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VARIATION IN BORNEAN FROGS
OF THE *AMOLOPS JERBOA* SPECIES GROUP,
WITH DESCRIPTION OF TWO NEW SPECIES

ROBERT F. INGER

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INTRODUCTION

Collections made at Nanga Tekalit, Sarawak, in 1962–63 and 1970 include large numbers of adult frogs fitting general descriptions of *Amolops jerboa* (Günther) (Boulenger, 1882; Inger, 1966). At this site, which is roughly 400 km from the type locality (Mt. Matang, Sarawak), we obtained three types of tadpoles immediately recognizable as larval *Amolops* by virtue of their suctorial abdominal disks. One of these is identical to Boulenger's (1893) description of larval *A. cavitympanum* (Boulenger), adults of which were also found at Nanga Tekalit. The other two larval types, referred to as *Amolops* larva A and *Amolops* larva B (Inger, 1966), are similar in having both beaks divided and very coarsely serrated and in the number of divided rows of denticles. However, they differ sharply in coloration, development of glands in the ventral fin and at the rear of the body, and to a lesser extent in other characters (see below).

The existence of these two larval types suggested the possibility that the adults identified as *A. jerboa* might represent two cryptic species not recognized in the field. As we reexamined these frogs, we discovered two general patterns on the rear of the thigh still visible despite more than 10 years in preservative. One pattern consists of moderately large light and dark areas that give the surface a blotched or pied appearance, and the other consists of a dark surface with fine dusting of small light spots (fig. 1).

After the more than 500 frogs from Nanga Tekalit were sorted into the "blotched" and "dusted" types, they were sexed and measured, and observations on other

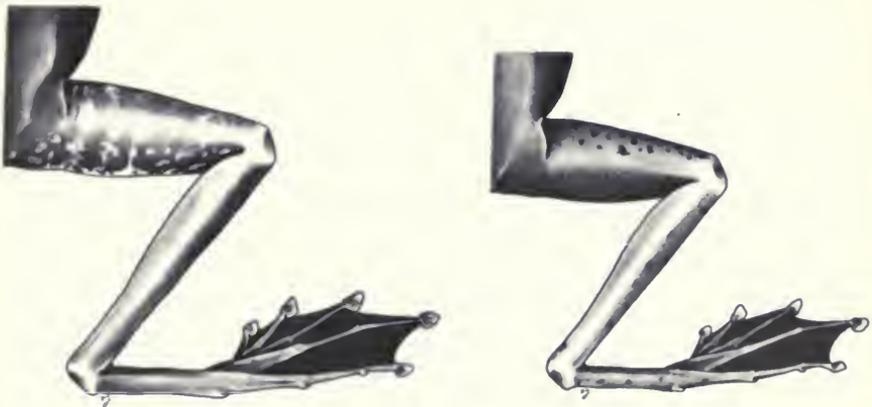


FIG. 1. Pattern of rear of thigh in frogs of the *Amolops jerboa* species group. Left, blotched or pied; right, dusted.

characters recorded. We then compared these two samples with each other and with samples from other areas of northern and western Borneo (fig. 2). The larvae from Nanga Tekalit were also compared with tadpoles collected elsewhere in Borneo. As a result of these comparisons, we conclude that a number of cryptic species have been grouped under a single name, *A. jerboa* (Günther).

MATERIALS AND METHODS

SPECIMENS EXAMINED

Map localities (fig. 2) are given in parentheses.

SABAH. Sungei Moyog, near Babagon, 22 km east of Kota Kinabalu (1), Field Museum of Natural History (FMNH) 1 plus larval series; 6 km east of Tuaran (2), FMNH larval series; Mt. Kinabalu (3), British Museum (Natural History) (BMNH) 1, Museum National d'Histoire Naturelle Paris 3 (syntypes of *Rana whiteheadi* Boulenger), BMNH 1; Sungei Bulungungan, 520 m, Mt. Kinabalu, FMNH larval series; Sungei Kaingeran, 640 m, Mt. Kinabalu, FMNH larval series; Sungei Kepungit, 790-915 m, Mt. Kinabalu, FMNH larval series; Sungei Liodan, 1,000 m, Mt. Kinabalu, FMNH larval series; Sungei Mamut, 425-850 m, Mt. Kinabalu, FMNH larval series; Tenompok, Mt. Kinabalu, FMNH 5.

SARAWAK. First Division: Mt. Matang (4), BMNH 2 syntypes of *Hylarana jerboa* Günther; Sungei China, Mt. Matang, FMNH 56 plus larval series; Tandjong Datu (5), FMNH 10. Second Division: Lupar River Valley (6), FMNH 5. Third Division: headwaters of Baleh River (7), FMNH 4 plus larval series; stream opposite Sungei Laie, headwaters of Baleh River (8), FMNH 10 plus larval series; mouth of Mengiong River (9), FMNH 17; Nanga Tekalit (10), FMNH 692 plus larval series. Fourth Division: Mt. Mulu (11), BMNH 3 plus larval series; Long Seniai, Akah River (12), FMNH larval series; Sungei Pesu Camp (13), FMNH 5 plus larval series.

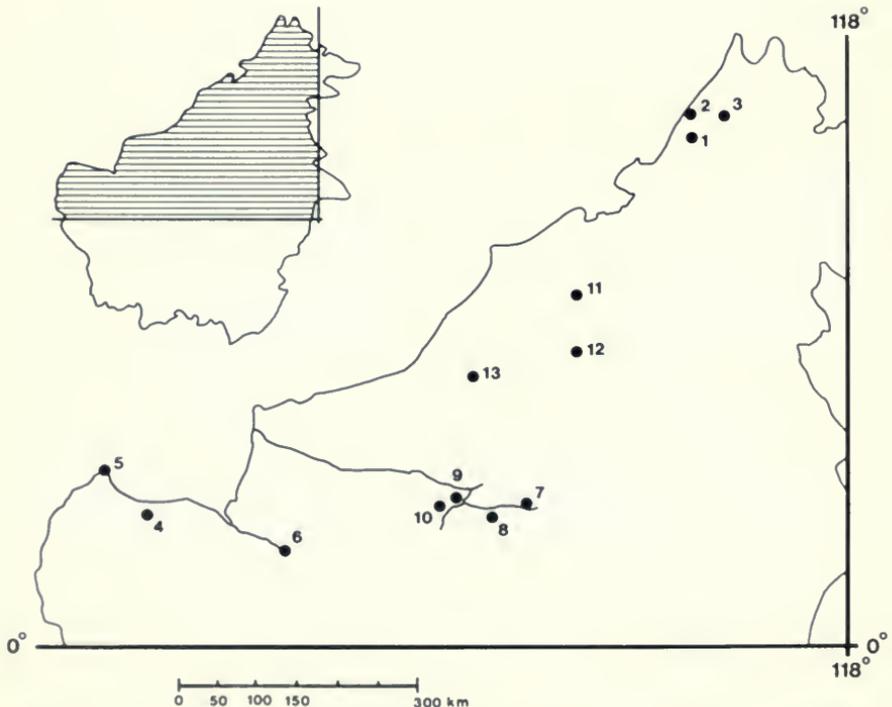


FIG. 2. Sources of samples of *Amolops jerboa* species group in western and northern Borneo. Code for numbered localities in Materials and Methods.

DATA COLLECTION

The characters of adults used were:

1. Snout-vent length (SVL).
2. Relative leg length—the ratio of tibia length, measured as described in Inger (1954), to SVL.
3. Relative head length—the distance from the rear of the jaw to the tip of the snout divided by SVL.
4. Relative head width—maximum head width divided by SVL.
5. Relative tympanum diameter—horizontal diameter divided by SVL.
6. Inner metatarsal length divided by SVL.

Measurements for characters 1 through 4 were made with dial calipers to 0.1 mm. For characters 5 and 6, measurements were made with an ocular micrometer at $\times 12$ and converted to millimeters.

7. Nuptial pad—extent of pad on medial edge of first finger. This character did not vary significantly among populations.
8. Pattern on the rear of the thigh (see p. 1).
9. Amount of pigmentation on ventral surface of tibia. This character was recorded in four states: A—heavy pigmentation over entire ventral surface; B—patches in which melanophores form continuous bands or spots across the surface; C—isolated, scattered melanophores; D—wide, longitudinal strip clear of melanophores.
10. Excision of web between fourth and fifth toes relative to subarticular tubercles of fourth toe. This character was recorded in five states: A—excision to proximal edge of distal subarticular tubercle; B—between distal and middle subarticular tubercle; C—distal edge of middle tubercle; D—center of middle tubercle; E—proximal edge of middle tubercle.

Tadpoles were staged using the system of Gosner (1960). The head-body length (HBL) was measured with an ocular micrometer from the tip of the snout to the end of the body. Other larval characters used are self-explanatory.

RESULTS

ADULTS FROM NANGA TEKALIT

The frogs having the blotched thigh pattern are clearly larger and have relatively longer legs and inner metatarsal tubercles (table 1), though overlap in each of these mensural characters is extensive, and the differences are not conspicuous to the human eye. Thus, we are not dealing with a simple case of intraspecific variation in a single character. At the very least, we appear to have polymorphism involving no less than four characters. Is there evidence that the two morphotypes may be reproductively and behaviorally isolated? Do the frogs themselves recognize two "species"? We have only three sets of observations on mating pairs, but all indicate reproductive isolation of the two morphotypes.

Five pairs were caught in amplexus and segregated until preserved. Each pair is matched with respect to thigh pattern and size. All have dusted thigh pattern, and all but one of these individuals are close to the mean SVL of the dusted form: ($\text{♀}-\text{♂}$) 63.3–35.6 mm, 62.8–35.6, 70.5–39.0, 66.3–38.1, 66.2–38.4. If mating is random with respect to pattern, the probability that one pair in amplexus would consist of matched individuals is .5, as the two types appeared to be equally abundant. The probability that all five pairs would be matched is .031. Three additional pairs (marked as numbers 515–16, 1339–40, 1396–97) were caught

TABLE 1. Comparison of adults of two morphotypes of *Amolops jerboa* species group from Nanga Tekalit, Sarawak.

Characters*	Blotched pattern		Dusted pattern		Student's <i>t</i> tests			
					Males		Females	
	Males	Females	Males	Females	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
No.	160	107	160	62
SVL	44.08 ± .25†	70.28 ± .29	38.25 ± .14	64.58 ± .41	20.22	<.001	11.44	<.001
T/SVL	.747 ± .008	.744 ± .003	.707 ± .002	.708 ± .004	12.62	<.001	7.72	<.001
HL/SVL	.406 ± .002	.400 ± .001	.399 ± .001	.403 ± .002	2.81	<.01	1.31	.20
HW/SVL	.333 ± .004	.342 ± .001	.328 ± .001	.342 ± .002	3.31	<.001	1.0	>.20
TYM/SVL	.099 ± .001	.064 ± .001	.100 ± .001	.065 ± .001	1.62	.10	2.47	.02
MT/SVL	.044 ± .001	.046 ± .001	.040 ± .001	.043 ± .001	9.34	<.001	6.21	<.001

*Abbreviations: SVL = snout-vent length; T/SVL = tibia length/SVL; HL/SVL = head length/SVL; HW/SVL = head width/SVL; TYM/SVL = tympanum diameter/SVL; MT/SVL = length of inner metatarsal tubercle/SVL.
 †Mean ± standard error.

TABLE 2. Distribution of two forms of the *Amolops jerboa* species group on streams of varying widths at Nanga Tekalit, Sarawak.

Pattern	Stream width (m)		
	2-4	5-8	10-20
Dusted	4	85	145
Blotched	20	261	44
			17

Values are numbers of frogs.

in amplexus on a small stream and, for purposes of other work (Inger, 1969), released after measurement. Although pattern was not recorded because we were not then aware of the taxonomic problem, the members of each of these three pairs fit the size range of the blotched form (table 3) and, therefore, were matched with respect to size groups: (\varnothing - δ) 76-43 mm, 78-46, 75-48.

On one night (May 19, 1963) frogs of this species complex were active on another small stream, and pairs were observed in amplexus, though not segregated after capture. All 36 individuals collected had the blotched pattern. Snout-vent range and mean for the 25 males and 11 females of this subset were approximately those of the entire blotched sample shown in Table 1: males 39.1-48.0 mm, mean $43.75 \pm .41$; females 68.5-75.2 mm, mean $71.95 \pm .60$. The aggregation was, therefore, essentially homogeneous, representing just one pattern-size morphotype.

The streams on which collecting was conducted at Nanga Tekalit varied in width from 2 to 60 m. The two morphotypes had overlapping but statistically distinct distributions (chi square = 156, $df = 3$, $P < .001$) with respect to stream size (table 2).

In view of these observations, we conclude that, at Nanga Tekalit, two populations exist that have attributes of sibling species: although very similar morphologically, they differ in pattern and size; males and females chose the morphologically "correct" mates; and the two populations have slightly differing ecological distributions.

ADULTS FROM OTHER AREAS

How are these populations related to frogs referred to *Amolops jerboa* from other parts of Borneo? *Rana whiteheadi* Boulenger (type locality Mt. Kinabalu, map locality 3), placed in the synonymy of *jerboa* (Inger, 1966), must be reconsidered in this context, as SVL of syntypes of *whiteheadi* are restricted to the size range of the large form from Nanga Tekalit (locality 10). The other Bornean localities (fig. 2) from which samples are available include Mt. Matang (type locality of *Hylarana jerboa* Günther) and Tandjong Datu in western Sarawak (localities 4 and 5); Mt. Mulu (locality 11) in northeastern Sarawak; and Mt. Kinabalu, Sabah (locality 3). It is clear, from a consideration of data in Table 3, that neither of the two adult morphotypes at Nanga Tekalit matches any other sample in the three characters distinguishing them. For example, the Matang series (presumed *A. jerboa* in the strict sense) agrees with the dusted form from Nanga Tekalit in size, but differs from it in pattern and in relative leg length; although agreeing with the blotched form at Nanga Tekalit in coloration, it is much smaller and has less extensive webbing. The only match among pairs of samples is between those from Matang and Tandjong Datu, which are only 100 km apart. The most likely explanations of the heterogeneity among samples in size, relative leg length, coloration, and extent of webbing shown in Table 3 are that there are as many as five forms or just one highly variable species. The latter alternative seems incompatible with the relationship of the two populations from Nanga Tekalit and with the evidence (see below) from larvae. We refer to this suite of populations as the *A. jerboa* species group.

LARVAE

At least eight morphotypes of *Amolops* larvae occur in Borneo. One, with undivided beaks, has been clearly associated with *A. cavitympanum* (Boulenger,

TABLE 3. Pattern, size, relative leg length, and extent of web in populations of *Amolops jerboa* species group.

Characters	Nanga Tekalit*	Nanga Tekalit†	Matang‡	Tandjong Datu	Kinabalu "large"§	Kinabalu "small"
	B	D	B	B	D	?
Thigh pattern						
SV ♂♂						
N	233	160	55	8	5	9
Range	34.5-51.0	33.0-43.0	32.1-39.3	35.5-39.1	43.9-47.1	31.5-37.0
\bar{x}	44.08	38.25	35.67	37.36	45.7	33.63
SV ♀♀						
N	107	62	3	...	2	1
Range	60.1-77.0	57.2-71.5	53.3-58.7	...	64.7-80.3	62.3
\bar{x}	70.28	64.58
T/SV ♂♂						
N	160	160	55	8	5	9
Range	.666-.849	.630-.765	.689-.798	.715-.759	.665-.683	.686-.760
\bar{x}	.747 (29<.720)	.707 (48>.720)	.752 (5<.720)	.733	.674	.727 (2<.711)
T/SV ♀♀						
N	107	62	3	...	2	1
Range	.682-.807	.635-.771	.767-.801667-.697	.727
\bar{x}	.744 (19<.720)	.708 (19>.720)	.780
Tibia pattern#						
A-B	5	10
B/C	1	5	2	...	1	...
C-D	24	20	23	8	2	...
Extent of web#						
A-B	22	17	10	4	1	...
C	1	8	12	4	3	2
D-E	1	...	3	...	4	8

*Form described as *A. poecilus* in this paper. †Form described as *A. phaeomerus* in this paper. ‡Type locality of *jerboa* Günther; sample includes two female syntypes. §Four syntypes of *whiteheadi* Boulenger plus one female from Whitehead's collection and three others (FMNH 130821-23) from Kinabalu.

||B = blotched, D = dusted; ? = pattern not clear. #See Materials and Methods for definitions of character states; B/C indicates individuals intermediate between these two states.

1893; Inger, 1966). The remainder (table 4) have at least the upper beak divided. Six of these seven develop a small outer metatarsal tubercle in tadpoles of stages 40 and 41 and, therefore, cannot be assigned to *A. kinabaluensis*. The seventh, not represented by a premetamorphic tadpole, is very similar to one of the other forms and is probably not the larva of *kinabaluensis*. As *A. cavitympanum* and *A. kinabaluensis* are the only Bornean *Amolops* not resembling *jerboa*, the most likely association of these seven larval types is with members of the *A. jerboa* species group. Only two of these larval forms can be assigned to populations of adults with reasonable confidence.

The two tadpoles of this species group caught at Nanga Tekalit differ sharply in coloration, as noted earlier. Type A (Inger, 1966, p. 270, fig. 52) is light greenish yellow in life, with large black spots on the body and caudal muscle and with the distal third of the tail usually devoid of spots. Type B (Inger, 1966) is brownish with a dense pattern of small dark spots on the body. The tail muscle is dark but usually has a few light areas forming narrow vertical bars. All larvae of type B older than stage 28 (Gosner, 1960) have large glands (two to four) in the ventral

TABLE 4. Summary of characters of larval morphotypes of *Amolops jerboa* species group; all larvae in stages 36 through 41 (Gosner, 1960).

Morpho- type	Surface projec- tions*	Glands of ventral fin	Rows of denticles		Serrae of beaks		Localities#
			Upper†	Lower‡	Upper§	Lower	
A**	absent	absent	3	V	5-8	7-8 (d)	Nanga Tekalit
B††	sharp	2-5	3	IV-V	6-8	7-8 (d)	Nanga Tekalit, Sungei Pesu
D	sharp	5-8	4	VI	16-18	19-24 (u)	Akah River, Mt. Mulu, Kina- balu
E	flat	4-8	4	V	7-9	11-16 (u)	Kinabalu
F	sharp	4-8	3	V-VI	6-9	5-8 (d)	Kinabalu
G	flat m	1-5	3	V	7-9	6-7 (d)	Tambunam
H	sharp m	3-5	3	V	5-8	6-7 (d)	Tuaran, Babagon

*Projections on head and body; m = tipped with melanin. †Number of divided rows. ‡Number of undivided rows. §Serrae on half of upper beak.

||Serrae on half of lower divided (d) beak in morphotypes A, B, F-H; on entire undivided (u) beak in morphotypes D and E. #Larvae in all stages. **Presumed larvae of *A. phaeomerus*. ††Presumed larvae of *A. poecilus*.

fin near its origin. No type A tadpole of any stage (stages 25 to metamorphosis examined) has glands in the fin. Both types have a lateral patch of large glands near the end of the body (and elsewhere, see Inger, 1966). These glands number from 10 to 20 (usually more than 12) per patch in all stages of type A, but never more than six in type B.

Two transforming young (FMNH 146194, 203498), both with vestiges of the suctorial disk and with the color pattern and number of glands (12 and 14) of larval type A, have the dusted thigh pattern. Two others (FMNH 137865, 146193), with vestiges of the disk and the coloration (brownish with obscured pattern) and number of body glands (four to six) of larval type B, have the blotched thigh pattern. As in other respects these metamorphosing young resemble the adults found at Nanga Tekalit, larval type A is assigned to the small, dusted adult morphotype and larval type B to the large, blotched adult morphotype.

Differences among the seven larval morphotypes¹ involve presence and nature of protuberances on the head and body, number of glands on the ventral fin, number of rows of denticles, division of the lower beak, and number of serrae on the beaks (table 4). Not shown in the table is the number of glands in the patch at the rear of the body: in larval type A there are 10 to 20 in a group; in all other forms a patch contains fewer than 10 glands.

Four tadpoles (FMNH 83024), stages 27 and 28, HBL 7.5-8.4 mm, collected at Long Seniai, Akah River, Sarawak, with a specimen of morphotype D, have both beaks divided, four to six serrae on each half of the upper and four to five on each half of the lower beak, and three divided rows of denticles on the upper lip. They lack glands in the ventral fin and spinules on head and body, but these states may be functions of early developmental stage (see table 5). A large sample of young tadpoles (FMNH 77571, 77573), none older than stage 25 and the largest only 5.4 mm HBL, collected at Matang, Sarawak, are very similar to the Long Seniai larvae in all these characters. The only difference between these two

¹Because of ontogenetic changes in certain characters (table 5), this paragraph refers only to tadpoles stage 36 and older.

TABLE 5. Ontogenetic changes in larvae of *Amolops phaeomerus* and *A. poecilus* at Nanga Tekalit, Sarawak.

Stages	Glands of ventral fin					Rows of denticles lower lip			Serrae of beaks									
	0	1	2	3	4	5	III	IV	V	Upper (½)				Lower (½)				
Morphotype A = <i>Amolops phaeomerus</i>																		
26-28	1	-	-	-	-	-	-	-	-	4	-	-	-	-	4	-	-	-
29-33	12	-	-	-	-	-	-	1	3	-	2	-	-	-	-	2	-	-
34-35	11	-	-	-	-	-	-	-	6	1	1	-	-	-	-	-	-	-
36-38	20	-	-	-	-	-	-	-	6	-	1	1	8	-	-	-	6	2
39	3	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
40-42	9	-	-	-	-	-	-	-	9	-	2	1	5	-	-	-	1	-
Morphotype B = <i>Amolops poecilus</i>																		
25	1	1	1	-	-	-	3	-	-	3	-	-	-	1	2	-	-	-
28	-	-	1	-	1	-	2	-	-	1	1	-	-	-	2	-	-	-
29-30	-	-	-	-	1	-	1	-	-	1	-	-	-	-	1	-	-	-
35	-	-	1	-	-	-	1	-	-	-	1	-	-	-	1	-	-	-
36-38	-	-	1	-	3	1	3	1	-	2	1	1	-	1	2	1	-	-
39	-	-	-	2	2	-	3	1	-	-	4	-	-	-	2	2	-	-
41-42	-	-	-	-	-	1	-	-	-	1	-	-	-	-	1	-	-	-

samples is the number of glands in the patch at the end of the body: five to nine in the older Long Seniai tadpoles and zero to one in the younger ones from Matang. This difference may also be a function of age. Although both samples were originally assigned to morphotype A (Inger, 1966), they are better placed in type B, F, or H.

Larval types A and B are syntopic at Nanga Tekalit. Larval types D, E (also so designated in Inger, 1966), and F are sympatric on Kinabalu, F being syntopic with D at 792 and 915 m and with E at 518-671 m. As D and E have overlapping altitudinal ranges on Kinabalu (792-915 m and 427-853 m, respectively) and as D occurs as low as 180 m elsewhere in Borneo, all three of these forms may be syntopic on Kinabalu. Thus, the larvae present a pattern similar to that of the adults: a number of morphotypes and, at several localities, two or more of the forms sympatric.

CONCLUSION

Patterns of variation of both adults and larvae from Nanga Tekalit resemble those of distinct sympatric species: separate clusters in multidimensional morphological space. This conclusion is strengthened by the observation of pairs in amplexus and by differing ecological distributions. These two populations appear to differ in important ways from those from the type localities of other forms in this species group—Matang, Sarawak (*jerboa*), and Kinabalu, Sabah (*whiteheadi*). They will be described below as new species.

Amolops whiteheadi (Boulenger) (see 'Kinabalu "large"' in table 3) should be reinstated as a distinct species, being relatively large and having a dusted thigh pattern, ventral surface of the tibia heavily pigmented, relatively short leg, and less webbing than *jerboa* (s.s.) and the new forms described here. The sample labeled 'Kinabalu "small"' in Table 3 probably represents the same form as the one listed by Matsui (1979) as *jerboa*; indeed, five of our specimens are from the

same locality (Liodan River near Bundu Tuhan) as Matsui's. One specimen (FMNH 157431) from Sungei Pesu, Sarawak, has the same broad head as Matsui's *Amolops* sp. A. (Matsui, 1979, p. 340, fig. 26C). It is our understanding that Dr. Matsui intends to describe both of these forms. The sample from Mulu is too limited (two adults) for taxonomic decision.

***Amolops phaeomerus*,² new species**

Diagnosis.—A small form of the *Amolops jerboa* species group, males 33–44 mm, rarely over 40.9 SVL, females 57–72 mm, rarely greater than 68.9 mm; rear of thigh dark brown, dusted with small irregular light spots (fig. 1, right); length of tibia relative to snout-vent usually less than .720. Mature larvae (stage 36 and older) lacking spinules on head and body, no glands in ventral fin, usually 5 undivided rows of denticles on lower lip, head and body pale (yellowish green in life) with large conspicuous black spots.

Holotype.—Field Museum of Natural History 136140, an adult female from Nanga Tekalit, Kapit District, Third Division, Sarawak. Collected in amplexus on the bank of the Mengiong River, Sept. 11, 1962, by Bernard Greenberg, R. F. Inger, and F. W. King.

Description of holotype.—Habitus moderately slender; head triangular; snout obtusely pointed, projecting slightly beyond lower jaw; eyes elevated; canthus sharp, slightly concave; lores slightly oblique, concave; nostrils lateral, just below canthal edge, closer to tip of snout than to eye; internarial distance equal to interorbital; latter slightly wider than upper eyelid; pineal spot visible, in line connecting anterior corners of orbits; tympanum distinct, diameter one-half length of eye, separated from eye by one-half tympanic diameter. Vomerine teeth weak, in short groups separated by width of one group, groups posterior to line connecting rear rims of choanae. Tongue deeply notched, without papilla.

Fingers slender, first slightly longer than second; tips expanded into disks having circummarginal grooves; disks of third and fourth fingers largest, one-half diameter of tympanum; no fringes of skin along fingers; no supernumerary subarticular tubercles.

Toes with disks similar to those of fingers in shape and size; webbing full to disks of all toes; excision of web between fourth and fifth toes distal to middle subarticular tubercle of fourth toe; a narrow fringe of skin along inner edge of first toe; inner metatarsal tubercle oval, shorter than distance between it and subarticular tubercle of first toe; a round, raised outer metatarsal tubercle.

Skin finely granular dorsally; a low, indistinct dorsolateral glandular fold; throat smooth; chest and abdomen weakly rugose.

Color in life chocolate brown dorsally on head and body with small dark spots on trunk; lores with indistinct dark streak below canthus; upper lip light brown with small obscure lighter spots; iris bicolored, upper two-fifths golden, lower three-fifths brown; a blackish brown band beginning behind eye reaching inguinal area, widest anteriorly, dorsal boundary sharp, ventrally fading into marbled brownish; limbs above with alternating grayish and dark brown crossbars, the darker ones wider; a short dark streak ventrally at insertion of arm.

Coloration of the ventral surfaces and rear of thigh was not recorded prior to

²From *phaios* (Gr.), dusky, and *meros* (Gr.), thigh, referring to the appearance of the rear of the thigh.

preservation. The rear of the thigh, after years in alcohol, is dark brown with a few small, irregular light spots. The throat and chest are dark brown and the abdomen and ventral surfaces of the legs whitish, with very few dots of melanophores on the legs. As dorsal and lateral coloration remain very close to the condition in life, probably the long period in preservative has not seriously affected the color of thigh and throat.

Measurements (mm): SVL 63.3; head width 19.1; head length 23.5; tibia 45.9; tympanum 4.2; inner metatarsal tubercle 2.6.

Paratypes.—All from the Baleh River basin, Third Division, Sarawak, in collections of Field Museum of Natural History: 307 from type locality, 17 from mouth of Mengiong River (downstream from type locality), and nine from small stream between Sungei Laie and Sungei Sujai in upper Baleh drainage. All were collected in the years 1962–63 and 1970–71.

Variation.—Males and females differ greatly in SVL and relative size of the tympanum (see table 1). Males have vocal sacs and distinct gular pouches. The light colored nuptial pad covers the dorsal surface of the first finger at its base and extends distally on the medial edge to the terminal phalanx.

Individual variation in size, body proportions, and webbing is given in Tables 1 and 3. Coloration of the rear of the thigh varies only in the amount of light spotting, never approaching the condition typical of the new species described below.

Larvae.—A complete developmental series from stage 25 onward ends with the two transforming young (FMNH 146194, 203498) associated with this species (p. 7). Descriptive notes and data on these tadpoles, referred to as type A, are given on p. 6, in Tables 4 and 5, and in Inger (1966, p. 270, fig. 52). Their distinctive features include: both beaks divided and coarsely serrated, smooth skin on head and body, usually five undivided rows of denticles on the lower lip, a large patch of 10 to 20 glands laterally at the end of the body, no glands in the ventral fin, and large, distinct black spots on head and body at all stages. Head-body lengths 11.25–14.67 mm in stages 36 through 41 (N = 32), maximum width divided by length .75–.82.

Referred larvae: FMNH 96012, 136324–31, 136333, 213637–45.

Comparisons.—Although similar in size to *A. jerboa* (s.s.) and the Kinabalu form designated "small" in Table 3, *A. phaeomerus* differs from *jerboa* in pattern of the thigh and relative length of the tibia and from Kinabalu "small" in extent of web and ventral coloration of the tibia (table 3). It resembles the Kinabalu "large" sample (table 3) in coloration of the thigh, but differs from that sample in size, webbing, and coloration under the tibia. Besides the differences between *phaeomerus* and *poecilus* (see below) discussed in the text, the two probably differ in coloration of the iris; uncertainty on this point stems from our failure to note this character in enough living frogs.

Amolops kinabaluensis is distinguished from *phaeomerus* by its larger size (females 75–92 mm, males 58–68 mm), stockier body, and lack of an outer metatarsal tubercle. The sunken tympanum of *A. cavitympanum* separates that species from all others in the genus.

Larvae of *A. phaeomerus* differ from those of other related species in lacking asperities on the head and body and in advanced stages in having large, well-separated black spots and 10 to 20 glands in the patch at the rear of the body.

Amolops poecilus,³ new species

Diagnosis.—A large form of the *Amolops jerboa* species group, males 34–52 mm, usually over 40.9 mm, females 60–78 mm, usually over 68.9 mm; rear of thigh pied or blotched (fig. 1, left) dark brown and cream (yellow in life); length of tibia relative to snout-vent usually greater than .720; mature larvae (stages 36 and older) with sharp, colorless spinules dorsally on head and body, 2–5 glands in ventral fin, usually 4 undivided rows of denticles on lower lip, head and body brownish without distinct spots.

Holotype.—Field Museum of Natural History 144532, an adult female from Nanga Tekalit, Kapit District, Third Division, Sarawak. Collected on Sungei Lawan, May 17, 1963, by F. W. King.

Description of holotype.—Habitus moderate; head triangular; snout obtusely pointed, projecting beyond jaw; eyes elevated; canthus sharp, slightly concave; lores slightly oblique, concave; nostrils lateral, below canthus, distinctly closer to tip of snout than to eye; internarial wider than interorbital; latter narrower than upper eyelid; pineal spot visible, in line connecting anterior corners of eyes. Tympanum visible, diameter slightly less than one-half length of eye, separated from eye by almost its own diameter. Vomerine teeth in small oblique groups, separated by less than width of one, groups on line connecting posterior third of choanae. Tongue deeply notched, without papilla.

Fingers slender; first and second subequal; tips expanded, disks round, with circummarginal grooves; disks of third and fourth fingers largest, two-thirds diameter of tympanum; fingers without fringes of skin; no supernumerary metacarpal tubercles.

Toes with disks similar in shape to those of fingers, disk of fourth slightly larger than those of outer fingers; webbing full on all toes, excision of web between fourth and fifth toes at level of proximal edge of outer subarticular tubercle of fourth toe; first toe with narrow fringe of skin on medial edge; inner metatarsal tubercle oval, slightly shorter than distance between it and subarticular tubercle of first toe; a small, round, raised outer metatarsal tubercle.

Skin shagreened above; indistinct dorsolateral fold; side of trunk coarsely granular; throat smooth; chest and abdomen rugose.

Color in life⁴ chocolate brown dorsally on head and body; side of snout darker; upper lip whitish, lower lip barred black and white; iris brown with crimson spot behind pupil; a dark brown to blackish brown band from eye to inguinal region, dorsal edge below dorsolateral fold sharp, ventral margin ragged, fading into spotted lower side; throat white to pale yellow; venter yellow; forelimb medium brown with dark brown speckles; leg dorsally barred with gray brown and blackish brown; leg yellow below.

In preservative rear of thigh dark brown with large, irregular light blotches (presumably yellow in life). Ventral surfaces of the leg have a few dots of melanophores. The yellow ventral color has faded to cream and the color of the iris is no longer discernible.

Measurements (mm): SVL 74.7; head width 25.2; head length 28.9; tibia 56.5; tympanum 4.4; inner metatarsal tubercle 3.4.

³From *poikilos* (Gr.), pied or blotched, referring to diagnostic pattern on rear of thigh.

⁴Based on notes made on series of 10 that included the holotype.

Paratypes.—All from Baleh River basin, Third Division, Sarawak, in collections of Field Museum of Natural History: 356 from type locality, one from small stream between Sungei Laie and Sungei Sujai in upper Baleh drainage. All were collected in the years 1962–63 and 1970–71.

Variation.—Sexual dimorphism in SVL and relative size of the tympanum is obvious (table 1). Other secondary sex characters are as described under *phaeomerus* (p. 10).

Individual variation in certain characters is given in Tables 1 and 3. The amount of dark pigmentation on the throat and chest varies greatly from faint mottling to completely dark brown. The form and amount of area covered by light blotches on the thigh vary among individuals, although the blotches are always present.

Larvae.—Transforming young having the thigh pattern of *poecilus* (p. 10) are the end point of a developmental series (morphotype B in text and tables 4 and 5). They represent only a portion of the larvae included under the heading B in Inger (1966, pp. 272–274). Their distinctive characters (larval stages ≥ 36) include: both beaks divided and coarsely serrated; sharp, colorless asperities laterally on head and body; two to five glands in ventral fin; usually four undivided rows of denticles on the lower lip; two to six glands in the patch at the rear of the body; and brown coloration with dense pattern of obscure, small dark spots. Head-body lengths 10.33–12.25 mm in stages 36 through 41 ($N = 11$), maximum width .77–.89 of head-body length.

Referred larvae: FMNH 135322–23, 135332, 146195, 158004, 213646–53.

Comparisons.—The large size, bold light marking on the thigh, and relatively long leg distinguish *A. poecilus* from other species in this group. *Amolops whiteheadi* (Boulenger), although similar in size (table 3), has shorter legs, lacks light blotches on the thigh, has the ventral surface of the lower leg heavily pigmented, and has less webbing. Differences between *A. poecilus* and *phaeomerus* are discussed above (p. 3). *Amolops kinabaluensis* and *A. cavitympanum* differ from *poecilus* as they do from all members of the *jerboa* group (see p. 10).

Larvae of *poecilus* differ sharply from those of *phaeomerus* in coloration and number of glands at the rear of the body, but generally resemble larval types D through H in these respects. However, *poecilus* larvae differ from types D and E in having the lower beak divided and from F, G, and H in having fewer rows of denticles on the lower lip and in having spinules restricted to the lateral surfaces of the head and body.

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