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Resurrection of *Amolops nepalicus* Yang, 1991 (Amphibia: Anura: Ranidae), with Comments on the Record of *A.* cf. *afghanus* in Nepal and China and the Validity of Two Other Junior Synonyms of *A. marmoratus* (Blyth, 1855)

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Abstract

The taxonomic validity of the controversial taxon, *Amolops nepalicus* Yang, 1991, is evaluated based on the examination of its holotype, along with topotypic *A. marmoratus* (Blyth, 1855) and *A. afghanus* (Günther, 1858), and other related congeners. Morphological comparison shows the holotype of *A. nepalicus* differs from its senior synonym *A. marmoratus* and all recognized species, supporting its valid species status. We provide a detailed redescription of the holotype based on a robust morphometric dataset and expanded comparisons with recognized congeners from the Pan-Himalayas and Southeast Asia. In addition, we discuss the remaining suspicious records of *A.* cf. *afghanus* in Nepal and China based on available specimens, and comment on the validity of two remaining junior synonyms of *A. marmoratus*, namely *Ixalus argus* Annandale, 1912 and *Rana latopalmata* Boulenger, 1882, suggesting that they may represent subjective synonyms of *A. gerbillus* (Annandale, 1912) and *A. panhai* Matsui and Nabhitabhata, 2006, respectively.

Key words: Cryptic diversity, Himalaya, Indochina, Taxonomy, Torrent Frogs, Tibet

Introduction

Located at the southern foothill of the eastern Himalaya, Nepal is well known for its dramatic topography and unique biodiversity. Among the Nepalese fauna, Torrent Frogs of the genus *Amolops* are of particular taxonomic interest (Wu *et al*. 2020). A total of four recognized species of *Amolops* are recorded currently from Nepal (Nanhoe & Ouboter 1987; Shah & Tiwari 2004), including *A. afghanus* (Günther, 1858), *A. formosus* (Günther, 1876), *A. marmoratus* (Blyth, 1855), and *A. monticola* (Anderson, 1871). Among them, two species, namely *A. afghanus* and *A. marmoratus*, belong to the *A. marmoratus* species complex (Dubois 1974, 2000; Nanhoe & Ouboter 1987; Yang 1991; Schleich & Kästle 2002; Shah & Tiwari 2004).

The nominate species of the complex, *Amolops marmoratus*, used to be considered a widespread taxon across the Pan-Himalayas and Indochina (Boulenger 1890, 1920; Dubious 1992). However, more recent taxonomic revision showed that previously recognized populations of *A. marmoratus* represent a species complex (Dever *et al.* 2012). With the restriction of true *A. marmoratus* to southern Myanmar and the recognition of *A. afghanus* and *A. indoburmanensis* in central and northern Myanmar (Dever *et al.* 2012), the previous records of *A. afghanus* and *A. marmoratus* in Nepal became allopatric to their conspecifics, and their taxonomic identities remain in question (Fig. 1; Lyu *et al.* 2019b; Frost 2020).

In relation to the Nepalese records of *A. marmoratus* and *A. afghanus*, the validity of the junior synonym, *A. nepalicus* Yang, 1991 warrants further evaluation. In the original description, Yang (1991) only compared his new

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form, *A. nepalicus*, against *A. afghanus*, stating that *A. nepalicus* differs from *A. afghanus* by having oblique rows of vomerine teeth (versus transverse). Later, Dubois (2000) considered both *A. afghanus* and *A. nepalicus* as junior synonyms of *A. marmoratus*. However, such taxonomic treatment by Dubois (2000) was based on a brief statement only without any available morphological or genetic data. For more than two decades, the taxonomy of *A. nepalicus* has remained controversial, with some regarding it as valid (Schleich & Kästle 2002; Shah & Tiwari 2004), while others treat it as a junior synonym of *A. marmoratus* (Dubois 2004; AmphibiaWeb 2020; Frost 2020).

Even after the restriction of true *A. marmoratus* to southern Myanmar (Dever *et al.* 2012), which implies a vitiation of the synonym status of *A. nepalicus* to *A. marmoratus*, the taxonomic validity of *A. nepalicus* has not been re-evaluated to date, and the species is still known only by the original description of the holotype (Yang 1991). Unfortunately, with the exception of snout–vent length, Yang (1991) did not provide measurements for any of the commonly used and standardized diagnostic morphometric characters (Watters *et al.* 2016). Additionally, no photos of the holotype of *A. nepalicus* are available. Without detailed morphological data and clear images of the holotype, it is impossible to reassess the taxonomic status of *A. nepalicus* with confidence.

Furthermore, with the delimitation of the *A. marmoratus* complex, the remaining junior synonyms of *A. marmoratus* in the Pan-Himalaya region are also vitiated, including *Ixalus argus* Annandale, 1912 in Southern Tibet, China and *Rana latopalmata* Boulenger, 1882 in southern Myanmar. It is likely that the synonymy of both of these names to *A. marmoratus* is problematic, and the taxonomic validity of both synonyms should be reevaluated.

In this study, we evaluate the validity of *A. nepalicus* through careful examination of its holotype, topotypes of *A. marmoratus*, true *A. afghanus*, *A.* cf. *afghanus* from Tibet and Nepal, and specimens of other closely related congeners from vouchered museum collections. Morphological comparison confirms that the holotype of *A. nepalicus* can be differentiated from true *A. afghanus*, true *A. marmoratus*, and all other recognized congeners. Based on our results, we resurrect and redescribe *A. nepalicus* as a valid species, provide a robust dataset of morphometric measurements, and present the first photographs of the holotype. We also discuss the validity of the remaining synonyms of *A. marmoratus*, namely *A. argus* and *A. latopalmata*, and provide taxonomic hypotheses as a framework for future systematic studies of this unique radiation of Asian anurans.

Materials and methods

Taxon sampling. Vouchered specimens were examined in major museum collections, including the Field Museum of Natural History, USA (FMNH), California Academy of Sciences, USA (CAS), the Museum of Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ), and Museum of Zoology at University of Michigan, USA (UMMZ) (Appendix I). Other museum/collection abbreviations used in this manuscript include Ansel Fong G.'s private collection of herpetofauna, France (AFG), Zoological Survey of India at Kolkata, India (ZSIC), and the Natural History Museum, UK (BMNH). Abbreviations for vouchered museum specimens examined follow Sabaj (2016). For the type specimens of *Ixalus argus*, *Rana latopalmata*, and *Amolops gerbillus* (Annandale, 1912), and other specimens that we could not examine in person, morphological data was obtained from literature (Boulenger 1882, 1920; Annandale 1912; Andersson 1939; Smith 1940; Ray 1999; Biju *et al.* 2010; Nidup *et al.* 2016; Fei *et al.* 2017; Yuan *et al.* 2018; Lyu *et al.* 2019a, b; Qi *et al.* 2019; Gan *et al.* 2020). Species group definitions follow Fei *et al*. (2005) and Wu *et al*. (2020) and their implications.

Morphological data and analyses. Morphometric data were collected by KW using a digital caliper to the nearest 0.1mm. Morphological characters and their definitions follow Dever *et al.* (2012) and include (acronyms in parentheses): snout–vent length (SVL), head length (HL), maximum head width (HD), internarial distance (IND), snout length (SNL), eye diameter (ED), interorbital distance at front (IODF), interorbital distance at rear (IODR), horizontal diameter of tympanum (TD), tympanum–eye distance (TYE), tibia length (TIB), femur length (FEM), hand length (HND), forearm length (FML), foot length (FTL), Finger III digital disc width (FDW3), Toe IV digital disc width (TDW4), and Finger III length (FL3). In addition to the previously defined and used characters, the following morphometric characters were also measured (definition after acronym): Finger I length (FL1), defined as the length of Finger I from tip to the base between Fingers I and II; Finger II length (FL2), defined as the length of Finger II from tip to the base between Fingers II and III; eye–nostril distance (END), defined as the distance between the anterior corner of the eye and the midpoint of the nostril; and snout–nostril distance (SND), defined as the distance between the tip of the snout to the midpoint of the nostril. Webbing formulas follow Guayasamin *et al*. (2006)

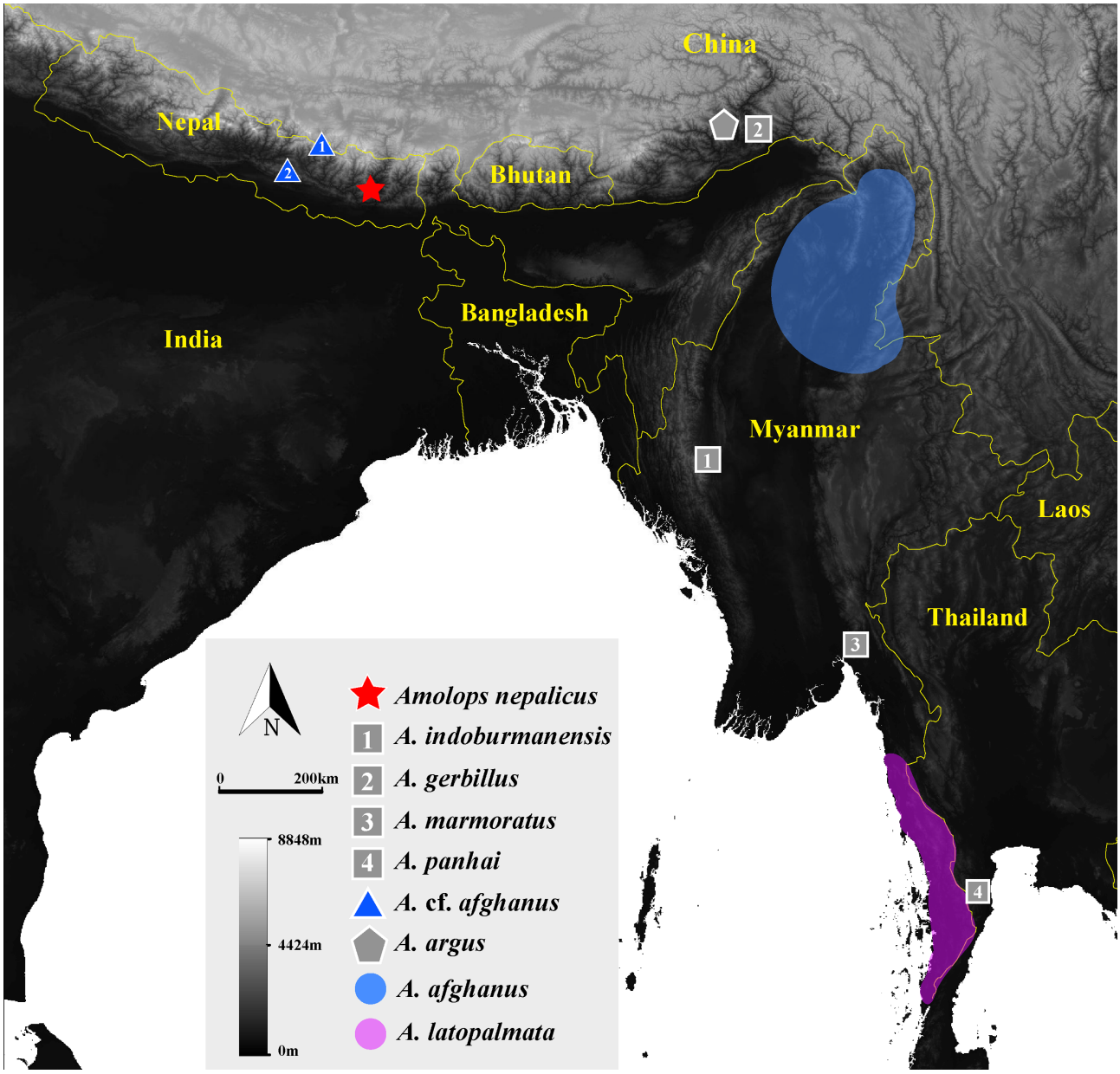

FIGURE 1. The distributions of the *Amolops marmoratus* complex in the Pan-Himalaya region. Star represent the type locality of *A. nepalicus* (on the Sabhaya Khola [=Sabha Khola], Sankhuwasabha District, Nepal); numbered rectangles represent type localities of recognized species of the complex; pentagon represents type locality of the junior synonym *Ixalus argus*; triangles represent localities of examined *A.* cf. *afghanus* in Tibet of China (1) and Nepal (2); and circles without the white-outline correspond to the shaded regions with the same color, which are either a vague type locality (i.e. Tenasserim [=Tanintharti Region] for *Rana latopalmata*), or confirmed distribution without a known type locality (i.e. no correct type locality of *A. afghanus*; see Dever *et al.* 2012).

Furthermore, the following qualitative characters were recorded: skin texture (i.e. rough or smooth, presence or absence of tubercles), presence of skin folds (i.e. supratympanic fold, dorsolateral fold), presence of glands (i.e. axillary, rictal, and dorsolateral glands), presence of sub-digital tubercles (i.e. metacarpal tubercles, inner metatarsal tubercle, outer metatarsal tubercle), arrangement of vomerine teeth (i.e. transverse or oblique), presence of vocal apertures and vocal sacs, presence of circummarginal grooves on Finger I, presence of a transverse groove on Finger I, and body coloration and ornamentation patterns (i.e. molted, spotted, banded, etc.). For maximum comparability and consistency, terminology in color descriptions follows Köhler (2012).

To control for covariance of different morphometric measurements, especially with respect to body size and head size, the following relative ratios were calculated and used for comparisons: HL/SVL, HW/HL, IND/HW,

SNL/HL, ED/IND, IODF/IODR, IODF/HW, IODR/HW, TIB/SVL, FEM/SVL, TIB/FEM, FL1/FL2, FL1/FL3, FL2/FL3, FDW1/FDW3, and TDW4/FDW3. Given species of the genus *Amolops* is known to display sexual dimorphism (Dever *et al.* 2012; Lyu *et al.* 2019a, b), comparisons and statistical analyses of morphometric data were done on males only, due to the lack of female specimens of *A. nepalicus*. END and SND were excluded from the Principle Component Analysis (PCA) due to their incomplete sampling. Raw measurements were square root transformed to ensure their normality, and PCA was conducted using R (http://www.R-project.org/). The One Sample T-Test was conducted using R to examine if the differentiating characters of *A. nepalicus* differ significantly from the examined populations of *A. marmoratus* and *A. afghanus*.

Results

Examination of the holotype of *A. nepalicus* largely confirms the original description by Yang (1991), except for SVL (37.3mm by Yang [1991] vs. 37.8mm in present study) and relative finger length of Fingers I and II (equal in length in Yang [1991] vs. first one longer, FL1 127% FL2) (Appendix II). Such differences can be explained by varying measurement methods, particularly for Finger II length.

Although the sample size is limited, we still find non-overlapping morphological differences that can differentiate the holotype of *A. nepalicus* from its current senior synonym, *A. marmoratus*, including the relative nostril position and relative head width (comparison section below; Table 1). Both non-overlapping, diagnostic characters are statistically different using One-Sample T Tests (comparison section below). PCA analysis shows that the first two principle components (PCs) account for 95% of the total variance, where PC1 loads most heavily on SVL, HL, and HW, and PC2 loads most heavily on TMD and FML (Appendix III). Visualization of the first two PCs shows clear separation of the holotype of *A. nepalicus* from *A. marmoratus*, *A. afghanus*, and *A. indoburmanensis* in morphospace (Fig. 2).

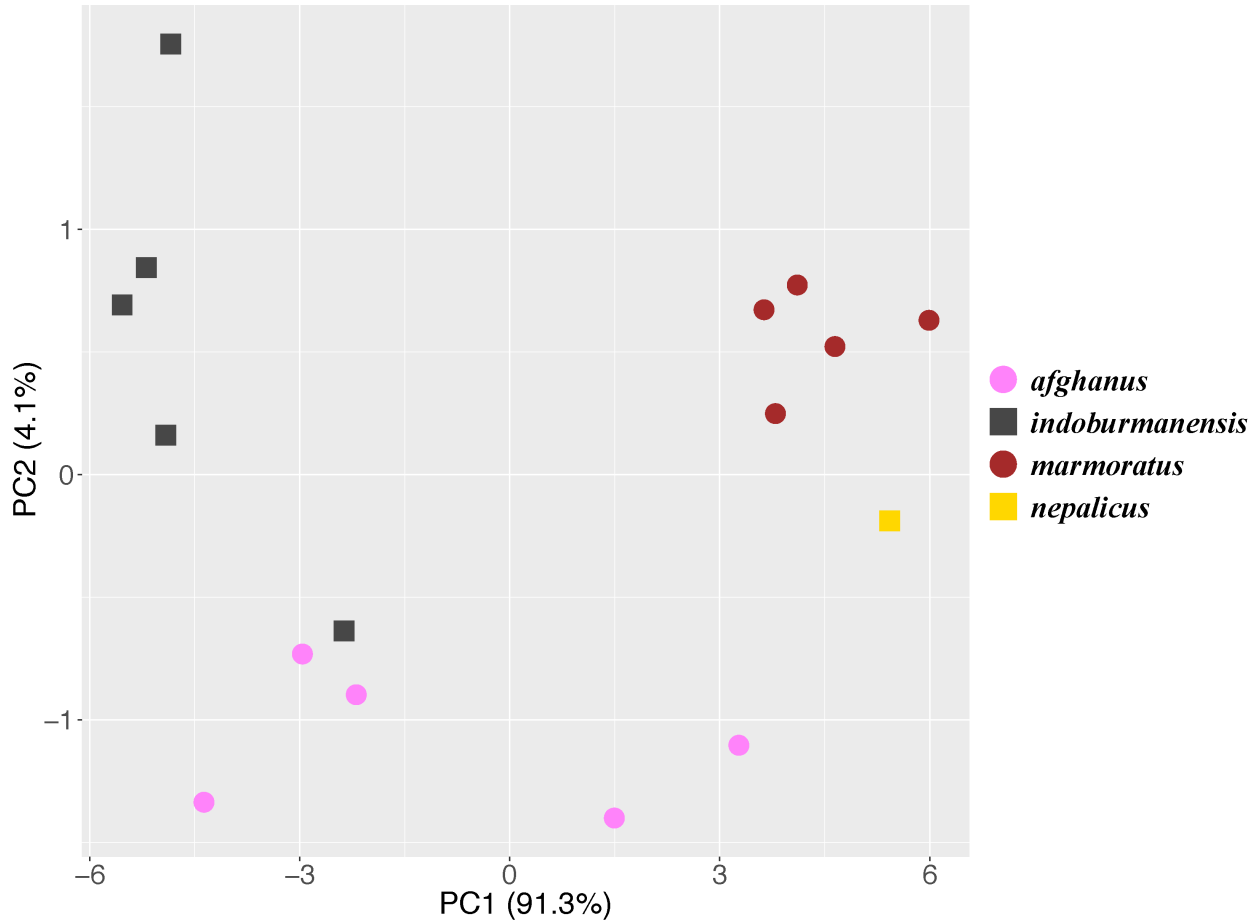

FIGURE 2. PCA plot of the first two major principle components (PCs) on the selected morphometric measurements among the true *A. afghanus*, topotypic *A. indoburmanensis*, topotypic *A. marmoratus*, and the holotype of *A. nepalicus*.

Together with the allopatric ranges of true *A. marmoratus* (Indochina) and *A. nepalicus* (Himalaya) (Zhang & Zhao 1978), we conclude that *A. nepalicus* should be resurrected as a valid species. To facilitate future taxonomic studies of *Amolops* in the Pan-Himalaya region, we provide a detailed redescription of the holotype of *A. nepalicus* and expanded diagnosis and comparisons against recognized congeners.

Taxonomic account

Amolops nepalicus Yang, 1991

(Table 1, Figs. 3, 4)

Chresonymy. *Staurois himalayana* (original collecting information by Douglas Lay, 1973)
Amolops marmoratus Dubois, 2000

Holotype. UMMZ 132063, adult male, collected 2km East of Barabise (=Barahabise), which is on Sabhaya Khola (=Sabha Khola), Sankhuwasabha District, eastern Nepal, elevation 2200ft (about 670m). Collected by Douglas Lay in May 1973.

Comment on the type locality. In the original description, Yang (1991) wrote "Sabhya Kbota, Nepal". However, upon exemption of the original museum record, the full locality information of the holotype is much more detailed: "Nepal: Barabise, 2200ft (Barabise is on Sabhya Khola, tributary of Arun River, ca. 3km NE of Khanbari)." According to the original record, the type locality is roughly at 27°25'34"N, 87°18'23"E, WGS 84.

Diagnosis. A small sized frog that can be diagnosed by a combination of the following characters: (1) body size small, SVL 37.8mm in adult male; (2) head relatively narrow, longer than wide, HW 86.2% HL in male; (3) nostril about midway between eyes and snout, END 106.0% SND; (4) Finger I longer than Finger II, FLI 127.2% FL2; (5) Finger I with distal disc, well developed, FDW1 60.8% FDW3, with transverse and circummarginal grooves; (6) tibia length equal to femur length, TIB 100.1% FEM; (7) both inner and outer metatarsal tubercles present, inner tubercle elongated, outer tubercle smaller; (8) background skin of dorsal surface of body rough but fine, with distinct larger tubercles scattered evenly; (9) lateral surface of body more granular, also with enlarged tubercles; (10) well developed glands present in incomplete series along dorsolateral junction of body on each side; (11) supratympanic fold distinct but thin, extending from eye to region posterior to shoulder joint, continuous with dorsolateral series of glands on dorsum; (12) tympanum distinct, annulus raised; (13) dual vocal sacs and vocal apertures present in male; (14) nuptial pads present on Finger I of male, without nuptial spines; (15) fingers free from webbing, toes fully webbed, weakly notched, webbing formula I0-0II0-0III0-0IV0-0V.

Redescription of holotype. Adult male, small in size, SVL 37.8mm. Head narrow, longer than wide, HW 86.2% HL; snout pointy, projecting slightly over lower jaw, SNL 36.8% HL; nostril oval, located about midway between snout tip and eyes, END 106.0% SND; canthus rostralis distinct, loreal region slightly concave; upper lips convex; eyes large, ED 130.7% IND; dorsal surface of head mostly smooth, with few enlarged, raised tubercles posterior to eyes; single rictal gland at corner of mouth on each side of head, bean shaped; tympanum distinct, with raised annulus, TMD 40.5% ED; supratympanic fold distinct, thin, covering the superior and posterosuperior sides of tympanum and connecting to dorsolateral series of glands. Vomerine teeth distinct, in two oblique rows, forming "\ /" shape; vocal aperture and dual vocal sacs present.

Background dorsal skin finely granular, with numerous enlarged, flat tubercles scattered evenly; dorsolateral glands forming incomplete series on each side of dorsum, in contact with supratympanic fold anteriorly and extending posteriorly toward pelvis; lateral skin of body granular, also with enlarged tubercles scattered. Ventral surfaces of head and body smooth; granular on posteroventral region of thigh and near cloaca.

Dorsal surfaces of limbs rough, with many small to medium tubercles, many tubercles forming longitudinal ridges on crus and thigh. Fingers long, slender, free of webbing, all with expanded discs, transverse grooves, and circummarginal grooves, FDW1 60.8% FDW3; Finger I longer than Finger II, FL1 127.2% FL2, relative finger lengths III>IV>I>II; enlarged nuptial pad present on Finger I, extending from base to distal end of subarticular tubercle, covering dorsal and posterior sides of finger; subarticular tubercles oval, distinct, I (1), II (1), III (2), IV (2); single supernumerary tubercle present on each finger except Finger I; inner and outer metacarpal tubercles large, elevated, fused medially. Toes long, fully webbed, webbing formula I0-0II0-0III0-0IV0-0V, all with enlarged discs, transverse grooves, and circummarginal grooves, TDW4 82.4% FDW3; relative toe lengths IV> V> III > II

> I; subarticular tubercles oval, smaller than those on fingers, I (1), II (1), III (2), IV (3), V (2); both inner and outer metatarsal tubercles present, inner tubercle elongated and larger, about three-times size of outer.

Coloration. After long-term preservation, the background coloration of the dorsal surfaces of the head and body is from Vinaceous Pink (Color 245) to pale Deep Vinaceous (Color 248). Irregularly shaped, Beige (Color 254) speckles are present and scattered on the top of the head and dorsal body surfaces. The enlarged flat tubercles of the posterior region on top of thel head and dorsum, the supratympanic folds, and the dorsolateral series of glands of the dorsum are darker Burnt Sienna (Color 38). The lateral surfaces of the head and body are Pale Pinkish Buff (Color 3), with fine, Deep Vinaceous (Color 248) speckles. The dorsal surfaces of the fore-limbs are mostly uniform pale Deep Vinaceous (Color 248); and hind limb surfaces are more distinctively patterned, with Mahogany Red (Color 34), marbled transverse patches, which are more distinct and saturated on the posterolateral regions of the thigh and crus. The ventral surfaces of the head, body, and limbs are uniform Buff (Color 5).

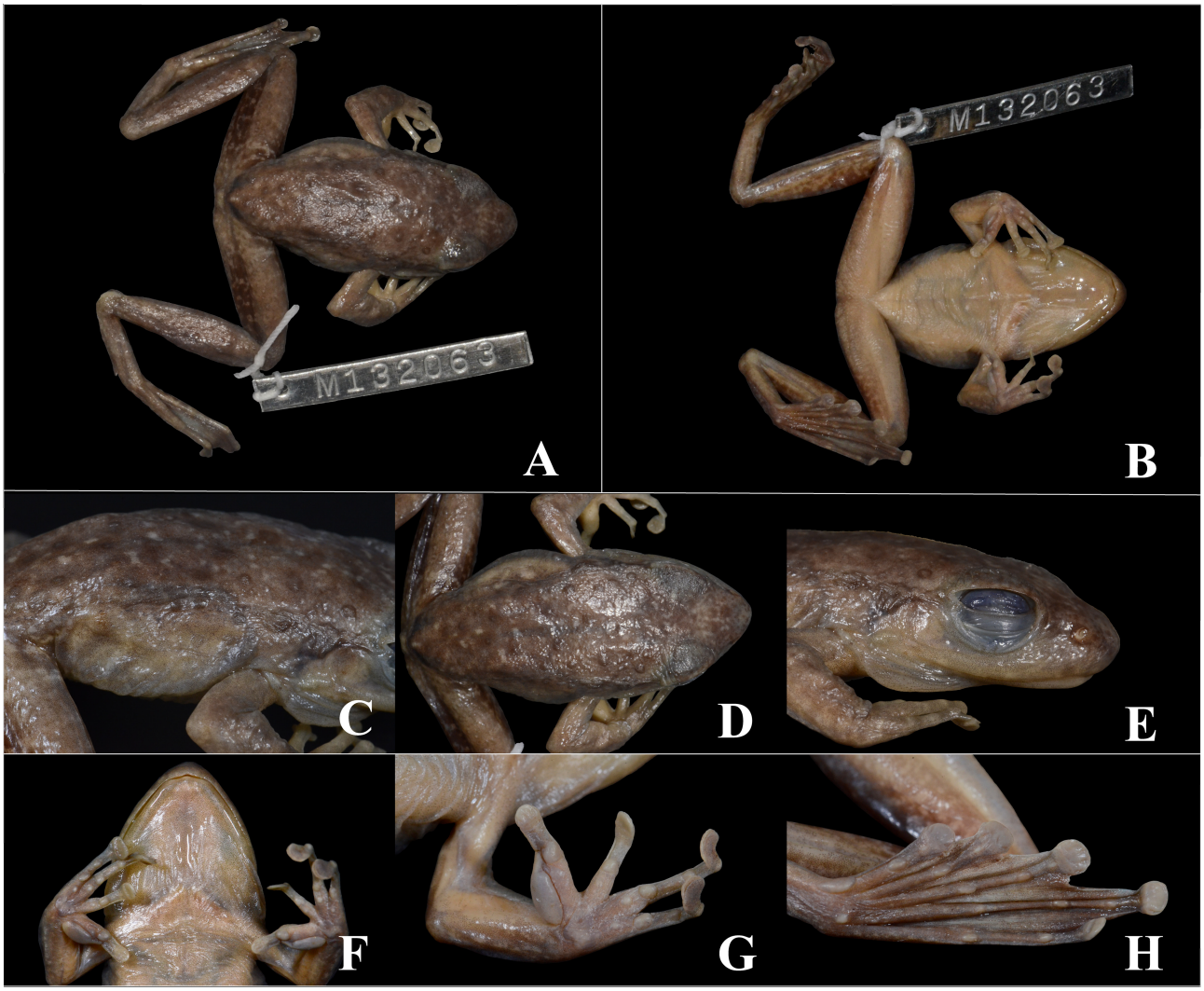

FIGURE 3. Photographs of the holotype of *A. nepalicus* UMMZ 132063 showing (A) dorsal view, (B) ventral view, (C) dorsolateral closeup of dorsum, (D) dorsal close-up of head and dorsum, (E) lateral close-up of head, (F) ventral closeup of head, (G) ventral close up of left hand, and (H) ventral close up of left foot. Individual images are not to scale. Photographs by Kai Wang.

Comparisons. *Amolops nepalicus* was considered as a junior synonym of *A. marmoratus*, and it is similar to *A. marmoratus* in having a small body size, enlarged tubercles on the dorsum, and by the presence of dual vocal sacs in adult males. However, *A. nepalicus* differs from *A. marmoratus* by having a relatively narrower head (HW 86.2% HL in male vs. 91.5–96.4% in males; One Sample T-Test p=0.0002), and a different nostril position (about midway between eye and nostril, END 106.0% SND vs. closer to snout, 118.8–125.0% in males; One Sample T-test, p=0.0001) (Fig. 4).

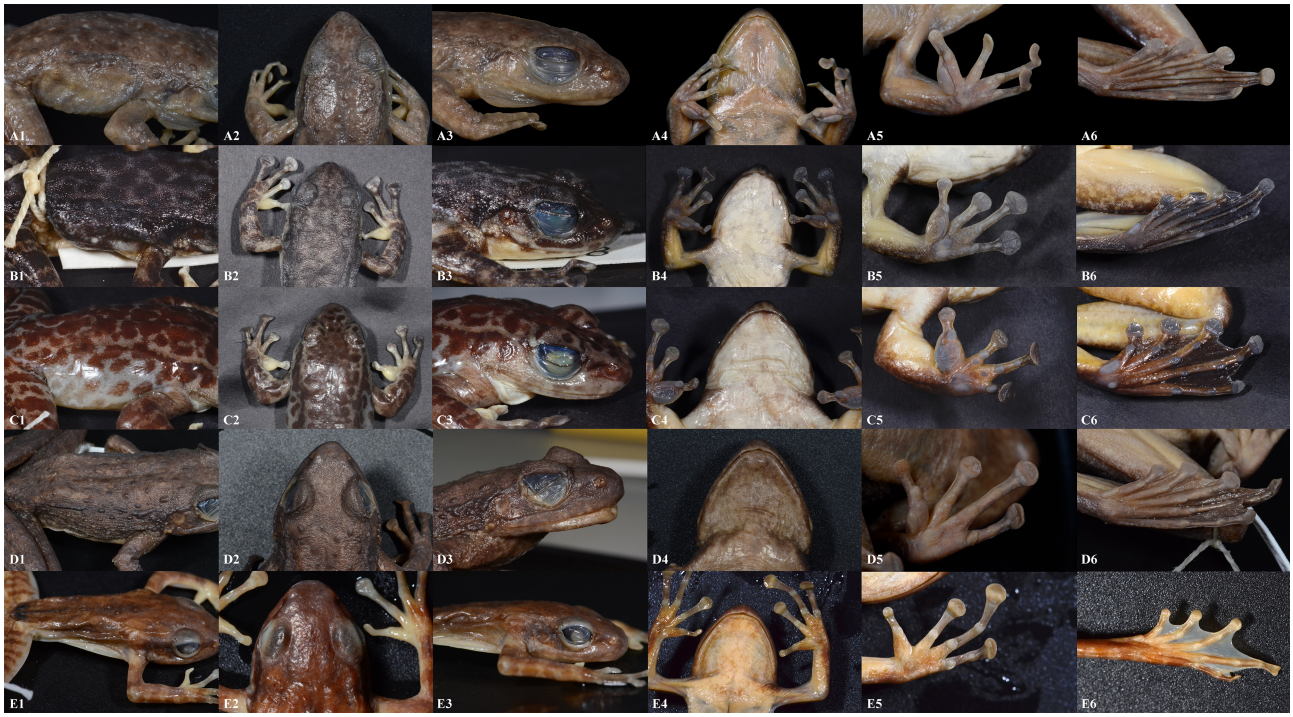

FIGURE 4. Comparisons between males of (A) *Amolops nepalicus* UMMZ 132063, (B) *A. marmoratus* CAS 240545, and (C) *A. afghanus* CAS 220182, as well as a female of (D) *A.* cf. *afghanus* from Nepal CAS 145816, and a juvenile of (E) *A.* cf. *afghanus* from China CAS 177645. Different columns show (1) skin texture on the dorsolateral surfaces of the body, (2) head shape, (3) other characters on the lateral head (i.e. nostril position and distinctiveness of tympanum and supratympanic fold), (4) gular pouch/vocal sacs, (5) relative finger length and shape and size of nuptial pads when applicable, and (6) webbing formula and subdigital tubercles of the foot (6). Individual images are not to scale. Photographs by Kai Wang.

For the remaining species of the *A. marmoratus* complex, *A. nepalicus* differs from *A. afghanus* by having a smaller body size (37.8mm vs. 43.5–67.1mm in males), oblique orientation of vomerine teeth (vs. mostly transverse), and by the presence of distinct, enlarged tubercles on the dorsum (vs. absence or presence but small and indistinct); from *A. assamensis* by having a smaller body size (37.8mm in male vs. ≥52.8mm in males) and a narrower head (HW 86.2 % HL vs. >100.0%); from *A. indoburmanensis* by having a smaller body size (37.8mm in male vs. 63.1–77.5mm in males), a relatively narrower head (HW 86.2 % HL in male vs. 94.0–99.7% in males), and by the presence of distinct, enlarged tubercles on the dorsal and lateral surfaces of the body (vs. absence); from *A. panhai* by the absence of axillary glands (vs. presence).

Compared to species of the *A. ricketti* group and *A. daiyunensis* group, *A. nepalicus* differs from *A. albispinus*, *A. hongkongensis*, *A. ricketti*, *A. sinensis*, *A. wuyiensis*, *A. yatseni*, and *A. yunkaiensis* by the absence (vs. presence) of nuptial spines on Finger I in males and by the presence of outer metatarsal tubercle (vs. absence); and from *A. daiyunensis* by the presence of distinct vomerine teeth (vs. absence). Compared to the *A. hainanensis* group, *A. nepalicus* differs from *A. hainanensis* and *A. torrentis* by the presence of vomerine teeth (vs. absence).

Amolops nepalicus differs from all members of the *A. monticola* group (*A. aniqiaoensis*, *A. archotaphus*, *A. akhaorum*, *A. bellulus*, *A. chakrataensis*, *A. chayuensis*, *A. chunganensis*, *A. compotrix*, *A. cucae*, *A. daorum*, *A. granulosus*, *A. iriodes*, *A. kohimaensis*, *A. mengdingensis*, *A. mengyangensis*, *A. monticola*, *A. minutus*, *A. nyingchiensis*, *A. tuanjieensis*, *A. vitreus*, and *A. wenshanensis*) by the absence of true dorsolateral folds (vs. presence), presence of enlarged tubercles on the dorsal and lateral surfaces of the body (vs. absence), and presence of outer metatarsal tubercles (vs. absence); from all members of the *A. mantzorum* group (*A. granulosa*, *A. jingjiangensis*, *A. loloensis*, *A. lifanensis*, *A. mantzorum*, *A. ottorum*, *A. shuichengensis*, *A. tuberodepressus*, and *A. xinduqiao*) by the presence of circummarginal grooves on Finger I (vs. absence); from *A. viridimaculatus* group (*A. viridimaculatus*) by the presence of gular sacs in males and presence of outer metatarsal tubercle (vs. absence).

For the remaining species of *Amolops* recognized to occur in the Pan-Himalayas and Southeast Asia, *A. nepalicus* differs from *A. formosus*, *A. himalayanus*, *A. pallasitatus*, and *A. splendissimus* by the presence of outer metatar-

TABLE 1. Morphological comparison between currently recognized congeners of the *A. marmoartus* complex in the Pan-Himalaya region, including *A. afghanus*, *A.* cf. *afghanus* from Nepal and China, *A. indoburmanensis*, *A. marmoratus*, and *A. nepalicus*. For sample size row, the numbers in parentheses indicate the differential sample size for END/SND, and * indicates the available data of *A. gerbillus* are obtained through literature. For remaining rows of data, numbers in parentheses indicate the average± standard deviation. "–" indicates not applicable or not available. M: male; F: female; J: juvenile.

	A. nepalicus	*A. marmoratus*		*A. afghanus*		*A.* cf. *afghanus* (Nepal)	*A.* cf. *afghanus* (Tibet, China)	*A. indoburmanensis*		*A. gerbillus*
Sex	M	M	F	M	F	F	F, J	M	F	–
Sample Size	1	6 (5)	6 (5)	5 (1)	4 (3)	1	1	5	5	1*
SVL (in mm)	37.8	37.0–42.9 (40.7±2.3)	69.9–74.2 (71.6±1.7)	43.5–67.1 (56.5±10.0)	69.0–88.7 (78.3±8.1)	61.3	28.6	63.1–77.5 (73.3±6.0)	65.5–100.9 (87.3±13.7)	33
HW/HL (%)	86.2	91.5–96.4 (94.7±2.1)	100.3–103.5 (101.7±1.2)	90.7–96.7 (92.8±2.4)	94.6–99.1 (97.0±1.9)	93.40	94.2	94.0–99.7 (97.4±2.9)	100.7–103.4 (102.2±1.1)	–
IND/HW (%)	31.1	27.2–32.4 (30.2±2.0)	25.1–28.6 (26.6±1.3)	28.6–32.0 (30.8±1.4)	26.7–28.2 (27.6±0.7)	28.70	34.3	25.7–29.2 (27.6±1.4)	25.9–29.0 (27.3±1.5)	–
SNL/HL (%)	36.8	38.8–41.0 (39.7±1.3)	37.0–43.7 (40.1±2.3)	38.3–40.6 (39.7±1.1)	37.9–41.5 (39.9±1.5)	38.50	39.7	37.8–41.4 (39.2±1.4)	38.3–41.4 (39.9±1.1)	–
END/SND (%)	106.0	118.8–125.0 (122.0±2.3)	131.1–136.8 (134.7±2.7)	108.1 (–)	125.8–132.5 (129.2±3.3)	122.00	86.4	–	–	–
ED/IND (%)	130.7	110.5–139.6 (125.3±11.7)	98.4–129.1 (109.9±10.6)	109.8–140.2 (120.7±11.6)	108.0–123.1 (114.7±6.9)	117.60	110.2	100.1–128.4 (107.8±11.9)	94.5–115.5 (104.1±9.3)	–
TMD/ED (%)	40.5	28.7–41.3 (35.8±4.8)	28.7–35.4 (32.8±2.5)	32.7–45.4 (39.9±4.8)	33.3–49.0 (39.4±7.1)	38.40	31.5	26.5–41.8 (35.6±6.7)	26.3–42.8 (33.6±6.0)	About 1/3
IODF/IODR (%)	72.2	68.1–75.9 (72.4±3.0)	71.9–74.5 (73.2±1.3)	68.2–69.5 (69.0±0.6)	68.5–73.1 (70.3±2.9)	71.0	71.7	66.8–71.7 (69.2±2.1)	68.9–74.8 (71.8±2.0)	–
FL1/FL2 (%)	127.2	100.0–119.7 (108.3±7.1)	117.1–125.9 (117.4±10.1)	90.4–96.4 (93.4±2.4)	86.3–95.6 (91.3±4.1)	103.5	83.4	108.2–119.9 (113.2±4.9)	104.6–120.7 (113.5±6.0)	<100.0
TIB/SVL (%)	60.6	56.3–63.2 (59.0±3.1)	58.5–63.2 (60.6±1.8)	60.9–64.9 (63.0±1.4)	60.1–66.1 (62.5±2.9)	59.8	62.6	59.3–63.6 (61.7±1.7)	57.5–64.5 (61.0±2.9)	–
FEML/SVL (%)	60.5	55.4–59.7 (56.6±1.8)	56.9–60.3 (58.6±1.4)	57.0–59.6 (58.5±1.1)	56.9–62.6 (58.8±2.6)	56.8	57.5	55.7–59.7 (58.1±1.9)	55.1–60.4 (58.0±2.2)	–
TIB/FEML (%)	100.0	101.3–108.2 (104.1±2.6)	101.1–104.8 (103.3±1.7)	106.0–112.6 (107.7±2.8)	104.2–109.3 (106.2±2.2)	105.3	108.9	102.8–112.0 (106.3±3.5)	102.8–107.4 (105.2±1.9)	–

.....continued on the next page

TABLE 1. (Continued)

	A. nepalicus	*A. marmoratus*		*A. afghanus*		*A.* cf. *afghanus* (Nepal)	*A.* cf. *afghanus* (Tibet, China)	*A. indoburmanensis*		*A. gerbillus*
FDW1/FDW3 (%)	60.8	58.1–67.7 (62.2±3.4)	55.9–76.7 (66.7±6.9)	56.0–67.1 (63.4±4.7)	51.6–70.7 (61.9±7.8)	70.3	66.9	58.3–66.9 (63.5±3.6)	57.8–68.5 (63.1±3.9)	–
TDW4/FDW3 (%)	82.4	77.1–93.5 (81.9±7.5)	72.0–83.2 (80.1±4.3)	74.3–88.5 (81.4±5.5)	74.8–79.6 (77.4±2.2)	87.4	63.1	83.1–92.2 (88.1±3.4)	82.9–95.0 (90.1±5.6)	–
Vomerine teeth orientation	Oblique	Oblique	Oblique	Mostly transverse	Mostly transverse	Oblique	Oblique	Oblique	Oblique	–
Vocal sacs	Present	Present	Absent	Present	Absent	Absent	Absent	Present	Absent	–
Outer metatarsal tubercles	Present	Present	Present	Present	Present	Present	Absent	Present	Present	Absent
Tubercles on dorsum	Present and extensive	Present and extensive	Present and extensive	Present but small and indistinct, or absent	Present but small and indistinct, or absent	Present and extensive	Present but weak	Mostly absent	Mostly absent	Present and extensive
Tympanum	Distinct	Distinct	Distinct	Distinct	Distinct	Distinct	Distinct	Distinct	Distinct	Visiable but not very distinct
Supratympanic fold	Well-developed	Well-developed	Well-developed	Well-developed	Well-developed	Well-developed	Well-developed	Well-developed	Well-developed	Moderately developed
Dorsolateral fold	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Dorsolateral series of glands	Present	Present	Present	Present	Present	Present	Present	Absent	Absent	Present

sal tubercle (vs. absence), presence of a circummarginal groove on Finger I (vs. absence), and presence of distinct, enlarged tubercles on the dorsal surface of the body (vs. absence); from *A. cremnobatus* and *A. kaulbacki* by the presence of vocal sacs in males (vs. absence); from *A. nidorbellus* by have a smaller body size (37.8mm in male vs. ≥76.4mm in males) and narrower head (HW 86.2% HL vs. >100.0%); from *A. gerbillus* by having large and distinct tympana (TMD 40.5% ED vs. about one-third, small and indistinct; Annandale 1912) and by the presence of outer metatarsal tubercles (vs. absence); from *A. caelumnoctis* and *A. medogensis* by the presence of enlarged tubercles on the dorsal and lateral surfaces of the body (vs. absence) and presence of vocal sacs in males (vs. absence); from *A. jaunsari* by having a narrower head (HW 86.2% HL vs. "as long as broad"; Ray 1999); from *A. longimanus* by having larger tympanum (TMD 40.5% ED vs. about one quarter; Andersson 1939) and by the presence of outer metatarsal tubercle (vs. absence); from *A. spinapectoralis* by the presence of outer metatarsal tubercle (vs. absence) and by the absence of conical spines on nuptial pads (vs. presence); and from *A. larutensis*, *A. gerutu*, and *A. australis* by the absence of axillary glands (vs. presence).

Discussion

Records of "*A. afghanus*" in Nepal and China. Owing the lack of genetic tissues and vouchered specimens, the taxonomic validity of the Himalayan species of the genus *Amolops* has long been under debate. In Nepal, even with the recognition of *A. nepalicus*, numerous questionable records of *A. afghanus* continue to exist in the literature. Dubois (1974) recorded the species from east-central Nepal, between Thondarkot (=Chandrakot) in the west and Sanghu in the East. Although we were not able to examine the 69 referred specimens of *A. afghanus* by Dubois (1974) (BMNH 1962.1093–1096, 1972.1056–1064; AFG 001–050, T001–008, NC001), the female specimen of *A.* cf. *afghanus* from central Nepal (near Bhimpedi) that we were able to examine agrees largely with our revised diagnosis of *A. nepalicus*, except for its nostril position (closer to the snout vs. about midway between eye and snout in the holotype of *A. nepalicus*) (Table 1; Fig. 3).

In relation to the Nepali records, "*A. afghanus*" has been also recorded in southern Tibet, China. Dubois (1974) first recorded "*A. afghanus*" from Tatopani in north-central Nepal, close to the Chinese border. Later J. R. Macey and T. J. Papenfuss collected a juvenile specimen of "*A. afghanus*" (CAS 177645) on the Chinese side of the border in Zhangmu Township, about 3km linear distance from Dubois's record at Tatopani, Nepal. Morphological examination shows that the referred juvenile female specimen from Tibet is distinct from the true *A. afghanus* by the absence of outer metatarsal tubercles and by having a different nostril position (much closer to the eye, END 86.4% SND vs. closer to the snout, 108.1–132.5%), and it differs from *A. nepalicus* by having a shorter Finger I (FL1 83.4% FL2 vs. 127.2%) (Table 1).

Given the allopatric distribution and isolation to true *A. afghanus* in northern Myanmar, it is safe to conclude that neither the Tibetan nor the Nepalese records of the "*A. afghanus*" are true *A. afghanus*. Although we feel confident in this conclusion, with the high level of morphological similarity among congeners within the *A. marmoratus* complex (Dever *et al.* 2012; Lyu *et al.* 2019b), and the paucity of available genetic material, the exact taxonomic identity of these Nepalese and Chinese records of *A.* cf. *afghanus* will require additional study of the referred specimens in the museum collections. Additionally, we recommend future studies collect *Amolops* specimens with genetic samples in Nepal, so that phylogenetic analyses can be used to confirm their taxonomic status.

Validity of *Ixalus argus* and *Rana latopalmata*. Similar to *A. nepalicus*, the taxonomic validity of previously recognized junior synonyms of *A. marmoratus* and *A. afghanus* also requires reevaluation, namely *Ixalus argus* from southern Tibet, China and *Rana latopalmata* from Tenasserim, southern Myanmar.

The names *Ixalus argus*, along with *Polypedates marmoratus* Blyth, 1855 and *P. afghanus* Günther, 1858, were first synonymized to *Rana latopalmata* Boulenger, 1882 (Boulenger 1920). However, as both *P. marmoratus* and *P. afghanus* have naming priorities over *R. latopalmata*, assuming this synonymizing act is correct, both *I. argus* and *R. latopalmata* should be considered as junior synonyms of either *A. afghanus* or *A. marmoratus*. Dubois (1974) first corrected the order of synonyms and considered both *I. argus* and *R. latopalmata* as junior synonyms of *A. afghanus*, and his taxonomy was followed by Yang (1991). A subsequent study by Dubois (1992) further considered *A. afghanus* as a junior synonym of *A. marmoratus*, which led to the synonymy of all three previous names (*A. afghanus*, *A. argus*, and *A. latopalmata*) with *A. marmoratus* (Dubois 2000; Bossuyt & Dubois 2001). Unfortunately, the above synonymies were all based on cursory statements only, with no detailed morphological data or comparisons provided.

With the vitiation of the above synonyms by recent phylogenetic work (Dever *et al.* 2012), our close examination of the original descriptions shows that *A. argus* is distinct from *A. marmoratus* but similar to *A. gerbillus*. According to Annandale (1912), *A. argus* is a small-sized species (SVL 27mm) that can be differentiated from *A. marmoratus* by having a different order of finger lengths (Finger I shorter than Finger II vs. equal or longer), as well as by the absence of metacarpal tubercles (vs. presence), and absence of outer metatarsal tubercle (vs. presence). *Amolops gerbillus*, which was described in the same publication as *A. argus* (Annandale 1912), is also a small-sized species that does not possess outer metatarsal tubercles. In fact, according to their original descriptions, the only differentiating character between *A. argus* and *A. gerbillus* is the absence of supratympanic folds in *A. argus* (vs. presence in *A. gerbillus*). However, the original illustration of the holotype of *A. argus* does indicate the presence of supratympanic folds (Annandale 1912: fig. 3, plate iii). In addition to the fact that the type localities of both species ("Renging" for *A. argus* and "Yembung" for *A. gerbillus*) are in close proximity within Abor County (about 24km linear distance) in southern Tibet, China, it is likely that both names represent the same taxon and constitute subjective synonyms to one another. If such synonym relationship is true, given that both *A. argus* and *A. gerbillus* were described together in the same publication, following the Article 24.2 of The International Zoological Nomenclature Code (International Zoological Nomenclature Commission, 1999), the future first reviser would need to decide the precedence of one name over the other.

Regarding the other synonym, *Rana latopalmata*, its original description is rather simple with limited useful information. Although Boulenger's (1920) redescription provided more morphometric measurements of the syntype females, his redescription of the species was based on specimens of different taxa (i.e. most likely *A. afghanus*, *A. indoburmanensis*, and *A. marmoratus* according to the locality information; Dever *et al.* 2012). Based on all information available to date, it is difficult to draw a conclusion about the taxonomic validity of *A. latopalmata* with confidence. However, the vague type locality of *A. latopalmata* (Tenasserim [=Tanintharyi Region], Myanmar) overlaps with the confirmed range and abuts the type locality of *A. panhai* (Matsui & Nabhitabhata 2006; Dever *et al.* 2012). Additionally, given that all diagnostic features of *A. latopalmata* presented in its original description agree with the diagnosis of *A. panhai*, it is possible that these two names constitute subjective synonyms of each other as well, and *A. latopalmata* (Boulenger 1882) would take naming priority over *A. panhai* (Matsui & Nabhitabhata 2006). Future studies should examine the type specimen of *A. latopalmata* at BMNH to confirm its taxonomic validity with regard to *A. panhai* and other congeners.

Despite improving taxonomic resolution for Himalayan lineages of *Amolops*, much work remains, and future taxonomic studies of the genus should focus on resolving the remaining controversial records regarding existing junior synonyms within the *A. marmoratus* complex. The results of this work also highlight the importance of evaluating available synonyms prior to describing new taxa from the Himalaya region.

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APPENDIX I. Specimens Examined.

Amolops afghanus (*N*=9): CAS 240973, 240883, 240889, Myitkyina District, Kachin State, Myanmar; CAS 224712–224715, 224363, 225233, Putao District, Kachin State, Myanmar.
Amolops cf. *afghanus* (*N*=2): CAS 145816, headwater of Rapti River, about 1–2mi west and downstream of Bhimpedi, central Nepal; CAS 177645, between the Chinese checkpoint and the national border on the Lhasa-Kathmandu Rd., Zhangmu, Tibet, China.
Amolops chayuensis (*N*=19): KIZ 014016–014026, 014028–014034, Baxoi, Tibet, China.
Amolops formosus (*N*=1): FMNH 190955, Nepal.
Amolops himalayanus (*N*=1): FMNH 15806, Sikkim, India.
Amolops indoburmanensis (*N*=10): CAS 21085, Sagaing Division, Myanmar; CAS 23151–23155, 233205, 235048, Chin State, Myanmar; CAS 221082, Rakhine State, Myanmar; CAS 240144, Magway Division, Myanmar.
Amolops marmoratus (*N*=12): CAS 222209, 222210, 222233, 222234, 240545, 240587, 240588, 240591, 240593, 240597, 240601, 240621, Mon State, Myanmar.
Amolops neplaicus (*N*=1): UMMZ 132063 (holotype), near Sabha Khola, Sankhuwasabha District, Province 1, Nepal.
Amolops nynchiensis (*N*=14): KIZ 016432 (holotype), 016418 (allotype), 016415–016417, 016419–016424, 016433, 012632, 012646, Nyingchi, Tibet, China.

APPENDIX II. Detailed morphometric measurements of the holotype of *Amolops nepalicus*, *A. marmoratus*, *A. afghanus*, *A.* cf. *afghanus*, and *A. indoburmanensis*. All measurements are in the unit of mm.

Measurements methods see the main text, and abbreviations include: snout–vent length (SVL), head length (HL), maximum head width (HD), internarial distance (IND), snout length (SNL), eye diameter (ED), interorbital distance at front (IODF), interorbital distance at rear (IODR), horizontal diameter of tympanum (TD), tympanum–eye distance (TYE), tibia length (TIB), femur length (FEM), hand length (HND), forearm length (FML), foot length (FTL), Finger I length (FL1), Finger II length (FL2), Finger III length (FL3), Finger III digital disc width (FDW3), Toe IV digital disc width (TDW4), eye–nostril distance (END), and snout–nostril distance (SND).

APPENDIX II.

Species	Catalog Number	Gender	SVL	HL	HW	IND	SNL	END	SND	ED	IODF	IODR	TD
Amolops nepalicus	M132063	M	37.8	16.3	14.0	4.4	6.0	3.5	3.3	5.7	8.0	11.0	2.3
A. cf. *afghanus*	CAS 177645	F, juvenile	28.6	10.4	9.8	3.3	4.1	2.1	2.4	3.7	5.3	7.4	1.2
	CAS 145816	F	61.3	23.8	22.2	6.4	9.2	5.0	4.1	7.5	11.3	15.9	2.9
A. marmoratus	CAS 222209	F	69.9	27.3	27.7	6.9	10.1	6.0	4.4	9.0	14.4	20.0	2.6
	CAS 222210	F	71.5	26.1	27.0	7.7	11.4	6.5	4.9	7.6	14.6	19.6	2.5
	CAS 222233	F	74.2	29.2	29.8	8.2	12.0			8.6	15.4	20.7	2.7
	CAS 240434	F	71.1	28.8	28.9	7.6	11.7	6.8	5.0	8.2	14.7	20.2	2.8
	CAS 240591	F	73.0	28.8	28.9	7.6	11.1	6.4	4.9	8.1	13.9	18.7	2.9
	CAS 240621	F	70.0	27.0	27.5	7.2	10.7	5.9	4.3	8.1	14.1	19.7	2.8
	CAS 240545	M	38.7	16.0	14.7	4.8	6.5			5.3	9.0	12.4	2.2
	CAS 240587	M	37.0	14.9	13.8	4.2	5.8	3.6	2.9	5.2	8.0	11.1	1.9
	CAS 240588	M	41.9	16.7	16.1	5.1	6.3	3.5	2.8	6.5	9.4	13.3	1.9
	CAS 240593	M	42.5	17.0	16.3	4.4	6.9	3.6	3.0	6.2	9.3	12.3	2.4
	CAS 240597	M	41.1	16.1	15.4	4.8	6.6	3.7	3.1	5.5	8.8	11.7	2.1
	CAS 240601	M	42.9	17.3	16.6	4.7	6.9	3.7	3.0	6.4	9.0	13.3	2.0
A. afghanus	CAS 224713	F	76.95	30.63	30.36	8.39	11.62			9.06	14.4	19.86	3.02
	CAS 240973	F	88.71	35.33	34.45	9.56	14.66	7.75	6.16	10.53	18.77	25.68	3.65
	CAS 224712	F	69.0	25.8	25.0	6.7	10.4	5.8	4.4	8.2	13.0	18.9	3.4
	CAS 225233	F	78.3	29.8	28.2	8.0	11.8	6.7	5.2	9.4	14.6	21.7	4.6
	CAS 240883	M	67.09	27.38	25.55	7.85	10.7	–	–	9.25	14.58	20.98	3.78
	CAS 240889	M	63.2	26.16	24.12	7.44	10.4	–	–	8.91	13.19	19.03	2.91
	CAS 224363	M	59.91	23.48	22.71	7.26	9.61	–	–	7.97	11.89	17.44	3.05
	CAS 221314	M	48.7	20.5	18.59	5.92	7.86	–	–	6.85	10.77	15.5	3.11
	CAS 224715	M	43.5	18.5	16.9	4.8	7.5	4.0	3.7	6.8	9.0	13.1	2.9
A. indoburmanensis	CAS 233205	F	87.0	33.1	34.2	9.9	13.7	–	–	9.4	17.6	24.6	3.1
	CAS 235155	F	65.5	26.5	26.7	7.7	10.7	–	–	7.3	13.7	18.3	3.1
	CAS 235048	F	97.0	37.1	38.0	9.9	14.2	–	–	11.4	19.4	26.8	3.0
	CAS 240144	F	100.9	37.7	38.9	10.2	15.0	–	–	10.7	19.2	26.8	3.4
	CAS 210185	F	86.1	34.0	34.5	9.2	13.4	–	–	10.1	16.3	23.7	3.5
	CAS 235153	M	77.4	30.5	28.8	8.4	12.0	–	–	9.0	15.9	23.1	2.4
	CAS 220182	M	63.1	25.5	24.0	6.2	9.7	–	–	7.9	13.3	18.6	3.3
	CAS 235151	M	73.2	28.4	28.3	8.1	11.8	–	–	8.2	13.9	20.4	3.0
	CAS 235154	M	77.5	30.3	30.0	8.0	11.9	–	–	8.1	14.2	21.3	3.3
	CAS 235152	M	75.5	29.0	28.9	8.2	11.0	–	–	8.2	14.2	20.1	2.5

APPENDIX II. (Continued)

Species	Catalog Number	Gender	TYE	TIB	FEM	HND	FML	FL3	FL1	FL2	FDW3	FTL	TDW4
Amolops nepalicus	M132063	M	1.6	22.9	22.9	12.3	8.7	7.3	6.3	4.9	2.2	20.3	1.8
A. cf. *afghanus*	CAS 177645	F, juvenile	1.4	17.9	16.5	10.9	5.5	7.1	3.7	4.4	1.3	14.7	0.8
	CAS 145816	F	3.4	36.6	34.8	17.1	11.9	11.1	7.6	7.4	3.1	29.6	2.7
A. marmoratus	CAS 222209	F	4.0	42.5	41.8	21.5	15.1	14.2	10.9	8.7	5.2	36.6	4.3
	CAS 222210	F	4.4	42.2	41.7	22.2	15.2	13.7	11.3	9.3	4.9	36.6	3.6
	CAS 222233	F	4.4	46.1	44.0	23.9	39.5	15.2	11.6	11.8	5.3	39.0	4.2
	CAS 240434	F	4.6	41.6	40.5	22.8	15.2	14.1	11.4	9.1	5.1	36.5	4.1
	CAS 240591	F	4.4	46.1	44.0	23.8	16.5	14.9	11.6	9.9	5.8	39.9	4.8
	CAS 240621	F	4.4	41.9	39.9	22.0	15.5	14.4	10.8	9.3	4.6	35.8	3.8
	CAS 240545	M	2.3	24.5	23.1	12.1	21.6	8.4	6.1	6.1	2.9	20.1	2.3
	CAS 240587	M	2.3	23.1	21.3	11.1	9.2	7.0	5.3	4.4	2.2	18.8	2.0
	CAS 240588	M	2.7	23.6	23.3	12.5	9.1	7.5	5.8	5.7	2.6	21.1	2.3
	CAS 240593	M	3.1	24.0	23.5	13.2	10.0	8.2	6.3	5.8	2.8	21.3	2.1
	CAS 240597	M	2.4	23.8	22.8	12.3	9.2	7.7	5.7	5.3	2.6	20.5	2.0
	CAS 240601	M	2.6	24.6	24.0	14.6	9.6	8.5	6.6	5.9	2.8	21.3	2.2
A. afghanus	CAS 224713	F	4.32	50.87	48.2	25.95	43.44	16	11.01	12.76	5.11	43.57	3.82
	CAS 240973	F	5.72	53.44	51.28	27.09	46.4	16.25	12.33	13.74	6.63	45.24	5.28
	CAS 224712	F	3.4	43.8	40.1	22.0	15.0	13.1	8.7	9.3	4.2	35.1	3.2
	CAS 225233	F	3.1	47.1	44.6	23.2	16.8	15.2	9.7	10.1	4.7	38.1	3.7
	CAS 240883	M	4.18	42.6	39.98	19.56	37.32	14.19	9.51	10.09	4.42	35.98	3.91
	CAS 240889	M	3.28	39.76	37.37	18.45	34.94	13.06	9.33	9.68	4.19	32.69	3.57
	CAS 224363	M	3.13	36.5	34.13	19.33	33.96	13.86	8.71	9.63	4.26	31.09	3.4
	CAS 221314	M	2.41	30.54	28.81	14.58	26.2	9.78	6.4	6.77	2.94	24.73	2.33
	CAS 224715	M	1.7	28.2	25.1	15.1	11.2	9.7	5.6	6.1	2.7	23.6	2.0
A. indoburmanensis	CAS 233205	F	5.0	54.7	52.5	29.8	46.6	17.1	11.9	11.3	5.5	46.6	5.2
	CAS 235155	F	4.4	42.2	39.3	19.3	33.9	13.4	9.6	8.5	3.9	34.2	3.2
	CAS 235048	F	6.1	56.9	55.3	26.9	20.8	15.0	12.4	11.0	5.5	47.0	4.7
	CAS 240144	F	5.6	58.0	55.6	28.2	20.4	17.8	14.1	11.7	6.9	48.3	6.4
	CAS 210185	F	4.6	53.0	49.6	25.2	18.0	15.8	11.0	9.5	6.6	43.9	6.3
	CAS 235153	M	3.4	48.2	43.1	23.5	40.6	13.9	9.7	9.0	5.7	40.2	5.1
	CAS 220182	M	3.5	37.4	35.6	19.6	30.9	11.8	9.4	8.1	4.3	31.0	3.6
	CAS 235151	M	4.9	46.6	43.6	21.7	39.0	14.9	9.9	9.1	5.1	37.9	4.4
	CAS 235154	M	5.1	48.5	46.3	23.3	17.5	13.7	9.9	8.8	5.3	40.7	4.7
	CAS 235152	M	4.8	45.8	44.6	23.1	15.5	13.8	11.3	9.4	5.3	38.7	4.9

APPENDIX III. Detailed results from the PCA analysis of morphometric measurements. Abbreviations of morphological characters are defined in the method section.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Standard Deviation	4.380051085	0.924782857	0.608110581	0.435304626	0.366528047	0.29592874	0.271786975	0.220942175
Proportion of Variance	0.91356	0.04072	0.01761	0.00902	0.0064	0.00417	0.00352	0.00232
Cumulative Proportion	0.91356	0.95429	0.9719	0.98092	0.98732	0.99149	0.99501	0.99733
Eigen	19.18484751	0.855223332	0.369798479	0.189490118	0.134342809	0.087573819	0.07386816	0.048815445
SVL	-0.226866413	0.102681806	-0.031758249	-0.086850352	0.098558837	-0.003239456	0.031144286	0.004124955
HL	-0.227023696	0.015746315	-0.025321155	-0.18137931	0.084145751	0.093560575	0.099369074	-0.148323358
HW	-0.226633619	0.101349843	-0.080369317	-0.074343259	0.065395554	0.035290444	-0.028435977	0.090034976
IND	-0.223644808	0.011594888	0.131828709	0.038522309	-0.024881138	0.049762103	-0.508186674	-0.429294733
SEL	-0.22683351	-0.008034235	-0.018415286	-0.112814993	0.109320032	-0.043286316	-0.123028097	0.222943811
ED	-0.215140911	-0.214349187	0.208533651	0.036415715	-0.418697868	0.566703384	0.072809878	0.116009313
IODF	-0.225080929	-0.0012068	0.10699286	0.07345173	0.146502069	0.32842704	0.31375353	-0.044444182
IODR	-0.225850747	-0.017645552	0.10573	-0.006891737	0.135996109	0.353347373	0.086135681	0.041490073
TMD	-0.155910054	-0.667026712	-0.631613398	-0.075606259	0.075675372	-0.010739247	0.167696133	-0.02613541
TYE	-0.195030317	0.323216773	-0.453946588	0.72443758	0.118636344	0.096665724	-0.100906451	0.148921168
TIB	-0.226024462	0.033616952	-0.038728989	-0.202084326	0.200849452	-0.00529779	-0.187821792	-0.121123636
FEM	-0.226093451	0.073173235	-0.110561275	-0.119403333	0.100959314	-0.02956166	-0.090984636	-0.310204457
HND	-0.223415573	0.090511419	-0.035521613	-0.323322195	-0.099703782	-0.180344183	0.086749351	0.39548624
FLL	-0.186555912	-0.459101087	0.497672789	0.370034134	0.437203226	-0.289338733	0.064243705	0.009653379
FL3	-0.223148989	-0.136043133	-0.004388883	-0.014302292	-0.190754487	-0.318064686	-0.373908943	0.230799582
FL1	-0.219997857	0.115698924	-0.053602846	0.077839845	-0.339927494	-0.367993881	0.468806924	-0.479918257
FL2	-0.218601131	-0.183150043	0.060537787	0.219189566	-0.536707994	-0.042228701	-0.211590322	0.012137006
FDW1	-0.222384625	0.141568829	0.156026299	0.096667837	-0.134551576	-0.220304304	0.276081108	0.131964442
FDW3	-0.225112194	0.141426624	0.046689903	-0.063721799	0.047898935	-0.123240665	0.09114757	0.336066641
FTL	-0.22644352	0.066107723	-0.052295055	-0.193028784	0.066982101	0.044960177	-0.134324537	-0.095632303
TDW4	-0.222592146	0.218594812	0.067657373	-0.031542579	0.121625691	0.032481945	0.057910494	-0.072284116