

Skin structures.—Throat smooth and not granulated, belly smooth. Both sides of the gape without warts, and distal edges of lower and upper jaws are smooth. Anterior end of mandible with symphyseal knob. Axilla-to-groin area is smooth. Middorsal area, lateral and posterior parts of the body present with larger warts. Both dorsal and ventral surfaces of arms covered with sharp and rough small warts on dorsal aspect. Thigh comparatively smooth on both anterior and posterior surfaces.

Coloration (in preservative).—Dorsum bluish grey and limbs light brown; back with many dark brown blotches, lateral surfaces of head with broad, dark brown bars; dorsal surfaces of limbs cross barred; all ventral surfaces immaculate cream-colored.

Distribution.—*Rentapia everetti* occurs in Borneo (Fig. 4; Frost 2015).

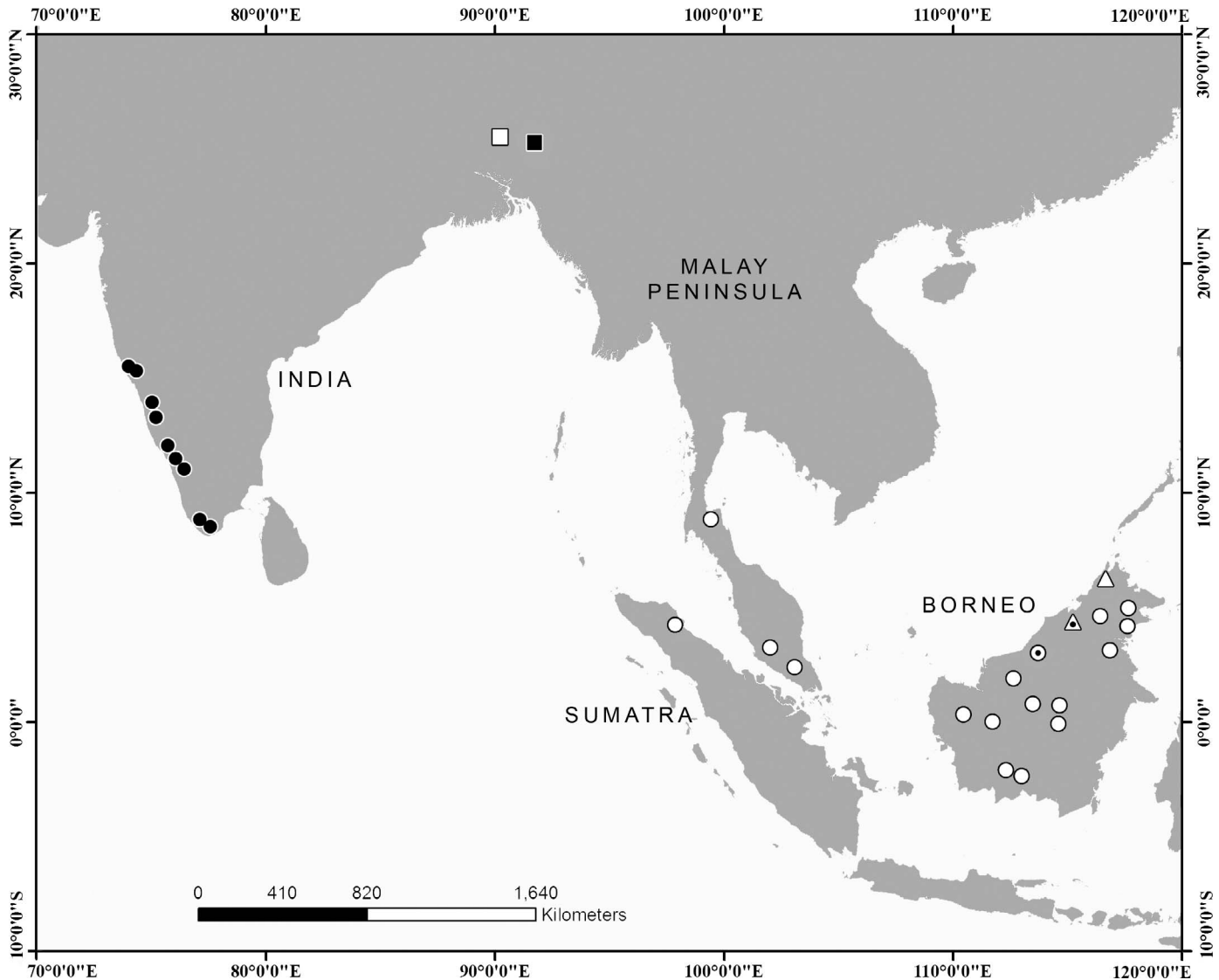


FIG. 4.—Collection localities for five species of arboreal toads in Southeast Asia, modified after Chan et al. (2016): *Bufoides kempii* (open square, type locality), *B. meghalayanus* (closed square, type locality), *Pedostibes tuberculatus* (closed circles), *Rentapia everetti* (open triangle, type locality of *R. rugosa* with a dot in the middle), and *R. hosii* (open circles, type locality with a dot in the middle).

Bufoides Pillai and Yazdani 1973
(Table 2; Figs. 2–4)

Type species.—*Ansonia meghalayanana* Yazdani and Chanda 1971.

Diagnosis (redefined herein).—A genus of small-bodied (SVL 29.8–47.2 mm), rupicolous toads, characterized by presence of supraorbital, preorbital, and postorbital ridges on the top of the head; presence of short, oval-shaped parotoid glands; absence of an externally visible tympanum; digit tips with rounded, poorly dilated discs; presence of seven presacral vertebrae; presence of a cartilaginous sternum; granular texture of the dorsal skin; absence of tarsal folds; and presence of basal webbing on fingers and complete webbing on toes (Table 2).

Comparison.—*Bufoides* can readily be distinguished from other oriental bufonid genera (characters in parentheses) by the absence of an externally visible tympanum (exposed in *Pedostibes*, *Blythophryne*, *Parapelophryne*, and *Rentapia*); presence of parotoid glands (absent in *Parapelo-*

phryne and *Pelophryne*); presence of cranial ridges (absent in *Pedostibes*, *Blythophryne*, *Parapelophryne*, and *Rentapia*); poorly developed digital discs on fingers and toe tips (well developed, widely dilated discs in *Pedostibes*, *Blythophryne*, and *Rentapia*); presence of seven presacral vertebrae (six in *Blythophryne*, eight in *Pedostibes*, *Parapelophryne*, and *Rentapia*); granular skin texture (glandular in *Pedostibes*); and the absence of tarsal folds (present in *Rentapia*).

Distribution.—*Bufoides* is restricted in distribution to the Garo and Khasi hills of the eastern Himalayas, with one species occurring on each of these hill ranges.

Included species.—*Bufoides kempii* (Boulenger 1919) comb. nov. and *Bufoides meghalayanus* (Yazdani and Chanda 1971).

Bufoides kempii (Boulenger 1919) comb. nov.
(Table 2; Figs. 3, 4)

Nectophryne kempii (Boulenger 1919:207).

Pedostibes kempii—Barbour (1934:192); Chan et al. (2016:13).

Diagnosis.—*Bufoides kemp* is diagnosed by small to moderate body size (SVL 17.4–29.8 mm); presence of nonkeratinized cranial ridges; presence of short, oval-shaped parotoid glands; absence of an externally visible tympanum; moderate degree of webbing on toes and basal webbing on fingers, with poorly developed terminal discs without lateral expansions.

Redescription of the syntypes.—Characters of Zoological Survey of India, Kolkata, India (ZSI) 18481A followed, when appropriate, by those of ZSI 18481B in parentheses. An adult and a subadult (unsexed) specimen, each measuring 29.8 mm (17.4 mm) SVL; head distinct from body, broader than long, HL 89.0% (87.0%) of HW, 30.0% (33.0%) of SVL. Nostril to snout distance less than distance between eye and nostril, NS 33.0% (23.0%) of EN. Snout rounded in dorsal and truncate in lateral views; canthal fold not pronounced. Loreal region flat; top of the snout concave; tympanum absent; a large conical tubercle present at the jaw angle. Parotoid glands lobulated, short, and bean-shaped, extending from the postorbital region to the axillary region on the dorsum. Interorbital space broader than internarial distance, IN 49.0% (64.0%) of IO. Upper eyelids with dense granules; narrower than interorbital distance.

Lower arm longer than head, LAL 139.0% (115.0%) of HL, 24.0% (26.0%) of SVL. Fingers webbed at the base, fingertips with small discs at tips, damaged and broken in the larger specimen. A large outer palmar tubercle present at the base of the palm.

Femur longer than tibia in the smaller specimen, FEL 37.0% (43.0%) of SVL, tibia broken in the larger syntype. Two oval metatarsal tubercles present; inner one larger than outer; tarsal ridge not discernible. Most of the toes damaged in both the specimens but the left foot of the smaller specimen shows partial webbing between Toes II and III, extending half the length of Toe III and similarly on Toe IV; toe tips with small discs.

Skin structures.—Dorsum granular with small conical warts scattered throughout; more intense toward lateral area than on the dorsal region. Venter with similar granules of smaller size; more intense on the posterior than on anterior end.

Coloration in preservative.—The larger of the two syntypes olive brown above with dark black flanks; the smaller specimen uniform black throughout; undersides without pattern, black in both specimens.

Distribution.—This species is known only from its type locality, Tura, in the Garo Hills of northeastern India.

Bufoides meghalayanus (Yazdani and Chanda 1971)

Ansonia meghalayana Yazdani and Chanda 1971.

Diagnosis.—*Bufoides meghalayanus* is diagnosed by small to moderate adult size (SVL 31.2–47.2 mm); presence of pre-, post-, and supraorbital ridges on the head; presence of short, oval-shaped parotoid glands; absence of an externally visible tympanum; digit tips with rounded, poorly dilated discs; granular texture of the dorsal skin; absence of tarsal folds; presence of basal webbing on fingers and nearly complete webbing on toes, with poorly developed terminal discs.

Description of a voucher specimen (WII uncatalogued, from Khasi Hills, Meghalaya, India).—An unsexed adult, SVL of 31.2 mm. Head depressed, a little

broader than long (HL 110.0% of HW, 35.0% of SVL); snout projecting beyond mandible, with a rounded tip in both dorsal and lateral views (ES 39.0% of HL, 14.0% of SVL); nostrils pointing downward, located midway between eyes, a little closer to snout tip than to the eyes (NS 202.0% of EN); loreal region slightly concave with an indistinct canthal fold. Preorbital, postorbital, and supra-orbital ridges on the head prominent; not keratinized. Loreal and internarial regions concave. Tympanum absent; parotoid glands slender and slightly elongate (PW 13.0% of PL; PL 48.0% of HL); extending downward from the postorbital ridge. Interorbital distance greater than upper eyelid width (IN 58.0% of IO).

Lower arm much shorter than the head (LAL 70.0% of HL); palm as long as the upper arm, with fleshy webbing extending only to the base of the fingers; relative lengths of fingers I < II < IV < III. Subarticular tubercles on fingers indistinct, outer palmar tubercle large and distinct.

Femur a little longer than the tibia (FEL 43.0% of SVL); foot nearly as long as tibia length (FOL 97.0% of TBL, 39% of SVL). Two metatarsal tubercles present, the medial one oval, the lateral one rounded; tarsal ridge absent. Toes with well-developed webbing; their relative lengths I < II < III < V < IV; digit tips with small fleshy discs without expanded terminal phalanges.

Skin structures.—Dorsal surfaces with small, almost uniform granular warts scattered all over the body; arms and legs. Ventral surfaces rough with granules sparsely distributed in the anterior region from the chin, across the throat to the axilla; densely granulated posteriorly.

Coloration in preservative.—Dorsum without pattern, uniform greyish brown; venter pale white in color throughout.

Distribution.—*Bufoides meghalayanus* has been recorded from a few localities in the Khasi Hills of Meghalaya near Mawblang, Cherrapunji. Other records from this region were provided by Deuti et al. (2012).

DISCUSSION

After Boulenger (1892, 1896) described *Nectophryne hosii* and *N. everetti*, Inger (1958) described *Pedostibes rugosus* from “Menuang, headwaters of the Baleh River” in Sarawak, based on a male holotype (Field Museum of Natural History, Chicago, USA [FMNH] 81297) and a female paratype. This taxon was diagnosed solely on the presence of “large oval parotoid glands, numerous round warts dorsally, and a sharp tarsal fold.” Upon describing this taxon, Inger (1958) remarked that only two species of *Pedostibes*, *P. hosii* and *P. rugosus*, have a sharply defined tarsal fold; thus, he eliminated *P. tuberculatus* from further comparisons and distinguished *P. rugosus* from *P. hosii* based on a set of characters. Two more congeners (after Barbour 1938), *P. kemp* and *P. everetti*, were neither mentioned nor compared. Among them, *P. kemp* is easily distinguishable from the rest of the species by lacking an externally visible tympanum (Boulenger 1919).

The diagnostic characters of *Pedostibes rugosus* in its original description coincide with those described for the taxon *P. everetti* by Boulenger (1896), which was apparently overlooked. Additionally, the type localities of these two taxa (i.e., “Menuang, headwaters of the Baleh River” for *P. rugosus* and “Mt. Kina Balu, north Borneo” for *P. everetti*)

are situated within the same biogeographical region of Borneo (Fig. 4). Malkmus et al. (2002) remarked on the similarity between *P. rugosus* and *P. everetti*, and cited Manthey and Grossman (1997), who suggested that none of the diagnostic characters of *P. rugosus* were distinct from character states exhibited by *P. everetti*. Although Inger (1966) mentioned additional morphological differences between *P. rugosus* and *P. everetti*, our reexamination of their type specimens leads us to conclude that Inger's (1966) characters are not sufficiently diagnostic to distinguish those species. This is further supported by the fact that *P. everetti* has seldom been mentioned in field-based scientific studies since the name *Pedostibes rugosus* came into being, essentially concealing the former taxon (e.g., see Das 2007; Matsui et al. 2007, 2015; Pyron and Wiens 2011; Ron et al. 2015). Our reexamination of the type specimens (BMNH 1947.2.18.27 and FMNH 81297, respectively) and original descriptions of these two taxa support Manthey and Grossman (1997) in that the morphological distinction between *P. rugosus* and *P. everetti* is effectively absent.

In the original description of *Nectophryne kempfi*, Boulenger (1919) distinguished it from "congeners" based on the following diagnostic characters: tympanum hidden; fingers with feebly dilated, truncated tips, 1/3 webbed; toes 3/4 webbed, tips rounded but not dilated; two small metatarsal tubercles, absence of tarsal fold; presence of prominent parotoid glands; and large, yellowish axillary spots. He also remarked on the similarity of *N. kempfi* with *N. maculata* in lacking an externally visible tympanum (Boulenger 1919). Barbour (1938: 192) transferred *N. kempfi* to *Pedostibes* with some degree of caution by stating "The four species of *Pedostibes* first mentioned and possibly this fifth one as well [*P. kempfi*] are alike..." where he refers to the taxa *P. tuberculosis*, *P. hosii*, *P. everetti*, and *P. altitudinis* [the lattermost of which currently represents a synonym of an unrelated species, *Ansonia fuliginea* (Mocquard 1890); see Frost 2015]. Additionally, even after revising *Pedostibes*, Chan et al. (2016) attributed the "Indian" species *kempfi* to this genus, making a remark on the uncertainty of this allocation. Moreover, limited taxon sampling has hindered Chan et al. (2016) from comparing this taxon with the other arboreal toad genus *Bufo* from the eastern Himalayan region.

When erecting it for the taxon *Ansonia meghalayana* Yazdani and Chanda 1971, Pillai and Yazdani (1973) characterized the genus *Bufo* based on the presence of cranial ridges, unwebbed fingers with dilated tips, almost fully webbed toes, and a concealed tympanum. Das et al. (2009) procured further specimens of *B. meghalayanus* from the type locality and identified an unstudied diversification within *Bufo* endemic to India by referring to specimen MFA 10134 collected from Tura, Garo Hills (the type locality of *Nectophryne kempfi*), which is not conspecific with *B. meghalayanus*. Prompted by its provenance, we suspect that this specimen could possibly represent the taxon *kempfi*. Furthermore, Das et al. (2009) identified a discrepancy from the original description, that the type series of *B. meghalayanus* has well-developed parotoid glands. Thus, both the taxa *Pedostibes kempfi* and *B. meghalayanus* share the following suite of morphological characters considered to be diagnostic: absence of an externally visible tympanum, presence of parotoid glands, and well-developed webbing in toes. The two species occur in two different hill ranges,

however: *B. kempfi* from Tura, Garo Hills and *B. meghalayanus* from Mawblang, Khasi Hills. Our reexamination the specimens of these two taxa complies with the above-mentioned set of similarities. Hence, we transferred the taxon *Pedostibes kempfi* to the genus *Bufo* in the new combination, *Bufo kempfi*. Whether *B. meghalayanus* and *B. kempfi* represent the same species or not, however, is a question that remains open for further research. Pending collection of new specimens referable to *P. kempfi* from the Garo Hills, we take a conservative stand and retain them to be specifically distinct.

The systematic status of the South and Southeast Asian bufonids at the generic level has long been problematic, as interpreted from the following examples. Once considered to be globally distributed, the genus *Bufo* Garsault 1764 was subjected to several systematic and taxonomic studies resulting in the reevaluation and recognition of several valid genera such as *Adenomus*, *Duttaphryne*, *Ingerophryne*, *Phrynooidis*, *Vandjikophryne*, and *Xanthophryne* (see Manamendra-Arachchi and Pethiyagoda 1998; Frost et al. 2006; Biju et al. 2009). All of these clades show a narrow, finite geographic distribution range (*Adenomus*: Sri Lanka; *Duttaphryne*, *Ingerophryne*, and *Phrynooidis*: South and Southeast Asia; *Vandjikophryne*: South Africa; and *Xanthophryne*: northern portion of the Western Ghats in peninsular India; Frost 2015). Similar cases are also known for certain genera that were once considered to be widely distributed, with some species showing disjunct distribution ranges. Examples include the transfer of *Ansonia ornata* Günther 1876 to *Ghatophryne* by Biju et al. (2009), and validation of *Pedostibes* from the synonymy of *Nectophryne* Buchholz and Peters 1875 by Barbour (1938). Frost (2015) suggested a similar scenario for *Pedostibes* according to its current definition by stating that, instead of providing a taxonomic remedy, Pyron and Wiens (2011) embraced a polyphyletic *Pedostibes*. Ron et al. (2015) also commented on the problem of a polyphyletic *Pedostibes*, and suggested generic transfer of the taxa *hosii* and *rugosus* to *Phrynooidis*, although they were not transferred formally. Chan et al. (2016) resolved this problem by erecting a new generic name *Rentapia* for the Sundaic species *hosii*, *everetti*, and *rugosus*. Because Chan et al. (2016) did not present a comprehensive taxon-sampling (e.g., *Bufo*) or examination of the name-bearing types, they provided some tentative conclusions at both generic and specific levels in some cases. Chan et al. (2016) expressed uncertainty with such species and thus made some provisional rearrangements within this clade. Our reexamination of the types and other material has revealed finer patterns within this group, and led to a few other taxonomic rearrangements.

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APPENDIX

Specimens Examined

- Bufoides kempi* (Boulenger 1919).—Garo Hills, Assam, Meghalaya, India: ZSI 18481A–B (syntypes).
- Bufoides meghalayanus* (Yazdani and Chanda 1971).—Meghalaya, Northeast India: WII uncatalogued.
- Pedostibes tuberculatus* Günther 1876.—Malabar (Western Ghats), South India: BMNH 1947.2.22.70–71 (syntypes); Tamil Nadu, South India: WII 38.6.91.
- Rentapia everetti* (Boulenger 1896).—Mt. Kina Balu, Sabah, Malaysia: BMNH 1947.2.18.27 (holotype); Menuang, headwaters of the Baleh River, Third Division, Sarawak, Malaysia: FMNH 81297 (holotype of *Pedostibes rugosus* Inger 1958).
- Rentapia hosii* (Boulenger 1892).—Mt. Dulit, Sarawak, Malaysia: BMNH 1947.2.19.29 (holotype); East Kalimantan, Indonesia: MZB 7779, 7780, 7864–67, 8891–99, 8900, 15454, 15455; Central Kalimantan, Indonesia: 3127, 3136, 8901–05, 10804, 10805, 11777, 11778, 17098; West Kalimantan, Indonesia: 4758, 4759, 4761, 7250; South Kalimantan, Indonesia: 6083–89; Aceh, Sumatra, Indonesia: 6904, FMNH 77369.
- Phrynooides juxtasper* (Inger 1966).—N. Borneo, Tauwau Dist, Kalabakan, Sungei Kadat: Museum of Comparative Zoology, Harvard, USA (MCZ) A-51649 (paratype).