Cryptic Torrent Frogs of Myanmar: An Examination of the *Amolops marmoratus* Species Complex with the Resurrection of *Amolops afghanus* and the Identification of a New Species

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Cryptic Torrent Frogs of Myanmar: An Examination of the *Amolops marmoratus* Species Complex with the Resurrection of *Amolops afghanus* and the Identification of a New Species

Jennifer A. Dever¹, Allison M. Fuiten², Özlen Konu³, and Jeffery A. Wilkinson⁴,⁵

We investigated diversity in the *Amolops marmoratus* species complex within Myanmar using both molecular and morphological characters from recently collected specimens. Based on congruence between multivariate analyses of quantitative morphological characters and phylogenetic analyses of nucleotide variation in the 16S ribosomal gene conducted on 43 out of 182 frogs examined, we recognize *A. marmoratus* for specimens from the states of Mon and Shan and northern Thanintharyi Division and designate a neotype for this species; resurrect *A. afghanus* ( Günther, 1858) from synonymy with *A. marmoratus* for specimens from the northern state of Kachin and designate a lectotype for this species; recognize *A. panhai* for specimens from Thanintharyi, a new country record; and describe a new species for specimens from the western states of Chin and Rakhine, and Sagaing Division.

Species Complex with the Resurrection of...
Fig. 1. Geographic distribution of specimens used in this study (circle = *A. afghanus*, triangle = *A. indoburmanensis*, square = *A. marmoratus*, and diamond = *A. panhai*).
Sequences were edited using SE-
O. (Table 1). Uncorrected
and from Myanmar (Table 1). After
from
Amolops
Nucleotide se-
per generation was plotted in
(Material Examined;
from Myanmar, China, India,
distance (TYE, from anterior edge of tympanum to posterior
mum distance between upper eyelids); tympanum diameter
width of head at its widest point); internarial distance (IND,
(SVL, from tip of snout to vent); head length (HL, from tip of
members of the same species (Vences et al., 2005; Fouquet et
erably higher than seen between individuals recognized as
individuals. Seventeen haplo-
types were observed among the Myanmar individuals with a
haplotype diversity of 0.904 (std. dev. 0.028). The overall
genic distance \( d \) for these 43 sequences was 0.11 with a
maximum distance of 0.20 observed between individual
CAS 229816 from Tanintharyi and several individuals from
Chin (CAS 234943, 235066–235068, 235070, 235071,
235151, 235153, and 235155) and Kachin (CAS 221313,
221314, 224451, 224466, 224491, 225230, 225244, 230228,
and 232997). These maximum genetic distances are consid-
erably higher than seen between individuals recognized as
members of the same species (Vences et al., 2005; Fouquet et
al., 2007). Upon comparing representatives from each
putative species with those of other species of Amolops
from GenBank, pairwise genetic distances (Table 2) ranged
from 0.12 (the distance between A. chunganensis, A. kantingensis,
corner of eye); distance from nostril to eye (DNE, from
center of nostril to anterior border of eye); eye width (EW,
distance from posterior to anterior corners of eye); eye width
front (EWF, distance between anterior corners of eyes); eye
width rear (EWR, distance between posterior corners of
eyes); eye lid width (ELW, transverse width of eyelid);
forelimb length (FLL, from elbow to tip of third finger);
hand length (HAL, from base of outer palmar tubercle to tip
of third finger); length of third finger (FL3, from base of
webbing between third and fourth finger to tip of third
finger); width of disk of third finger (FDW3, greatest
horizontal width); thigh length (THL, from vent to knee);
tibia length (TIL, from knee to ankle); foot length (FL, from
proximal end of inner metatarsal tubercle to tip of fourth
toe); length of fourth toe (TL4, from proximal edge of third
subarticular tubercle to tip of toe); width of disk of fourth
toe (TDW4, greatest horizontal width). Skin texture, dorsal
coloration, ventral coloration, and the presence of supra-
tympanic folds, circummarginall grooves, dorsolateral folds,
axillary glands, vomerine teeth, hind limb banding, and
forelimb banding were all noted. To determine differentia-
tion among individuals, Principal Component Analysis
(PCA) was performed using the program R (R Development
Core Team, 2008) with functions procmp and biplot,
treating data for males and females separately. All variables
were tested for normality using the Shapiro-Francia test in
the Nortest package written in R (http://cran.r-project.org/
web/packages/nortest/). Based upon Bonferroni corrected
\( p \)-values using multtest package of R (Ge et al., 2003), only
one and two variables were non-normal, for females and
males, respectively. The PCA was performed on log_{10}
transformed data matrix (zero centered but unscaled for
variance [Everitt and Hothorn, 2006]). Values for the first
principal component (PC1) and second principal compo-
ment (PC2) were combined to calculate PCA scores for each
specimen and plotted. The biplot function in R was used to
plot both the principal component scores and loadings onto
the same graph. In addition, a one factorial Analysis of
Variance (ANOVA) was performed for males and females
separately for each putative species using an online ANOVA
program (Kirkman, 1996).

RESULTS

Sequence data and phylogenetic analysis.—Nucleotide se-
dquence data from the 16S gene (704 bp) were obtained for
43 individuals of Amolops from Myanmar (Table 1). After
alignment, 201 sites were found to be variable and 153 sites
were parsimony-informative with an average number of
differences of 61.91 among individuals. Seventeen haplo-
types were observed among the Myanmar individuals with a
haplotype diversity of 0.904 (std. dev. 0.028). The overall
genic distance \( d \) for these 43 sequences was 0.11 with a
maximum distance of 0.20 observed between individual
CAS 229816 from Tanintharyi and several individuals from
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and 232997). These maximum genetic distances are consid-
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al., 2007). Upon comparing representatives from each
putative species with those of other species of Amolops
from GenBank, pairwise genetic distances (Table 2) ranged
from
0.12 (the distance between A. chunganensis, A. kantingensis,
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and CAS 240603) to 0.24 (the distance between A. torrentis and CAS 235070) with an overall mean genetic distance of 0.12. Two pairs of previously submitted sequences of *Amolops* described as distinct species (*A. kantingensis* and *A. mantzorum*; *A. liangshanensis* and *A. loloensis*) had genetic distances of zero, indicating they may in fact be from members of the same species. Upon further examination of base composition, these sequences were 99.4% and 99.9% identical, respectively. Based on these results, we suggest that the voucher specimens from which these sequences were taken be examined for confirmation of their species status.

The results of the Bayesian and MP analyses are congruent trees with nearly identical topologies, the differences being the support values for the clades. Only the Bayesian analysis results are presented (Fig. 2). Clades among specimens from Myanmar were well supported by significant bootstrap and BC values (≥0.95), and three additional distinct subclades within the clade representing individuals from Chin and Rakhine were found. All other species, except for *A. marmoratus* and *A. panhai*, formed separate clades from the Myanmar specimens of *Amolops*. *Amolops marmoratus* from China (KIZ) and *A. marmoratus* from Thailand (KUHE 19089) were in two separate clades of the four clades of specimens from Myanmar. *Amolops panhai* (KUHE 20133) was in a basal clade with a specimen (CAS 229816) from Tanintharyi (Fig. 2).

**Morphological data**—We found no obvious variation in morphology among the specimens of *Amolops* from Myanmar. All possessed circummarginal grooves on the fingers, thick supratympanic folds, vomerine teeth, paired gular pouches, and nuptial pads in males. In addition, all lacked distinct raised dorsolateral folds and a distinct annulus around the tympanum. However, differences in body size, coloration, and patterning were observed among adult frogs from three distinct geographic regions: eastern and southeastern Myanmar (Mon, Shan, and Tanintharyi; Fig. 3A), northern Myanmar (Kachin; Fig. 3B), and western and southwestern Myanmar (Chin, Rakhine, and Sagaing; Fig. 3C). Among males and females, 21 morphometric characters were analyzed (Table 3). ANOVA results (Table 4) of males from the three regions produced highly significant values for all characters (*P* < 0.0001) and significant to highly significant values for characters for females (*P* < 0.04–0.0001), with the exception of three characters (hand length, forearm length, and third finger length).

Both males and females of *Amolops* from Mon, Shan, and Tanintharyi were significantly smaller than those collected from Chin, Kachin, Rakhine, and Sagaing. Principal component analyses for males and females performed separately indicated that males were significantly more distinct in morphospace, forming three groups that correspond with major clades in the phylogenetic analyses (Fig. 4). The first two axes (PC1 and PC2) explained more than 94.3% and 77% of the variation for males and females, respectively. For both sexes, the loadings for all 21 characters were positive and similar in magnitude, thus the PC1 reflected the variation in size (Table 5; 91.2% and 67% for males and females, respectively). Males from the states of Mon and Shan consistently had smaller features than males from the states of Chin, Kachin, and Rakhine (Fig. 4) based on the PC1 scores alone. Males from Chin and Rakhine were significantly larger overall and within this region geographic subclusters could be distinguished by PC1 alone and were congruent with clades recovered in the phylogenetic

**Table 2.** Pairwise Genetic Distances for the 16S rRNA Gene (704 bp) among the Species of *Amolops* Used in This Study. Bold characters highlight distances between species of *Amolops* collected from Myanmar.

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Voucher cat. no.</th>
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analyses. Characters that most contributed to this pattern included TYE, TDW4, FDW3, ELW, DNE, and TD (Table 5).

Kachin males were intermediate in size when compared to those from Chin, Mon, Rakhine, Sagaing, and Shan. In comparison, the PCA results for females showed less distinction, with PC1 explaining only 67% of the variation (Fig. 5), and females from Chin, Kachin, and Rakhine overlapped significantly. Similar to what was observed for males, the most significant variables for the distribution of females included TYE, TDW4, and FDW3. Indeed, the correlation coefficient between the PC2 scores of males and those of females was highly significant, indicating that the same morphometric characteristics contributed to the observed separation of groups (Table 5; r = 0.96; Pearson's

![Fig. 2. The phylogenetic consensus tree derived from partial DNA sequences of the mitochondrial gene (16S) based on Bayesian analysis. Numbers above branches are Bayesian support values; numbers below branches are nonparametric bootstrap proportions for parsimony analysis of the consensus alignment (* indicates less than 60% bootstrap support).](image-url)
correlation coefficient). Although males and females exhibit sexual dimorphism in the features considered, these differences are likely to be largely isometric.

We interpret the geographic distribution of samples, the high degree of genetic differentiation, the results of phylogenetic analyses, and morphological differences between Burmese specimens of *Amolops* as evidence for the existence of four species. Therefore, we restrict *A. marmoratus* to specimens from the states of Mon and Shan, and northern Tanintharyi Division, elevate *A. afghanus* from synonymy for specimens from Kachin State, recognize *A. panhai* for other specimens from Tanintharyi Division (Fig. 6), and describe a new species (see below) for specimens from the states of Chin and Rakhine, and Sagaing Division.

**Amolops marmoratus** (Blyth, 1855)

**Neotype.**—CAS 240603, adult male, Myanmar, Mon State, Thaton District, Kyaikhto Township, 10 Minutes Camp, along YeTakon Chaung, 17°26'38.5"N, 97°5'57.3"E, A. K. Shein, S. L. Oo, K. S. Lwin, and Y. M. Win, 1 February 2008.

**Diagnosis.**—This species differs from all other members of *Amolops* by a combination of the following characters: relatively small body size (male mean SVL 42.7 mm, female mean SVL 75.4 mm); vomerine teeth well developed; dorsal surface granular; dorsum with dark mottling on lighter background; posterior of thighs with light mottling on dark gray; first finger with circummarginal and transverse grooves on disk; first finger slightly shorter than second; outer metatarsal tubercle present (indistinct in some specimens); males with dual gular pouches and white nuptial pad on first finger.

**Description of neotype.**—Small body, SVL 41.4 mm (slightly smaller than Blyth’s originally described specimen); head broad, flat and triangular, longer (16.2 mm) than wide (15.2 mm); snout sloping from eye to a point just below nostril, projecting upward beyond jaw in profile, snout tip rounded in dorsal view; canthus rostralis distinct, curving inward from eye to nostril; loreal region strongly concave; nostril closer to tip of snout than eye, projecting lateral from canthus, longitudinally oval, angled medially and dorsally towards tip of snout, posterior edge with small tubercle; interorbital and frontal areas flat; eyes large (6.3 mm), pupil horizontal; internarial distance (5.0 mm) wider than interorbital distance (3.7 mm); tympanic indistinct, small (1.9 mm; same as original description) and round, diameter approximately 30% that of eye, separated from eye by approximate tympanum diameter, annulus not apparent, surrounded by tubercles of various sizes; vomerine teeth week, on oblique patches separated from choanae by half the length of one patch and from each other medially by one fourth the length of one patch, lateral edges hidden by lingual shelf in ventral view; tongue horizontally wide, medially with U-shaped notch, posterior half free; paired gular vocal sacs form darkened pouches, vocal apertures as small, narrow slits just inside commissures of jaws.

Forearm and hand length (elbow to tip of third finger) 51% SVL. Fingers long and slender, with tips of all fingers expanded to disks with circummarginal and transverse grooves, disk of third finger largest (3.2 mm), approximately 1.7 times larger than size of tympanum; webbing and lateral fringes absent on hand; relative finger lengths III > IV > II > I, third finger shorter than forearm; large round protruding subarticular tubercles on midventral ridge, subarticular formula (digit number in Roman numerals, subarticular tubercle count in Arabic numbers) I (1), II (1), III (2), IV (2); no supernumerary on palmar surface; inner and outer metacarpal tubercles large, flat, indistinct ovals, touching medially; white velvety nuptial pad, extending from base of first finger, which is widened, to distal end of subarticular tubercle, with a lateral extension to base of disk.

Legs long, heels overlap when legs at right angles to body; tibiotarsal articulation reaches beyond snout; mean tibia
length approximately 57% mean length of body; toes fully webbed (same as original description), webbing formula I1–1/1 II1–1/1 III1–1/1 IV1–1/1 V following Myers and Duellman (1982) as modified by Savage (1997) with fringes reaching to disks; disks of toes slightly smaller than those of fingers with circummarginal and transverse grooves; oval subarticular tubercles on all toes, subarticular formula I (1), II (1), III (2), IV (3), V (2); inner metatarsal tubercle narrow, elongate, flat, and grayish; outer metatarsal tubercle small, raised, distinct, and white.

Skin granular throughout dorsal surface (as described originally by Blyth); raised tubercles present on sides, back of thigh to vent, just below tympanum and along dorsolateral row but distinct dorsolateral fold absent; skin smooth.

Table 3.

<table>
<thead>
<tr>
<th>Character</th>
<th>Amolops afghanus (n = 36)</th>
<th>Amolops marmoratus (n = 8)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SVL</td>
<td>86.4 ± 7.3</td>
<td>75.4 ± 2.9</td>
</tr>
<tr>
<td>HL</td>
<td>31.8 ± 2.2</td>
<td>27.4 ± 0.9</td>
</tr>
<tr>
<td>HW</td>
<td>31.9 ± 2.6</td>
<td>28.0 ± 1.3</td>
</tr>
<tr>
<td>TD</td>
<td>3.9 ± 0.4</td>
<td>2.9 ± 0.3</td>
</tr>
<tr>
<td>TYE</td>
<td>4.2 ± 0.7</td>
<td>3.9 ± 0.5</td>
</tr>
<tr>
<td>DNE</td>
<td>7.3 ± 0.6</td>
<td>6.3 ± 0.6</td>
</tr>
<tr>
<td>IOD</td>
<td>8.0 ± 0.8</td>
<td>6.7 ± 0.5</td>
</tr>
<tr>
<td>IND</td>
<td>9.0 ± 1.0</td>
<td>8.0 ± 0.4</td>
</tr>
<tr>
<td>EW</td>
<td>9.3 ± 0.8</td>
<td>8.2 ± 0.5</td>
</tr>
<tr>
<td>EWF</td>
<td>17.4 ± 1.3</td>
<td>15.1 ± 0.6</td>
</tr>
<tr>
<td>EWR</td>
<td>24.4 ± 1.7</td>
<td>21.2 ± 0.8</td>
</tr>
<tr>
<td>ELW</td>
<td>7.6 ± 0.7</td>
<td>6.7 ± 0.5</td>
</tr>
<tr>
<td>TL</td>
<td>49.1 ± 4.1</td>
<td>43.1 ± 1.9</td>
</tr>
<tr>
<td>THL</td>
<td>47.9 ± 4.2</td>
<td>42.1 ± 2.3</td>
</tr>
<tr>
<td>FL</td>
<td>42.0 ± 3.6</td>
<td>37.8 ± 1.9</td>
</tr>
<tr>
<td>HAL</td>
<td>24.0 ± 3.4</td>
<td>22.7 ± 1.1</td>
</tr>
<tr>
<td>FLL</td>
<td>40.5 ± 3.4</td>
<td>37.6 ± 2.0</td>
</tr>
<tr>
<td>FSL</td>
<td>15.0 ± 2.0</td>
<td>14.6 ± 0.8</td>
</tr>
<tr>
<td>FDW3</td>
<td>5.8 ± 2.0</td>
<td>5.5 ± 0.3</td>
</tr>
<tr>
<td>TL4</td>
<td>22.6 ± 2.1</td>
<td>20.7 ± 1.2</td>
</tr>
<tr>
<td>TDW4</td>
<td>5.1 ± 0.7</td>
<td>4.3 ± 0.6</td>
</tr>
</tbody>
</table>

Adult males:

<table>
<thead>
<tr>
<th>Character</th>
<th>Amolops afghanus (n = 29)</th>
<th>Amolops marmoratus (n = 20)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SVL</td>
<td>71.1 ± 7.5</td>
<td>42.7 ± 2.3</td>
</tr>
<tr>
<td>HL</td>
<td>26.4 ± 2.5</td>
<td>15.9 ± 0.9</td>
</tr>
<tr>
<td>HW</td>
<td>25.9 ± 2.8</td>
<td>15.3 ± 1.1</td>
</tr>
<tr>
<td>TD</td>
<td>3.1 ± 0.4</td>
<td>2.0 ± 0.2</td>
</tr>
<tr>
<td>TYE</td>
<td>3.5 ± 0.7</td>
<td>2.0 ± 0.3</td>
</tr>
<tr>
<td>DNE</td>
<td>5.9 ± 0.5</td>
<td>3.5 ± 0.3</td>
</tr>
<tr>
<td>IOD</td>
<td>6.4 ± 0.8</td>
<td>3.9 ± 0.2</td>
</tr>
<tr>
<td>IND</td>
<td>7.6 ± 1.1</td>
<td>4.8 ± 0.3</td>
</tr>
<tr>
<td>EW</td>
<td>8.3 ± 0.7</td>
<td>5.7 ± 0.5</td>
</tr>
<tr>
<td>EWF</td>
<td>14.8 ± 1.3</td>
<td>9.4 ± 0.6</td>
</tr>
<tr>
<td>EWR</td>
<td>20.7 ± 1.7</td>
<td>13.1 ± 1.0</td>
</tr>
<tr>
<td>ELW</td>
<td>6.7 ± 0.6</td>
<td>4.1 ± 0.5</td>
</tr>
<tr>
<td>TL</td>
<td>40.8 ± 5.5</td>
<td>24.4 ± 0.9</td>
</tr>
<tr>
<td>THL</td>
<td>39.4 ± 4.6</td>
<td>23.6 ± 1.3</td>
</tr>
<tr>
<td>FL</td>
<td>34.7 ± 4.3</td>
<td>21.1 ± 1.1</td>
</tr>
<tr>
<td>HAL</td>
<td>20.3 ± 2.5</td>
<td>13.3 ± 0.8</td>
</tr>
<tr>
<td>FLL</td>
<td>34.7 ± 3.7</td>
<td>22.5 ± 1.2</td>
</tr>
<tr>
<td>FSL</td>
<td>12.5 ± 1.6</td>
<td>8.5 ± 0.5</td>
</tr>
<tr>
<td>FDW3</td>
<td>4.8 ± 0.8</td>
<td>3.1 ± 0.2</td>
</tr>
<tr>
<td>TL4</td>
<td>18.8 ± 2.5</td>
<td>11.5 ± 0.6</td>
</tr>
<tr>
<td>TDW4</td>
<td>4.2 ± 0.8</td>
<td>2.3 ± 0.2</td>
</tr>
</tbody>
</table>
on ventral surface (differs from original description);
dorsum of arms and legs with scattered indistinct flat
tubercles; supratympanic fold short and indistinct,
existing from eye to just behind tympanum; multiple small
globular rictal glands on right side, single rictal gland on left
side, just posterior to jaw.

 Measurements of neotype (mm).—SVL 41.4; HW 15.2; HL
16.2; DNE 3.4; EW 6.3; ELW 4.4; IOD 3.7; IND 5.0; EWR
14.0; EWF 9.5; TD 1.9; FLL 23.1; HAL 13.8; FL3 8.5; FDW3
3.2; THL 24.5; TIL 23.5; FL 20.4; TL4 11.2; TDW4 2.4.

 Color in preservative.—Dorsum with distinct dark mottling
interspersed with lighter chain pattern, patterning continuing
onto sides (Fig. 3); light ventral surface (similarly
described in original description). Upper lip mottled.
Nuptial pads on first fingers white; distinctive banding on
forelimbs and hind limbs extending onto hands and feet;
posterior of thighs with a light cream mottling on a dark
gray background.

 Variation.—See Table 3 for measurements. All comparative
specimens conform to description of neotype, with the
following exceptions: sexual dimorphism observed with
females being significantly larger than males, female mean
SVL 75.4 mm (range 69.8–79.0), male mean SVL 42.7 mm
(range 38.2–48.1); females with heads slightly wider (mean
of 28.0 mm) than long (mean of 27.4 mm); vomerine teeth
in short oblique rows (CAS 221669, 221671, 222209,
240588, 240589) or transverse rows (CAS 240434, 240591,
240595, 240597); outer metatarsal tubercle indistinct (CAS
221669, 221670, 221674, 240593, 240597, 240602); upper
lip solidly dark (CAS 215272, 221668–221670, 240434,
240595).

 Comparisons.—Amolops marmoratus differs from all species of
Amolops and two similar looking species of Odorrana found
within Myanmar and neighboring countries based on the
following characters: gular pouches present in males (absent in
A. bellulus, A. dainiyunensis, A. granulosus, A. himalayanus, A.
jinjiangensis, A. kantgingensis, A. kaulbacki, A. liangshanyenischis,
A. lifanensis, A. loloensis, A. mantzorum, A. medogensis, A.
nidorbellus, A. ricketti, and A. viridimaculatus); nuptial pads
present on base of first finger in males (absent in A.
akhaorum); spinules absent on upper lip of males (present in
A. akhaorum); vomerine teeth strongly developed (weakly
developed in A. akhaorum and A. panahi, absent in A.
dainiyunensis, A. daorum, A. hainanensis, A. hongkongensis, A.
torrentis, and A. wuyiensis); distinctive dorsolateral folds
absent (present in A. akhaorum, A. aniqiaoensis, A. arch-
ophalus, A. chapaensis, A. chinghansensis, A. compotrix, A.
cremnobatus, A. cuca, A. gerbillus, A. iroides, A. kohimaensis, A.
longimanus, A. mengyungensis, A. minutus, A. monticola, A.
nasicus, A. ricketti, and A. vitrea); diagnostic fringe of skin
on third finger absent (present in A. formosus and O.
chapaensis); parotid-like swelling above tympanum absent
(present in A. longimanus); visible axillary glands absent
(present in A. larutensis and A. panahi); conical spines on
nuptial pads absent (present in A. ricketti and A. spinapector-
alis); circummarginal and transverse grooves present on disk
of first finger (absent in A. bellulus, A. formosus, A. granulosus,
A. jinjiangensis, A. kantgingenis, A. liangshanyenischis, A. lifanen-
sis, A. loloensis, A. mantzorum, A. nidorbellus, and A. viridimaculatus);
first finger slightly shorter than second (first finger substantially shorter than second in A. assama-
ensis); outer metatarsal tubercle present (absent in A.
akhaorum, A. bellulus, A. daorum, A. gerbillus, A. granulosus,
A. hainanensis, A. himalayanus, A. jinjiangensis, A. kaulbacki,
A. kohimaensis, A. lifanensis, A. loloensis, A. mantzorum, A. otaphus,
A. ricketti, A. spinapectoralis, and O. gennatina); distinct dark
mask through eye extending to anterior flank of body and
white band on upper lip absent (present in A. bellulus);
narrow gold stripe on canthus absent (present in A. akhaorum);
dorsum with dark motting interspersed with light chain pattern (dorsum dark purple with yellow spots in
A. caelumnootis and A. splendidissimus, brown with distinct
green spots in A. nidorbellus and A. viridimaculatus, green
with distinct brown motting in A. medogensis); one or more
large white spot on each flank absent (present in A. daorum).

Amolops marmoratus is morphologically very similar to A.
afghanus and the new species described below but differs in
male being significantly smaller in size, and by dorsum
having dark motting interspersed with lighter chain pattern
and distinct granular skin that continues onto sides (dorsum
with light reticulation on more extensive brown background in A. afghanus and dorsum brown with faint lighter
reticulation or scattering of darker brown spotting or both
in new species), and posterior of thighs with light cream
motting on dark gray background (light cream speckling or
reticulation on brown background in A. afghanus and solid
brown in new species).

 Remarks.—The single type specimen was stated in the
original description to have been collected from “Schwe
Gyen, Pegu” by Captain Berdmore. Schwe Gyen, Pegu
(Shwegyin, Bago) is a city at the confluence of the Shwegyin River and Sittaing River in the eastern part of Bago Division. However, because species of *Amolops* are not typically found in large lowland rivers, the type locality may reflect a general reference to the Shwegyin River valley itself that originates near the border with Kayin State. This valley is approximately 270 to 300 km south of the collecting sites in Shan State but only approximately 45 to 90 km north of the collecting sites in Mon State for specimens of the present study. The sites from Mon State are also from streams of the Sittaing watershed. The type material was examined by Anderson (1871, 1878) but not by subsequent researchers and presumed to be lost (Chanda et al., 2000). Herein we therefore designate a neotype and provide a detailed description of *A. marmoratus* based upon the neotype and 28 specimens collected from the states of Mon and Shan and the northern Tanintharyi Division. We compare this description with the following original description by Blyth.

Fig. 4. Plot of components 1 and 2 resulting from PCA of males. *Amolops marmoratus* (closed circle), *A. afghanus* (closed square), and *A. indoburmanensis* (X). Direction and magnitude of the vectors reflect the degree of contribution by the morphometric characteristics used in the analysis. Morphometry: SVL = snout to vent length, HL = head length, HW = head width, IND = internarial distance, IOD = interorbital distance, TD = tympanum diameter, TYE = tympanum to eye distance, DNE = nostril to eye distance, EW = eye width, EWF = front eyelid width, ELW = eyelid width, FL = forelimb length, HAL = hand length, THL = thigh length, TIL = tibia length, FL3 = third finger length, FDW3 = third finger disk width, TL4 = fourth toe length, TDW4 = fourth toe disk width.
(1855). “Hind-feet completely webbed. Tympana very small. Skin granulose above and on the belly. Colour black above, ventral surface slightly granular; dorsum with light reticulation; dorsal surface with light reticulation or reticulation on brown; first finger with circummarginal and transverse grooves; oval subarticular disk; disks of toes slightly smaller than those of fingers with circummarginal and transverse grooves; oval subarticular tubercles on all toes, subarticular formula I (1), II (1), III (2), IV (2); supernumerary tubercles not apparent; inner and outer metacarpal tubercles vague (probably due to age of specimen).

Arms long, forearm and hand length (elbow to tip of third finger) approximately 50% SVL; fingers long and slender, lacking webbing, as stated in original description, with tips of all fingers expanded to disks with circummarginal and transverse grooves; disk of third finger largest (4.5 mm), much larger than tympanum (contrary to statement in original description); relative finger lengths III > IV > II > I, third finger shorter than forearm; large protruding subarticular tubercles on midventral ridge; subarticular formula I (1), II (1), III (2), IV (2); supernumerary tubercles not apparent; inner and outer metacarpal tubercles absent; dorsal region of left thigh damaged near vent.

Skin smooth on both dorsal and ventral surfaces with only a few small indistinct tubercles present on sides and near vent; supratympanic fold short and thick, extending from eye curving around and ending behind tympanum; tubercles in temporal region not apparent (probably due to age of specimen); indistinct rictal glands present on one side of head at posterior end of jaw.

Measurements of lectotype (mm).—SVL 80.9; HW 29.6; HL 29.7; DNE 5.6; EW 12.0; ELW 6.4; IOD 7.4; IND 7.8; EWR 22.9; EWF 15.2; TL 26.9; FL 36.9; HAL 24.2; FL 3 13.8; FDW 4.5; THL 39.8; TIL 49.2; FL 38.8; TL 4 21.7; TDW 4.2.

Color in preservative.—Color pattern faded overall, ventral surface light; pattern absent on arms, legs, and feet.

Variation.—See Table 3 for measurements. All comparative specimens conform to description of lectotype, with the following exceptions: sexual dimorphism observed with females being significantly larger than males, female mean SVL 81.1 ± 7.0 mm (range 67.7–94.1), male mean SVL 51.5 ± 3.7 mm (range 45.6–62.9), males with paired gular pouches and white nuptial pads.

As with lectotype, vomerine teeth are linear and transverse in female specimens CAS 221313, 221361, 221362, 225233, 233114, but are slightly oblique in female specimens CAS 221322 and 240896, and oblique in female
specimens CAS 221323 and 233012; they are oblique in all male specimens except CAS 225230–225232, 233013, which are transverse, and CAS 224363 and 232915, which are globular. Unlike the lectotype, all specimens have moderate to extensive tuberculation in the temporal region; all female and some male specimens (CAS 221314, 224362, 225230–225232, 232914, 232915, 232936, 233013, 233113) with distinctly visible tympanum, but tympanum obscured by tubercles in several male specimens (CAS 224363, 240882, 240883, 240889, 240890, 240892–240895). All specimens with light colored rictal glands more distinct than lectotype, some male specimens (CAS 224363, 232914, 240890, 240892) with small white spinules on these glands. Unlike lectotype, all female specimens with dorsal granulation, some with scattered dorsal tubercles (CAS 221361, 233012, 233114, 240896); CAS 221313, 221322, 221323, 221361, 221362, 224362, 224363 with thicker supratympanic fold; CAS 221322, 221323 with more pronounced scattered tubercles on dorsal aspect of tibia; CAS 224362, 224655, 232914, 232915, 232936, 232996, 233012, 233013, 233113,
Amolops afghanus

A. kaulbacki

Amolops

A. compotrix, and A. nidorbellus

5 mm.

A. mengyangensis and two similar looking species of

Amolops marmoratus sensu

is similar to A. loloensis

A. daiyunensis

A. afghanus

A. jinjiangensis

differs from all other

A. mantzorum

69

A. lifanensis

and A. cucae); circummarginal and transverse grooves

A. viridimaculatus

are significantly larger in A. hainanensis

A. bellulus

A. viridimaculatus

A. ricketti

A. archontophus, A. chakrataensis, A. cunchanensis, A. compotrix, A.

cremnobatus, A. caeae, A. gerbillus, A. irodes, A. kohimaensis, A. longimanus, A. mengyangensis, A. minitus, A. monticola, A. nasicus, A. tornotus, and A. vitreus; diagnostic fringe of skin on third finger absent (present in A. formosus, A. macrorynchus, and O. chaepaensis); parotid-like swelling above tympanum absent (present in A. longimanus); visible axillary glands absent (present in A. larutensis and A. panhai); conical spines on nuptial pads absent (present in A. ricketti and A. spinapectoralis); circummarginal and transverse grooves present on disk of first finger (absent in A. bellulus, A. formosus, A. granulosus, A. jinjiangensis, A. kangtingensis, A. liangshanensis, A. lifanensis, A. loloensis, A. mantzorum, A. nidorbellus, and A. viridimaculatus); first finger slightly shorter than second (first finger substantially shorter than second in A. assamanensis); distinct dark mask through eye extending to anterior flank of body and white band on upper lip absent (present in A. bellulus); narrow gold stripe on canthus absent (present in A. akhaoorum); dorsum with light reticulation on more extensive brown background (dorsum dark purple with yellow spots in A. caelumoctis and A. splendissimus, brown with distinct green spots in A. nidorbellus and A. viridimaculatus, green with distinct brown mottling in A. medogensis); one or more large white spot on each flank absent (present in A. daorum).

Amolops afghanus is similar to A. marmoratus and the new species described below but males are intermediate in body size (mean SVL of 51.5 mm, compared to mean 42.7 mm for A. marmoratus and mean SVL of 71.1 mm for new species) but exhibit relatively larger tympanum diameter (TW/SVL of 5.1%) than males of A. marmoratus (4.7%) and new species (4.4%). Females of A. afghanus are significantly larger in body size (mean SVL of 81.1 mm) than females of A. marmoratus (mean SVL of 75.4 mm). Amolops afghanus has less granulation on dorsal surface than A. marmoratus but is not as smooth dorsally as in new species. Amolops afghanus has a dorsum with light reticulation on a more extensive brown background (more extensive dark mottling interspersed with a light chain pattern in A. marmoratus and a brown background with faint lighter reticulation or scattering of darker brown spotting or both in new species), and posterior of thighs consist of fine light cream speckling or reticulation on brown background (light cream mottling on dark gray background in A. marmoratus or solid brown in new species).

**Comparisons.**—Amolops afghanus differs from all other members of Amolops and two similar looking species of Odorrana found within Myanmar and neighboring countries based on the following characters: gular pouches in males (absent in A. bellulus, A. daiyunensis, A. granulosus, A. himalayanus, A. jinjiangensis, A. kangtingensis, A. kaubacki, A. liangshanensis, A. lifanensis, A. loloensis, A. mantzorum, A. medogensis, A. nidorbellus, A. ricketti, and A. viridimaculatus); nuptial pad present at base of first finger in males (absent in A. akhaoorum); spinules on upper lip absent in males (present in O. geminata); vomerine teeth strongly developed (weakly developed in A. akhaoorum and A. panhai, absent in A. daorum, A. daiyunensis, A. hainanensis, A. hongkongensis, A. torrentis, and A. wuyiensis); distinctive dorsolateral folds absent (present in A. akhaoorum, A. aniqaoensis, A. archontophus, A. chakrataensis, A. cunchanensis, A. compotrix, A. crennobatus, A. caeae, A. gerbillus, A. irodes, A. kohimaensis, A. longimanus, A. mengyangensis, A. minitus, A. monticola, A. nasicus, A. tornotus, and A. vitreus); diagnostic fringe of skin on third finger absent (present in A. formosus, A. macrorynchus, and O. chaepaensis); parotid-like swelling above tympanum absent (present in A. longimanus); visible axillary glands absent (present in A. larutensis and A. panhai); conical spines on nuptial pads absent (present in A. ricketti and A. spinapectoralis); circummarginal and transverse grooves present on disk of first finger (absent in A. bellulus, A. formosus, A. granulosus, A. jinjiangensis, A. kangtingensis, A. liangshanensis, A. lifanensis, A. loloensis, A. mantzorum, A. nidorbellus, and A. viridimaculatus); first finger slightly shorter than second (first finger substantially shorter than second in A. assamanensis); distinct dark mask through eye extending to anterior flank of body and white band on upper lip absent (present in A. bellulus); narrow gold stripe on canthus absent (present in A. akhaoorum); dorsum with light reticulation on more extensive brown background (dorsum dark purple with yellow spots in A. caelumoctis and A. splendissimus, brown with distinct green spots in A. nidorbellus and A. viridimaculatus, green with distinct brown mottling in A. medogensis); one or more large white spot on each flank absent (present in A. daorum).

Amolops afghanus is similar to A. marmoratus and the new species described below but males are intermediate in body size (mean SVL of 51.5 mm, compared to mean 42.7 mm for A. marmoratus and mean SVL of 71.1 mm for new species) but exhibit relatively larger tympanum diameter (TW/SVL of 5.1%) than males of A. marmoratus (4.7%) and new species (4.4%). Females of A. afghanus are significantly larger in body size (mean SVL of 81.1 mm) than females of A. marmoratus (mean SVL of 75.4 mm). Amolops afghanus has less granulation on dorsal surface than A. marmoratus but is not as smooth dorsally as in new species. Amolops afghanus has a dorsum with light reticulation on a more extensive brown background (more extensive dark mottling interspersed with a light chain pattern in A. marmoratus and a brown background with faint lighter reticulation or scattering of darker brown spotting or both in new species), and posterior of thighs consist of fine light cream speckling or reticulation on brown background (light cream mottling on dark gray background in A. marmoratus or solid brown in new species).

**Remarks.**—The discovery that Amolops marmoratus sensu stricto is more limited in Myanmar to eastern Bago Division, Mon State, Shan State, and northern Tanintharyi Division and probably the states of Kayin and Kayah, which are between Thailand (from which the KUHE 20133 specimen that forms a clade with A. marmoratus from Myanmar was collected) and the type locality of A. marmoratus, requires that we reexamine the available names from the list of synonyms for this species to consider any that may be appropriate for the specimens from Kachin State. Amolops kakhienensis (Anderson, 1878) is a possible name since the type locality is stated as “fields, in the Nampoung valley, 1,000 feet”, which is between the city of Bhamo and the Chinese border in the state of Kachin. This species was synonymized into A. marmoratus by Boulenge (1890, 1920). However, Amolops afghanus (Günther, 1858) is the older available name. The type locality is stated as Afghanistan in the original description. Subsequent researchers have argued that this type locality is mistaken (Annandale, 1912) as no
other species of *Amolops* is known from Afghanistan and the syntype was part of a large collection of plants and animals collected by William Griffith during his expeditions in Afghanistan, northeastern India, and Myanmar (Griffith, 1847) and then sent to the British Museum (BMNH) by the East India Company after his death.

Although Griffith described in his journal the specimens of fish, birds, snakes, and plants he collected or received (Griffith, 1847), he did not mention collecting any frog. He does detail an expedition he made into Myanmar from Assam, India from February to May 1837. He began his travel from Sadiya in Assam to the Noa Dihing River, traveling up the river and then crossing the Patkai Mountain Range at the northern end of the Naga Hills into Myanmar, in particular into the Hukawng Valley of Kachin State. He traversed the Hukawng Valley in a southern direction to Mogau, traveling south along the Mogau River to the Irrawaddy River. From here he traveled by boat to Bhamo then exited Kachin State into Mandalay Division to Inywa, and finally to Yangon. It is clear that his route bisects the sites from which specimens from Kachin State were collected for the present study. He may have therefore easily collected the two tadpoles and one adult female syntype for *A. afghanus* from Kachin State during this expedition, although he may also have collected the specimens from Assam, India during this or other expeditions.

We therefore remove *A. afghanus* from synonymy of *A. marmoratus* to accommodate the specimens from Kachin State and provide a detailed description of this species using the adult syntype from which the original description was made by Günther as follows: “Fingers free. Palatine teeth in a straight line between the posterior choana, interrupted in the middle. Skin smooth. Tympanum very small, the size of a sucker. Toes completely webbed. Three inches long”. We designate this specimen as the lectotype, and include an additional 57 specimens from Kachin State (28 adult females and 29 adult males) to account for additional morphological variation.

*Amolops indoburmanensis*, new species

Indoburman Torrent Frog

**Figure 7**

**Holotype.**—CAS 235070, adult male, Myanmar, Chin State, Mintatt District, Mintatt Township, Twi Rein Village, 21°35’55.4”N, 93°51’59.9”E, A. K. Shein, T. Nyo, and L. Shein, 23 March 2006.


**Diagnosis.**—*Amolops indoburmanensis* differs from all other members of *Amolops* by a combination of the following characters: large body size (male mean SVL of 71.0 mm, female mean SVL of 86.5 mm); vomerine teeth well developed; dorsal surface mostly smooth with small tubercles along posterior region of sides; dorsum brown with scattering of darker brown spotting or very faint lighter reticulation or both; posterior of thighs brown; first finger with circummarginal and transverse grooves on disk; first finger slightly shorter than second; males with dual gular pouches and gray nuptial pads on first finger.

**Description of holotype.**—Relatively large body size, SVL 77.9 mm; body moderately stocky; head broad, flat and triangular, width of head (29.2 mm) slightly greater than length (28.5 mm). Snout sloping from eye to a point just below nostril, projecting upward beyond jaw in profile, rounded in dorsal view; canthus rostralis distinct, curving inward from eye to nostril; loreal region strongly concave; upper lip thick, strongly flared outward; nostril closer to tip of snout than eye, lateral to and below canthus, longitudinally oval, angled medially and dorsally towards tip of snout, posterior edge with small tubercles; interorbital and frontal areas flat; pineal body not visible; eyes large (8.7 mm), 74.7% snout length (11.6 mm), pupil horizontal; internarial distance (8.7 mm) wider than interorbital distance (6.9 mm); interorbital distance narrower than upper eyelid width (7.4 mm); temporal region swollen; tympanum visible, small (2.3 mm) and round, diameter approximately 26.5% that of eye, separated from eye by over twice tympanum diameter, annulus not apparent, surrounded by tubercles of various sizes; vomerine teeth strongly developed, in short oblique patches constricted anterolaterally and expanded and rounded posteromedially, approximately 13 small teeth dispersed along edges of each patch, lateral ends just anterior to midline of choanae, posterior edges behind choanae, separated from each other by less than half the length of one patch; choanae as medially obtusely pointed triangles lateral edges hidden by lingual shelf in ventral-lateral view; tongue medially notched, posterior half free; paired gular pouches, vocal apertures as narrow slits just inside commissures of upper and lower jaws.

Arms thick and long, forearm and hand length (elbow to tip of third finger) 50.2% SVL, when adpressed; relative finger lengths III > IV > II > I, third finger shorter than forearm; tips of all fingers expanded to disks with circummarginal and transverse grooves, disk of third finger largest (6.2 mm), over twice the size of tympanum; webbing and lateral fringes absent on hand; large round protruding subarticular tubercles on midventral ridge, subarticular formula I (1), II (1), III (2), IV (2); indistinct supernumerary tubercle present at base of each finger; inner and outer metacarpal tubercles large, wide and flat, narrowly separated, inner tubercle slightly triangular with medial obtuse point and slightly wider than outer oval tubercle; gray velvety nuptial pad, extending from base of first finger to distal end of subarticular tubercle, with a lateral extension to base of disk.

Legs long and broad; heels overlap when legs at right angles to body; tibiotarsal articulation reaches beyond snout; tibia approximately 52.4% length of body; toes fully
webbed, webbing formula \( II^{1/2} III^{1/2} IV^{1} V \) with fringes reaching to disks; disks of toes smaller than those of fingers with circummarginal and transverse grooves; oval subarticular tubercles on all toes, subarticular tubercle formula \( I (1), II (1), III (2), IV (3), V (2) \); inner metatarsal tubercle narrow, elongate, and flat, 31.9% length of first toe; outer metatarsal tubercle absent.

Skin middorsally smooth becoming tuberculate laterally; dorsum of arms and legs with scattered indistinct flat tubercles; venter smooth on throat and chest, becoming granular on abdomen and thighs; dorsolateral folds absent; supratympanic fold short and thick, extending from eye to just behind tympanum; small flat tubercles cover area from below nostril, through loreal region, below eye, to behind tympanum; four small globular linearly positioned rictal glands on left, three on right, just posterior to jaw, covered with small white spicules that become minute as they extend onto posterior end of upper lip.

**Measurements of holotype (mm).—** SVL 77.9; HW 29.2; HL 28.5; DNE 6.7; EW 8.7; ELW 7.4; IOD 6.9; IND 8.7; EWR 22.5; EWF 16.5; TD 2.3; FLL 39.1; HAL 22.5; FL3 13.9; FDW3 6.2; THL 46.3; TIL 47.5; FL 40.8; TL4 21.7; TDW4 4.9.

**Color in preservative.—** Dorsum brown scattered with irregularly shaped darker brown spots from snout to vent; dorsal aspect of forelimbs and hind limbs brown without pattern; webbing slightly darker brown without pattern; venter brown on throat and chest, lighter on abdomen and thighs; posterior of thighs appear solid brown with naked eye but as fine dark brown reticulation on lighter brown background under stereoscope; fingers and toes including disks brown without pattern.

**Variation.—** See Table 3 for measurements. All paratypes and referred specimens (see Material Examined) conform to description of holotype, with the following exceptions.

![Fig. 7. Amolops indoburmanensis, CAS 235070, adult male in dorsal view, in preservative. Scale bar = 3 mm.](image-url)
Sexual dimorphism observed in adults with females (mean SVL of 87.0 ± 6.0 mm, range 62.82–106.0 mm) significantly larger than males (mean SVL of 71.1 ± 7.4 mm, range 59.4–85.6 mm), which have paired gular pouches along with lightly white pigmented nuptial pad on first finger. Vomerine teeth rows are transverse in female specimens CAS 216568, 216569, 216572, 216593, 219954, 219955, 220262; however, slightly oblique in female specimens CAS 216496, 216591, 216592, 216571, and male specimen CAS 216597; and globular, as in holotype, in female specimens CAS 210185, 235066, 235071, and male specimens CAS 216567, 216570, 219953, 220263, 221973, 220264, 235067–235069. Most specimens with extensive tuberculation in temporal region between eye and tympanum and surrounding tympanum, some (CAS 219953, 235066–235069, 235071, 235151–235154) with tubercules obscuring tympanum, others (CAS 216597, 219954, 219955, 235217) with small whitish tubercules around tympanum, annulus slightly raised anteriorly but obscured by supratympanic fold posteriorly; all specimens with well developed light colored rictal glands, some (CAS 210185, 216567, 219953, 219954, 220264, 221973, 235067–235069) with small white spinules on these glands. All specimens have smooth dorsum lacking tubercules except for CAS 216567 and 220264, which have indistinct dorsolateral rows of tubercules, and CAS 216597, which with these indistinct rows of dorsolateral tubercles has few small indistinct tubercles scattered on dorsum; all female specimens with granulated dorsum, and all specimens with slight to moderate tuberculation on thigh and tibia. All specimens examined with a brown dorsum, most with darker brown spotting, concentrating on head, and an obscured lighter reticulation; however, some (CAS 235067–235069) with darker brown spotting but no reticulation, and others (CAS 210185, 219953–219955) with lighter reticulation but no darker brown spotting. Very faint banding on dorsal aspect of arms and legs of CAS 216569, 220263, 220264, and only on legs of CAS 210185, 216172, 219953, 235066, 235069, 235071, remaining specimens without visible banding. Some specimens (CAS 219953–219955, 235066–235069, 235071) darkly pigmented throughout venter, others (CAS 216496, 216567–216572, 216591–216593, 216597) with dark spotting or reticulation on throat and chest but lighter abdomen and legs, while others (CAS 210185, 220262–220264, 221973) are light throughout venter. Outer metatarsal tubercle not apparent in female specimens CAS 210185, 219955, 235066, and male specimens CAS 235067–235068, slightly visible in female specimens CAS 216568, 216569, 216571, 216591–216593, 219953, 219954, 235071, and male specimen CAS 235069, and clearly visible in females specimens CAS 216496, 216572, 220262, and male specimens CAS 216567, 216570, 216597, 220263, 220264, 221973.

Comparisons.—Amolops indoburmanensis differs from all other members of Amolops found within Myanmar and neighboring countries based on the following characters: dual gular pouches present in males (absent in A. bellulus, A. dajiyunensis, A. granulosus, A. himalayanus, A. jinjiangensis, A. kantgingensis, A. kaulbacki, A. langshansensis, A. langanensis, A. loloensis, A. mantzorum, A. medogensis, A. nidorbellus, A. ricketti, and A. viridimaculatus); nuptial pads on base of first fingers present in males (absent in A. akhaorum); spinules on upper lip in males absent (present in O. geminata); vomerine teeth strongly developed (weakly developed in A. akhaorum and A. panhai, absent in A. daorum, A. dajiyunensis, A. himalayanus, A. hongkongensis, A. torrentis, and A. wujiensis); distinctive dorsolateral folds absent (present in A. akhaorum, A. antiquaensis, A. archotaphus, A. chakrataensis, A. chunganiensis, A. compotrix, A. cremnobatus, A. cucae, A. gerbillus, A. iroides, A. kohimaensis, A. longimamus, A. mengyangensis, A. minutus, A. monticola, A. nasicis, A. tornotus, and A. vitrea); diagnostic fringe of skin on third finger absent (present in A. formosus, A. macrorhynchs, and O. chapaensis); parrotid-like swelling above tympanum absent (present in A. longimamus); visible axillary glands absent (present in A. larutensis and A. panhai); conical spines on nuptial pads absent (present in A. ricketti and A. spinpectoralis); circummarginal and transverse grooves present on disk of first finger (absent in A. bellulus, A. formosus, A. grano, A. jinjiangensis, A. kantgingensis, A. liangshanensis, A. lifanensis, A. loloensis, A. mantzorum, A. nidorbellus, and A. viridimaculatus); first finger slightly shorter than second (first finger substantially shorter than second in A. assamensis); distinct dark mask through eye extending to anterior flank of body and white band on upper lip absent (present in A. bellulus); narrow gold stripe on canthus absent (present in A. akhaorum); brown dorsum with scattering of darker brown spotting or very faint lighter reticulation or both (dorsum with yellow spots on dark purple background in A. caelumnos and A. splendissimus, distinct green spots on brown background in A. nidorbellus and A. viridimaculatus, and distinct brown mottling on green background in A. medogensis); one or more large white spot on each flank absent (present in A. daorum).

Amolops indoburmanensis is very similar to A. afghanus and A. marmoratus. However, dorsum with much reduced lighter reticulation, or darker brown spotting, or both on brown background (dorsum of A. marmoratus with more extensive dark mottling on lighter background, and dorsum of A. afghanus with light reticulation on more extensive brown background); posterior of thighs solid brown (light cream mottling on dark gray in A. marmoratus and light cream speckling to reticulation on brown in A. afghanus); dorsum mostly smooth, with some tuberculation along posterior region of sides (dorsum of A. marmoratus coarsely granulated throughout and dorsum of A. afghanus with less granulation on dorsal surface but not to the extent of A. indoburmanensis). Males of A. indoburmanensis (mean SVL of 71.1 mm) are significantly larger than males of A. afghanus (51.5 mm) and A. marmoratus (42.7 mm), and females of A. indoburmanensis (mean SVL of 86.5 mm) are significantly larger than females of A. marmoratus (75.4 mm), but cannot be as readily distinguished from females of A. afghanus (81.1 mm).

Remarks.—Given that A. marmoratus is restricted in Myanmar to eastern Bago Division, Mon State, Shan State, and northern Tanintharyi Division and probably the states of Kayin and Kayah, and A. afghanus to Kachin State (possibly also northern Sagaing Division), we proposed A. indoburmanensis to accommodate populations from Chin State, Rakhine State, southern Sagaing Division, and western Bago Division. However, the results of the phylogenetic analyses show that A. indoburmanensis consists of three subgroups that are genetically distinct and exhibit significant differences in size from all others. Further study of A. indoburmanensis may reveal additional species diversity.

Etymology.—The specific epithet is an adjective that refers to the Indo-Burman Mountain Range from where the new
species is found. This mountain range is separated into three blocks from south to north as the Arakan Yoma (Rakhine State) and Chin Hills (Chin State and Manipur State, India) from which the species has been found and the Naga Hills (between Nagaland, India and Sagaing Division) from which it is assumed to occur.

DISCUSSION

Herein, we report A. panhai from Myanmar for the first time. The range extension is not unexpected as the specimens were collected in Tanintharyi Division between the type locality and the most northern known locality in Thailand (Matsui and Nabhitabhata, 2006). Our sequence data from the Tanintharyi specimen of A. panhai differed by only one base pair (a T-C transition) from that reported by Matsui et al. (2006). The northern most known locality for A. panhai in Myanmar is only approximately 23 km southeast of A. marmoratus in our study. However, the specimens of A. marmoratus and A. panhai in our study came from two different watersheds in Tanintharyi (Tavoy River and Tenasserim River watersheds, respectively). Sampling streams between these two localities may better delineate the ranges of these two species or indicate whether they occur in sympathy.

Myanmar is, simply speaking, a country with an elongated inverted U-shaped montane border surrounding a central lowland. The montane border consists of, from west to east, the Indoburman Range (between western Myanmar and eastern Bangladesh and eastern India), eastern Himalayan syntaxis (between northern Myanmar and southern Tibet), Sinoburman Range (between northeastern Myanmar and northwestern Yunnan, China), Shan highlands (much of eastern Myanmar into southwestern China, Laos, and northwestern Thailand), and the Tenasserim Range (between southeastern Myanmar and southwestern Thailand to the Isthmus of Kra). Interspersed are other north-south mountain ranges, such as the Kuman Range in the north that separates the Chindwin River watershed from the upper Irrawaddy River watershed, and the Bago Yoma in the south that separates the lower Irrawaddy River from the Sittaing River watershed.

These mountain ranges are the result of orogeny associated with sequential collisions of Gondwanan blocks with the Laurasian plate beginning in the mid to late Triassic. The Sinoburmanalaya block collided with the Asian plate in the late Cretaceous producing the Sinoburman Range. The Burman plate collided with the southern edge of the Sinoburmanalaya block resulting in the Shan Highlands on the Sinoburmanalaya block. These eastern highlands are bordered by the Sagaing fault along their western edge. The collision of the Indian plate with the Eurasian plate by the end of the early Eocene and the subsequent subduction of the Indian plate with the Burman plate (late Miocene) initiated the building of the Indoburman Range in the late Eocene and early Oligocene thus resulting in the inverted U-shaped mountains surrounding and isolating the central lowlands of Myanmar from the Indian and Indochina lowlands (Bender, 1983; Hutchison, 1989; Metcalfe, 1998; Satyabala, 2003).

It is possible that the A. marmoratus complex is an example of secular migration, diversifying from A. marmoratus to A. afghanus, and A. indoburmanensis as the complex expanded its range from the Shan Highlands northward and westward along the forest streams of the newer western mountains of the Indoburman Range.

Whether there is overlap of ranges between A. marmoratus in the Shan Highlands, A. afghanus and A. indoburmanensis in the Sinoburman and Indoburman Ranges will require further sampling of intermediate areas in northern Shan State and Sagaing Division. However, because these frogs are ecologically restricted to mountain streams, they are not expected to be found in the central lowlands of Myanmar. It is also important to compare, both morphologically and molecularly, populations outside of Myanmar currently assigned to A. marmoratus and superficially similar looking species (i.e., A. assamensis) in Northeast India and Nepal to better understand the phylogenetic relationship and taxonomy of this complex.

Our findings have conservation implications. Amolops marmoratus was ranked as a species of Least Concern “in view of its wide distribution and presumed large population” (van Dijk et al., 2004). However basing species inventories solely on morphological characteristics often leads to an underestimation of diversity which Stuart et al. (2006) noted as a common problem for Southeast Asian ranid management. Indeed, both molecular and morphological data suggest that a much greater level of diversity exists within Myanmar than originally reported. It should be recognized that four discrete evolutionary units (one of which, A. indoburmanensis, shows a high degree of within group diversity) whose distribution is limited to a much smaller geographic region than that of A. marmoratus sensu lato and whose population numbers may be much smaller and more susceptible to extinction (Bickford et al., 2007). Further research on these species is needed to determine population sizes and properly designate their conservation status. The taxa recognized herein have significantly smaller geographic distributions; hence, greater concern regarding their conservation status may be warranted.

MATERIAL EXAMINED

Amolops afghanus: BMNH 1947.2.27.93 (lectotype); CAS 221313, 221314, 221322–221323, 221361–221362, Myanmar, Kachin State, Putao District, Machanbaw Township, Ahtonga Village; CAS 221441, Myanmar, Kachin State, Putao District, Naung Mon Township, Aureinga Camp; CAS 221538, Myanmar, Kachin State, Putao District, Naung Mon Township, Rabaw; CAS 224362, 224363, Myanmar, Kachin State, Putao District, Nagmung Township, Shin-San-Ku Camp; CAS 224448, 224449, 224451, 224466, 224467, Myanmar, Kachin State, Putao District, Nagmung Township, Hkakabo Razi National Park, Gaw Let Village; CAS 224491, 224497, 224655, 224656, Myanmar, Kachin State, Putao District, Nagmung Township, Hkakabo Razi National Park, Lan Sa Htu Village; CAS 224712, 224713, 224715, Myanmar, Kachin State, Putao District, Nagmung Township, West of Hton Hlra Village; CAS 224742, 224744, Myanmar, Kachin State, Putao District, Nagmung Township, Ta Se Htu Village; Myanmar, Kachin State, Putao District, Nagmung Township, Ba Bawt Village; CAS 225197, 225207, 225216, 225230–225233, 225238, 225244, 225247, 225535, Myanmar, Kachin State, Putao District, Naung Mon Township, Au Yin Ga Camp; CAS 225537, Myanmar, Kachin State, Putao District, Machanbaw Township, Htan Ga Village; CAS 230228, Myanmar, Kachin State, Putao District, Machanbaw Township; CAS 232338,
Myanmar, Kachin State, Ta Nai Township, Shin Bawe Yan, border of Hukaung Wildlife Sanctuary, beside Ledo Road; CAS 232914, 232915, 232936, 232940, 232941, 232996, 232997, 233004, 233007, 233008, 233012, 233013, 233031, Myanmar, Kachin State, Myitkyina District, Moeyin Township, Indawgyi Wildlife Sanctuary, Hepy Village, Hepy stream; CAS 232982, 232996, 232997, Myanmar, Kachin State, Myitkyina District, Moeyin Township, Indawgyi Wildlife Sanctuary, Hepy Village, Kyar Phu Stream; CAS 233113, 233114, 235878, Myanmar, Kachin State, Myitkyina District, Moeyin Township, Indawgyi Wildlife Sanctuary, Nanmun Village.

Amolops indoburmanensis: CAS 235066–235069 (paratypes), 235070 (holotype), 235071 (paratype), Myanmar, Chin State, Mintatt District, Mintatt Township, Twi Rein Village; CAS 233204, 233205 (paratypes), Myanmar, Chin State, Phalum District, Haka Township, Chun Kyone; CAS 234943, Myanmar, Chin State, Mintatt District, Mintatt Township, Hele Yaw Village; CAS 235151–235155 (paratypes), Myanmar, Chin State, Mintatt District, Mintatt Township, Bae Stream, near Khwee Rein Village; CAS 210185, Myanmar, Sagaing Division, Alaungdaw Kathapa National Park, Sunthaik Chaung (tributary to Hkaungdin Chaung); CAS 216590–216593, 216597, Myanmar, Rakhine State, Gwa Township, Rakhyine Yoma Elephant Range, Ye Bya Camp; CAS 216496, Myanmar, Rakhine State, Than Dawa District, Gwa Township, Rakhyine Yoma Elephant Range, Elephant Camp; CAS 216567–216572, 216591–216593, 216597, 220176–220185, 220251, Myanmar, Rakhine State, Gwa Township, Rakhyine Yoma Elephant Range, Ye Bya Stream Camp; CAS 220277–220285, 220288–220290, 220342, 220349, Myanmar, Rakhine State, Gwa Township, Rakhyine Yoma Elephant Sanctuary; CAS 220262–220264, Myanmar, Rakhine State, Gwa Township, Rakhyine Yoma Elephant Sanctuary, Kyat Stream camp; CAS 220351, Myanmar, Rakhine State, Gwa Township, Rakhyine Yoma Elephant Sanctuary, Khoko Gwe Creek; CAS 221973, Myanmar, Rakhine State, Gwa Township, De-Pok Village camp; CAS 221986, Myanmar, Rakhine State, Gwa Township, Kyauk Win Gyi Camp; CAS 235217, Myanmar, Chin State, Mindat District, Kanpatlet Township, Ke Har Stream; CAS 219917, 219953–219955 (paratypes), 219959, 219960, 220551, 234717–234721, Myanmar, Chin State, Mindat District, Kanpatlet Township, Nat Ma Taung National Park; CAS 235023, Myanmar, Chin State, Mindat District, Mindat Township, Mindat District, Bow Village; CAS 234851, Myanmar, Chin State, Mindat Township, Mindat District, upper Bee Hoe Village.

Amolops marmoratus: CAS 210640, 210641, Myanmar, Shan Division, Tuanggyi District, 17 miles west of Kalaw; CAS 215272, 221668–221675, Myanmar, Shan Division, Tuanggyi District, Kalaw Township, Wat Phu Ye Camp; CAS 222209, 222210, Myanmar, Mon State, Kyaihtoki Township, Kyaiht-Hti-Lo Wildlife Sanctuary (tributary of Moe Baw Chuang); CAS 222233, Myanmar, Mon State, Kyaihtoki Township, Kyaiht-Hti-Lo Wildlife Sanctuary, Nga Bat camp, near the Kyaiht-Hti-Lo Pagoda; CAS 240434, Myanmar, Mon State, Kyaihtoki Township, Kinmon Chuang Village, Kadat stream; CAS 240586–240600, 240602, 240603 (neotype), Myanmar, Mon State, Kyaihtoki Township, 10 Minutes Camp, along YeTakon Chuang; CAS 240601, Myanmar, Mon State, Kyaihtoki Township, Kinmon Chuang Village, Zaung Naing stream; CAS 240621, 240623, Myanmar, Mon State, Kyaihtoki Township, 10 Minutes Camp, Yae Myang Gyi stream; CAS 243875, Myanmar, Tanintharyi Division, Dawei District, Yebyu Township, Tanintharyi Nature Reserve; NMNH 564959, 564966, 564967–564972, Myanmar, Mon State, Kinmun, Kyaihtkiyo Wildlife Sanctuary.

Amolops panhai: CAS 229816, Myanmar, Tanintharyi Division, Dawei District, Thayet Chuang Township, East of Mai Ke Village, border of Nwa La Bo Reserve Forest, Ngwe Tunang stream.

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