

**Morphology and Systematics of
Kalophrynus interlineatus-pleurostigma Populations
(Anura: Microhylidae: Kalophryninae) and a Taxonomy
of the Genus *Kalophrynus* Tschudi, Asian Sticky Frogs**

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Sticky Frogs, *Kalophrynus* Tschudi, are a small group of Southeast Asian species with their greatest diversity in Borneo. Two species, *K. interlineatus* (Blyth) and *K. pleurostigma* Tschudi, were proposed as residents of Myanmar (Burma), northern and southern populations respectively. An analysis of morphological variation in Burmese specimens and comparison with small samples from throughout the distribution of the *interlineatus-pleurostigma* group of species demonstrates variable levels of regional differentiation, which I interpret as evidence of speciation. This interpretation recommends the restriction of *K. pleurostigma* to Sumatra populations and *K. interlineatus* to peninsular Myanmar and adjacent mainland Southeast Asian populations. The northern Borneo populations have the largest body size of any members of this group and represent a new species, *K. meizon*. The Philippine populations, *K. sinensis* Peters, are confirmed as unique as proposed recently by Ohler and Grosjean (2005). The populations from northern Myanmar also represent a distinct taxon, *K. anya*, and differ from *K. orangensis* (India and Bangladesh) and *K. interlineatus* (peninsular Myanmar and Southeast Asia). To assist the on-going discovery of new species of this cryptic frog group, I provide a taxonomic resumé of all currently recognized species of the genus *Kalophrynus* and a diagnostic key to all species of *Kalophrynus*.

KEYWORDS: nomenclature, anatomy, morphometrics, tropical Asia, Myanmar, Thailand, Sumatra, Borneo, Philippines, Amphibia, *Kalophrynus*

Tschudi (1838) recognized the uniqueness of the Sticky Frogs with the erection of a new genus, *Kalophrynus*. Simultaneously he described *K. pleurostigma* for a specimen from Sumatra, thereby establishing this taxon as the type species of *Kalophrynus*. The Sumatran origin has not been questioned, although few Sumatran specimens are available to provide a thorough examination of variation of topotypic *K. pleurostigma* in the broadest sense of all Sumatran populations.

The scarcity of Sumatran specimens and the widespread occurrence of presumably similar appearing frogs from southern Myanmar through Southeast Asia to Borneo and the Philippines led to the name *pleurostigma* being applied to the larger-bodied Sticky Frogs in this area. This concept of *K. pleurostigma* had its foundation in Parker's review (1934) of the Microhylidae. Therein, he recognized four of the eight species of *Kalophrynus* described prior to his review. He considered the broadly distributed *K. pleurostigma* as consisting of two subspecies (n nominate and *interlineatus*). This concept persisted for sixty years until Matsui et al. (1996) recognized the two

subspecies as full species with *K. interlineatus* for the northern populations and *K. pleurostigma* for the southern ones.

During our Myanmar Herpetological Survey's (MHS) country-wide survey of the composition and distribution of the herpetofauna of Myanmar, I noted the absence of populations of any *Kalophrynus* species in central Myanmar (between 18° to 23°N). This area was visited repeatedly between 1997 and 2009 by our MHS teams. This absence and a preliminary examination and comparison of a few individuals from northern and peninsular Myanmar encouraged me to examine more closely the morphology of Burmese *Kalophrynus*. That examination led me to broaden the investigation to include samples of *interlineatus-pleurostigma* frogs from throughout the range of these two species. The first part of this report details the results of that study. My literature review for the preceding morphological analysis informed me of the scattered nature of the published records on the species of *Kalophrynus* and the absence of consistent characterization of the now 25 species of this genus. I have attempted a review of the *Kalophrynus* literature and offer a series of standardized species accounts for every recognized species of this genus through September 2014.

Owing to the long term adoption of *K. pleurostigma* as a broadly distributed Asian species with two subspecies, I assumed at the beginning of my analysis of Burmese *interlineatus-pleurostigma* populations that these populations represented a single clade. The Asian-wide populations are not a single clade as I will demonstrate later in a discussion of recent molecular phylogenetic studies. Nevertheless, my focus remains on these populations as they have been historically treated as a single species, which had not undergone a detailed morphological examination, i.e., the major goal of this study. For convenience, I refer to these broadly distributed populations as the *interlineatus-pleurostigma* group, a phenetic paradigm and not a clade.

MATERIALS AND METHODS

The morphometric characters are standard ones for the study of frog morphology and are defined in the Appendix 2. *Character definitions*. Sex and maturity for the frogs examined were determined by dissection. I note my preference again for abbreviated labels, such as HeadL and SnEye, for character names versus the usual initial abbreviations, i.e., HL and SE, which are uninformative to all but frog specialists. I developed a set of color pattern characters for the Sticky Frogs. Although I am not totally satisfied with these defined traits, I argue that this qualitative approach to the major features of *Kalophrynus* coloration is less subjective than verbal descriptions and, further, allows statistical examination of intra- and interpopulational variation.

Whether descriptive or qualitative, recording coloration (i.e., both color and pattern) of preserved specimens remains subjective owing to the varying degrees of fading, manner of original preservation, and other factors. Our recent MHS specimens, their field descriptions, and, in some cases, photographs give me confidence in my coding and recording of coloration traits for them but leaves me much less confident of my data from older specimens (extra-Myanmar) from other collections. The erection of a coding scheme for documenting the various features of color pattern attempts to overcome some of the subjectivity resulting from preservation related changes in coloration (I use coloration to include the color of an individual and the pattern of color marks, e.g., stripes, blotches, spots, etc.). The coding reduces the arbitrariness of recording and analysis of pattern, but problems remain; these are noted in the analysis of coloration traits.

The samples are identified in Appendix 1. *Specimens examined*. Although the impetus for this project was Burmese frogs, perusal of the literature and my initial examination of specimens from outside of Myanmar indicated the necessity of a wider geographic exploration of morphological variation and eventually encompassed the entire range of the *interlineatus-pleurostigma* group

(also see Ohler and Grosjean 2005). Although my study encompasses the entire range of this group, I limited my sampling to seven sites within the group's total range. With the exception of the Thai-Indochina sample, the samples each derives from a limited geographic area (see Appendix 1). All statistical analyses were performed with SYSTAT version 12. Students' *t* tests determined whether adult females and males were significantly different ($P = 0.05$); body proportions were arcsine-transformed to approximate normal distributions for each sample. Proportions are reported in the text as the original proportions, not their arcsine-transformed values. I use the standard leaf-shape definitions, commonly illustrated in botanical text, for describing the outline shape of head and body.

Because *K. pleurostigma* has been identified as the species of southern peninsular Myanmar and the remainder of the Malayan Peninsula, this study needed to characterize *K. pleurostigma* in a broader geographic area than Myanmar and further to confirm that *K. pleurostigma* from this mainland area was the same as the Sumatra population, i.e., the topotypic population. The available Sumatra specimens are few, and I discovered from a colleague, H. Kaiser, that the type specimen of *K. pleurostigma* had deteriorated badly. *Kalophrynus pleurostigma* is the type-species of the genus, hence the designation of a neotype has been proposed (Zug and Kaiser 2013). I provide a description of the neotype herein and a brief diagnosis of the genus *Kalophrynus*. Although this detour is seemingly extraneous to a study of Burmese frogs, it has become evident during the past decade that the majority of the presumed widespread tropical Asian frog species are multi-species complexes. To resolve the nomenclature for a narrow regional sample frequently creates uncertainty in the taxonomic identity of populations elsewhere in the range of the former pan-Asian species.

RESULTS

Morphology and Variation

Sexual dimorphism.—Five of the regional samples are sufficiently large to test for sexual dimorphism in adults: northern Myanmar (Sagaing only; 5 females, 4 males); central peninsular Myanmar (Tanintharyi; 7, 4); Thai-Indochina (Thailand, Laos, Vietnam, Cambodia; 4, 7); north-central Sarawak (Samarahan & Sri Aman; 11, 7); and Philippines (Bohol; 9, 17). Of the Myanmar samples, only two proportions, SnEye/SVL (38 % females, 42 % males) and EyeD/HeadL (32 %, 35 %), were significantly dimorphic in the northern sample. In contrast, the central peninsular sample had no dimorphic measurements or proportions, although the coloration trait HeadMid was dimorphic with median head stripe usually distinct in females and absent or indistinct in males. The Thai-Indochina, Sarawak, and Philippine samples are strongly size dimorphic with females as the larger sex. All measurements except Tymp are dimorphic in the Philippine samples; tympanum width averages larger (3.6 mm) in females than in males (3.4 mm) but with strong overlap and high variance. All measurements are dimorphic in Sarawak frogs, and all but TarsL in the Philippine individuals. Of the proportions, HndL/SVL is also significantly different in all three samples with shorter legs in Sarawak and Philippine females (means 142 % females, 150 % males; 153 %, 157 % Philippines; respectively) and slightly longer in Thai-Indochina females (134 %, 133 %). Sarawak females also have significant shorter tarsi (54 %, 58 % TarsL/ThghL). Of the non-metric traits, Philippine males have significantly stronger webbing of the hindfoot (1.8, 2.6 WebIII2) but no other significantly dimorphic traits. The Sarawak frogs have males with darker sides of the trunk (LatTrnk) and all other traits are monomorphic. Thai-Indochina frogs display no dimorphism in non-metric traits. The type series of *K. orangensis* contains five adults; they fall in a narrow size of range of 35 to 38 mm SVL, suggesting an absence of sexual dimorphism; no traits could be tested for dimorphism owing to small sample size and absence of trait quantification.

Morphometrics.— Although small, the Burmese samples reveal similar size ranges for adults from the three geographic areas: north Myanmar (Sagaing and Kachin); southeast main Myanmar (Mon, limited to five immature individuals); and central peninsular Myanmar (Tanintharyi). Additionally, the adult females and males are of equal size. The females' mean SVLs (Table 1) are the same in the north and south samples, although the north (Sagaing) sample has a broader range, which encompasses the minimum and maximum SVLs of the southern sample. Male SVL ranges of both Myanmar samples are also contained within the size range of their respective female samples. Body measurements are typically considered to be highly correlated with SVL. Such is not the case in the Tanintharyi sample. For the Tanintharyi adult sample ($n = 11$), only HeadL, SnEye, and ThghL have correlation coefficients greater than 0.50, $R = 0.70, 0.71, 0.66$, respectively. This low correlation probably results from the limited size range (i.e., absence of juveniles) of the sample and the sample's small size.

In spite of the similarities in body length in the northern and southern Burmese samples, the southern sample averages larger than the northern one in all measurements and strikingly so in all segments of the hindlimb; thus, hindlimbs are distinctly longer in the southern sample. This difference in limb length is evident in the HndIL/SVL proportion (Table 1). The proportional lengths of the components, however, do not differ; CrusL is 90 % and 87 % of total hindlimb length, north and south, respectively, and the ranges are nearly identical. The same proportional similarities exist for TarsL and HndfL. The Mon sample includes only juveniles, and it shows the same pattern of differences from the north sample as the southern sample. The Mons' mean HndIL/SVL is the highest (Table 1) of the three Burmese samples but that may result from the comparison of a sample of juveniles to samples of adult females.

TABLE 1. Select morphometric features of adult females from several geographic areas within distribution of the *Kalophrynus interlineatus-pleurostigma* species group. Character abbreviations are defined in the Appendix. The values are mean±standard deviation, minimum and maximum values; mm for SVL and percent for proportions.

Sample	SVL	HeadL/SVL	SnEye/HeadL	Tymp/EyeD	HindIL/SVL	CrusL/ThghL	HndfL/ThghL
Location							
Sagaing $n = 5$	41.2±4.46	27.2±1.4	37.7±2.2	74.8±13.7	117±5.3	90.0±5.3	87.3±8.2
	36.4–47.1	24.9–28.9	35.2–40.8	60.6–92.5	110–125	81.2–95.9	78.5–95.5
Mon $n = 5$ immatures	32.2±2.17	33.7±2.4	37.3±7.0	80.6±10.3	147±5.9	88.1±7.8	88.0±5.5
	29.6–34.5	31.3–36.8	27.5–44.7	67.6–93.8	142–154	79.5–100.8	82.0–96.6
Tanintharyi $n = 7$	40.9±1.52	30.6±0.8	39.7±1.1 1	85.1±10.0	139.5±5.2	87.3±4.4	87.6±2.2
	39.3–43.7	29.6–31.9	38.2–41.3	72.1–100.0	132–147	82.6–93.1	84.9–90.9
Thai-Indochina $n = 4$	44.7±1.68	31.7±2.9	39.3±2.3	81.2±4.0	133±6.5	87.2±2.6	86.2±4.3
	42.8–46.4	29.3–35.7	35.9–41.0	76.2–84.8	127–142	84.9–90.0	82.6–92.2
Sumatra $n = 1$ neotype	34.5	28.7	41.4	89.7	152	80.7	65.9
Sarawak $n = 11$	54.8±3.95	32.0±1.5	41.1±6.20	101±7.0	141.7±6.6	88.8±1.7	77.9±4.1
	48.2–60.2	29.0–34.7	36.2–46.4	89.5–112.0	136–157	85.2–91.0	71.2–86.6
Philippines $n = 9$	42.3±1.82	30.6±1.9	40.4±2.5	83.0±6.1	153.5±6.1	93.1±8.3	88.0±8.5
	39.4–45.7	28.1–34.2	36.6–45.2	54.8–104	142–163	76.9–106.3	79.8–104.4

HeadL and the other head measurements are slightly smaller in the northern sample (Table 1). The proportion HeadL/SVL illustrates this difference (Table 1). The other head proportions are also less in the northern sample, and again the Mon sample is similar to the southern (Tanintharyi) sample.

Comparisons of extra-Myanmar samples show the Thai-Indochina sample's metrics overlap broadly the ranges of most Tanintharyi sample traits, although the hindfoot proportion (HndfL/ThghL) is smaller in the Thai-Indochina sample. The mean HndfL/SVL proportion of Thai-Indochina is intermediate between that of Sagaing and Tanintharyi, although its range largely overlaps Tanintharyi. The single Sumatra adult female is smaller than adult females from any other locality (Table 1), although not smaller than some adult males from elsewhere. The Sumatra female has proportionately longer hindlimbs (HndfL/SVL) than any adult Burmese female, although this proportion is within the ranges of Borneo and Philippine females. The Sumatra female differs strikingly from all other females in its relative small hindfoot length (HndfL/ThghL; Table 1). Borneo females average significantly larger than females from any other area, and for my samples, there is no overlap in SVL ranges. Relative hindfoot length of Borneo females is intermediate between that of Sumatra and Burmese females. Philippine females match the Tanintharyi and Thai-Indochina ones in all body metrics, although they average larger in relative hindlimb and crus lengths; ranges of these latter two proportions, however, overlap with those of the Tanintharyi and Thai-Indochina samples.

Only SVL and head metrics are available for *K. orangensis*. The body size of the three adult females overlaps the lower range of adult Burmese females. I am unable to compare the head morphometrics of the *K. orangensis* type series owing to a presumed error in the reported measurements of head dimensions (Dutta et al. 2000: table 1). Accepting their SVL data as correct, their HeadL measurements are too small, and SnEye and NarEye too large; HeadW and EyeD appear correct. This conclusion derives from a comparison with the samples from Myanmar and elsewhere. The problem is highlighted by adding SnEye and EyeD from their table; the resulting sum equals or exceeds HeadL. HeadL should equal roughly the sum of these two values plus Tymp. The other aspect indicating an error in their head length measurements is that HeadL/SVL proportions for their data range 20–23 % in contrast to 28–36 % for my combined samples. TarsL of *K. orangensis* was measured although these data were not reported in the description.

External morphology.— The shape or dorsal outline of all *K. interlineatus-pleurostigma* group-members is a cordate to conical/triangular body with a smooth transition from of head and neck to the body. Limbs are of moderate length and sturdy. The dorsal surface from nape to trunk is strongly glandular, consisting of compact skin with contiguous columnar epidermal glands (Fig. 1A–B). These glands appear structurally similar to those of the parotoid glands of *Rhinella marina*, hence they are likely granular glands with a syncytial cellular column surrounding a narrow lumen or duct that opens to the exterior. This dorsal glandular sheet of skin is like a cloak and extends from the middle of the head to above the vent and laterally onto the sides of the body, apparently with glandular tissue columns gradually decreasing in height and becoming less compact, and merges into the thinner, although still glandular, skin of the sides. The merger of the thicker, glandular trunk skin with the dorsal head skin is smooth in most populations; only in the Borneo specimens is the transition marked by a slight transverse ridge. Some researchers (e.g., Parker 1934) report the presence of parotoid glands; however, there is no delineation of the skin on the posterodorsal surface of the head and the supra-axillary region into an elevated gland. In contrast to the trunk, the thick skin ends abruptly dorsolaterally on the head and ventrolaterally in the preaxillary region thereby creating a distinct supratympanic fold continuous with a broad preaxillary fold (Fig. 1C). A white to cream stripe (commonly mislabeled a dorsolateral fold) extends from the tip

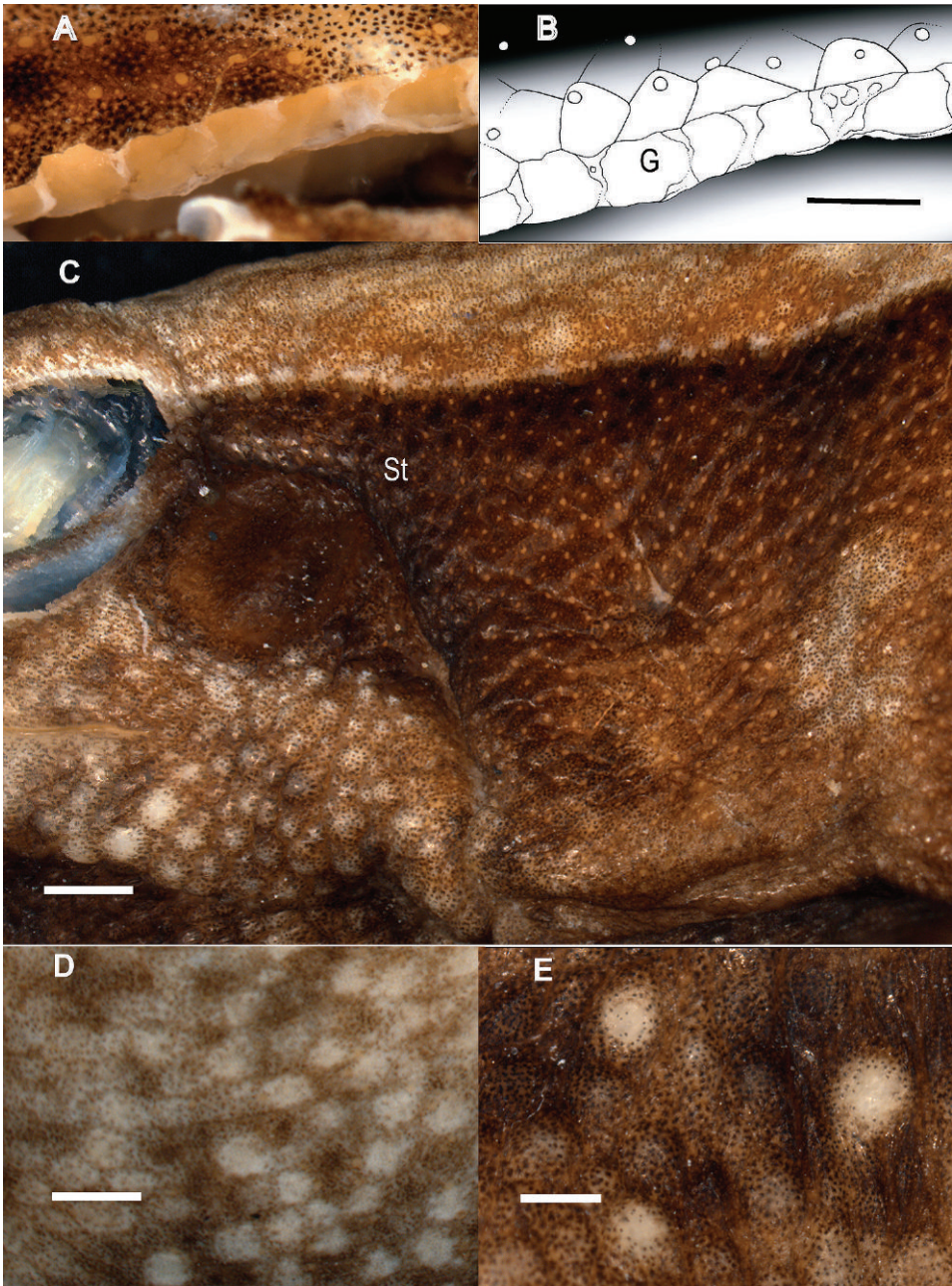


FIGURE 1. Morphology of the glandular skin of a northern Myanmar *Kalophrynus* individual (USNM 537421). (A) compact, columnar macroglands comprising the skin in the dorsolateral pre-inguinal region; (B) sketch of the preceding image A to assist the identification of structures; incision is immediately below and parallel to white diagonal dorsolateral stripe; tile-like pattern on dorsal surface identifies individual macroglands, each with a single duct opening (lighter area in each tile); (C) lateral view of head and neck displaying the abrupt termination of thick glandular skin, equivalent to a supratympanic fold; (D) belly pebbly skin just anterior to pubic area; (E) white glandular epidermal patches on chest. Abbreviations: D, dorsolateral stripe; G, columns of glandular tissue; St, supratympanic fold. Scale bars equal 1 mm in figures B, D, E, and 10 mm in C.

of the snout to the inguinal region, running diagonally on the side of the trunk from dorsolateral on the shoulder angling downward to a mid-lateral position at inguina. It is not a discrete glandular ridge or fold, as its tissue composition is identical to the skin on either side of this light stripe. The entire surface of the glandular cloak bears small flattened circular tubercles of two sizes, small and smaller. The dorsal surface of the head lacks the thickened columnar skin and its surface bears numerous tiny spiculate tubercles. Ventrally, the skin's surface is tuberculate with small, flattened, circular tubercles (Fig. 1D) from chin to rear of the chest and the abdomen (belly) paved with large flattened tubercles; a few small, white 'macroglans' (Fig. 1E) are scattered from chin to pelvis. Although histological data are lacking, these 'macroglans' appear to be unpigmented tubercles, otherwise they are the same as other ventral tubercles. The preceding description is applicable to all adults from all samples.

The appearance of the head is similar in individuals of all samples. The tip of the snout usually bears a short pointed proboscis. The canthus rostralis is sharply defined and the loreal or lore is a flat vertical surface. The nares lie anteriorly on the lower edge of the canthus, about one-third of the distance from snout tip to the anterior border of orbit, although this character is variable within a locality and with differences in the mean position (NarEye/SnEye) among the samples. In the Mon juveniles, Tanintharyi adults, and the two Sumatran specimens, the nares are nearest the midpoint (55, 56, 56 %, respectively), whereas they are somewhat closer to the snout in the northern Myanmar, Borneo, and Philippine samples (59, 58, 59 %, respectively) and closest (64 %) to the tip of the snout in the Thai-Indochina sample; all samples have broad ranges (~15 %) of the measurement. The NarEye/HeadL means (22–25 %) are similar in all samples and less variable than NarEye/SnEye. Eyes are moderately large (means ~30 % EyeD/HeadL) with horizontal, elliptical pupils. Tympanum is exposed and visible; it is modest sized, its diameter usually smaller than the diameter of the orbit (Table 1). The tympanum averages smallest in the northern Myanmar sample and largest (i.e., equals eye diameter) in the Borneo sample (Tymp/EyeD, Table 1). The upper annulus (rim) of the tympanum is usually partly covered by the bottom edge of the supratympanic fold.

Fore- and hindlimbs are well-developed, moderately slender, and of moderate length, hindlimbs are about twice the length of forelimbs. Forefeet are web-free. Finger tips are bluntly rounded. Fingers are of moderate length, and most individuals in all populations have a phalangeal formula of $3 > 2 \approx 1 > 4$ or $3 > 2 \approx 1 \approx 4$, although a few individuals have the first finger slightly longer than second one. The underside of forefoot has well-developed tubercles (Fig. 2A). A large round to oblong outer palmar tubercle occupies most of the palm and is encircled distally by four well-developed tubercles at the base of each finger. All four digits bear large basal or proximal subarticular tubercles, and the third digit has a second, well-developed subarticular tubercle beneath the proximal phalanx, thus a sub-articular formula of 1 1 2 1 from first to fourth finger. In two Laos individuals, the third finger had a third small tubercle distally, i.e., 1 1 3 1. Hindlimbs are moderately robust, and the crus is slightly shorter than the thigh (Table 1); the hind-foot and crus are commonly equal-sized or nearly so. The ankle (tarsus) is the shortest segment of

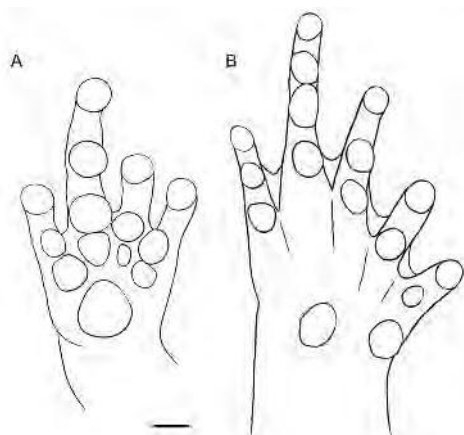


FIGURE 2. Schematic ventral view of the right (A) fore- and (B) hindfoot of *Kalophrynus anya* sp. nov. (USNM 537420). Scale bar equals ~1 mm.

the hindlimb, slightly more than half the length of the thigh (average 55–59 % TarsL/ThghL for all populations). Hindfoot is modestly webbed (Fig. 2B) with webbing varying in development between toes, basal between the first and second and second and third digits, and moderate between the third and fourth and fourth and fifth digits. The webbing formulae (means) for extent of webbing on the fourth toe vary among populations (Table 2): WebIII2 averages 1.0 (north Myanmar), 2.3 (Tanintharyi), 2.0 (Indochina), 2.1 (Borneo), and sexually dimorphic for the Philippine sample with 1.8 (female) and 2.6 (male); WebIV2 averages 0.9, 1.7, 1.2, 1.3, respectively and 1.8 (female) and 2.2 (male) for the Philippine sample. Thus, Philippine males have the most extensive webbing and Tanintharyi adults next, although in no population is the hindfoot fully webbed. The two Sumatran specimens display 1.5 WebIII2 and 1.0 WebIV1, values within the range of the other populations. Toes are of moderate length, tips bluntly rounded, and all populations share a 4>3>5>2>1 phalangeal formula. The plantar surface bears moderate sized, round inner and outer metatarsal tubercles, usually of similar size although occasionally the inner is half the size of the outer. The five distal plantar tubercles at the base of the toes are variously developed, although always evident. Each toe except the fifth has a well-developed basal subarticular tubercle. First and second toe have only the basal tubercle; third toe usually has a second more distal tubercle, uncommonly a third one (two Laos specimens); fourth toe usually has a third distal tubercle, uncommonly a fourth one (two Laos specimens). The condition of subarticular tubercles on the fifth toe is variable. One tubercle is the most prevalent condition and typically it is moderately developed; however, about a third of the Sarawak toads had no tubercle and where present, the tubercle was small, weakly developed. In Philippine specimens, a single tubercle was always present, although weakly developed in some. For the northern and peninsular Myanmar, and Thai-Indochina frogs, slightly more than half had two tubercles and the remainder one tubercle; tubercles ranged from weakly to moderately well-developed. The Sumatran adult female had a single tubercle and it was distal rather than basal as in most specimens examined. The toes' most common subarticular tubercle formulae are 1 1 2 3 1 and 1 1 2 3 2.

TABLE 2. Select morphological features of adults from the regional samples of the *Kalophrynus interlineatus-pleurostigma* species group. Character abbreviations are defined in the Appendix. The values are means.

Sample	Hindfoot	Webbing	Roof of Mouth	Coloration				
Location	WebIII2	WebIV2	Buccal Fold	HeadMid	DorsNap	IngSpt	HndIbr	Chin
Sagaing <i>n</i> = 5	0.9	0.9	rectangular edged	1	0.8	1.2	0.2	1.3
	0.5–1	0.5–1		0–2	0–2	0–2	0–2	0–2
Mon <i>n</i> = 5 immatures	1.7	0.9	rectangular edged	0.8	0.2	2	0.6	0.6
	1–2	0.5–1		0–2	0–1	2–2	0–2	0–2
Tanintharyi <i>n</i> = 7	2.3	1.6	rectangular edged	1.1	1.4	2	1.4	1.7
	2–3	1–2		0–2	0–2	2–2	0–2	1–2
Thai-Indochina <i>n</i> = 4	2	1.25	rectangular edged	0.7	0.7	1.8	1.4	1.5
	2–2	1–2		0–2	0–2	0–2	0–2	0–2
Sumatra <i>n</i> = 1 neotype	2	1.5	denticulate edged	0	1	2	0	.
Sarawak <i>n</i> = 11	2.1	1.2	blunt-lobed edged	0	0.1	2	0.7	0.3
	2–2.5	1–2		0–0	0–1	2–2	0–1	0–1
Philippines <i>n</i> = 9	1.8	1.8	blunt-lobed edged	0.1	1.3	1.5	0.7	0.8
	1–3	1–2.5		0–1	0–2	1–3	0–1	0–1

Oral morphology.— The tongue is moderately large, broadly oblong to obovate in outline, smoothly truncated on its rear edge, and variably attached. In the Sumatra and some Borneo frogs, the posterior quarter or less of the tongue is free, about half is free in Borneo and Philippine individuals, and half to two-thirds is free in north and south Burmese and Thai-Indochina specimens. The roof of the mouth (Fig. 3) bears three transverse folds (dermal pharyngeal folds of Parker 1934) (Fig. 3; also see Fei et al. 2005:fig. 349). These folds appear to be edentulous in all individuals examined and lack underlying bony support (not evident in a small series of x-rays). The anterior-most fold is the vomerine fold; the second fold (postorbital) extends transversely between the posterior quarter of the orbits; and the third fold (buccal) lies transversely just behind the orbits. Size and shape of these folds vary among the different populations (Table 2). In the Sumatran specimens (*K. pleurostigma* sensu stricto), the vomerine fold is pair of long, straight-edged folds extending from the labial edge of the mouth to near the midline, with a short gap between the left and right folds. The postorbital fold is a low, smooth-edged fold and is followed closely by the high, edentulous buccal fold which has a strongly serrated free edge. Each serration has the shape of a tri-crowned tooth, although there is no evidence of dentine or enamel in these ‘denticles.’ I recommend the use of the term palatal folds as the folds lie on the primary palate and are anterior to the epiglottal opening into the pharynx.

In the northern Myanmar sample, the vomerine fold is a broad, smooth-edged double flap and somewhat undulatory; left and right sides are separated by moderate gap. This morphology is largely shared by the Mon, Tanintharyi, Thai-Indochina, Borneo, and Philippine specimens. The left and right folds are narrowly separated in the Borneo and Philippine specimens. Owing to various states of preservation, observed relative size and undulation of the folds may be considered tentative observations. The extent of the medial hiatus appears more consistent within regional samples. Differences in the morphology of the postorbital folds seem more robust. The northern Myanmar specimens have a moderately broad flap divided into five or six unequal-sized lobes; the fold is paired in Tanintharyi individuals and distinctly separated at the midline, the left and right sides each with two or three lobes. In the Indochinese specimens, morphology is similar to Tanintharyi although it ranges from a short lobular fold of well-separated lobes to left and right lobular folds separated medially. Borneo individuals have a moderately wide, continuous lobular fold, and there is a similar morphology in Philippine specimens with the folds ranging from strongly undulatory to broad lobes. The buccal fold extends across the entire breadth of the buccal cavity in all specimens from all localities. Regional differences occur in the relative height and lobular shape of the fold. Height or its appearance may possibly be influenced by preservation, whereas the lobular nature of the fold probably not. Northern Myanmar individuals have a buccal fold of ten or more closely abutting rectangular lobes; Tanintharyi individuals have a similar morphology although the lobes appear shorter and more round-edged. Borneo and Philippine frogs have folds comprised of variously shaped, short blunt lobes.

The apex of the lower jaw is similar in individuals from all localities. The lower jaw has a

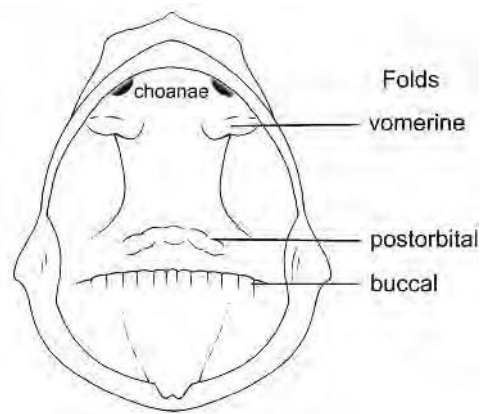


FIGURE 3. Schematic depiction of the roof of the mouth of a *Kalophrynus anya* sp. nov., emphasizing the palatal folds. Only the basal portion of the tongue is shown, epiglottis and esophageal opening are not shown, and lower jaw is foreshortened.

smooth, labial margin and anteriorly curves downward forming a concave edge with a small blunt odontoid process in the middle (tip of the jaw). It is edentulous. The upper jaw lies rearward of the tip of snout, producing a distinctly under-hung (subterminal) jaw. The upper jaw bears tiny teeth, often hidden by the labial mucosa.

Coloration.— The color characters were analyzed for sexual dimorphism. No differences in the frequency between females and males were observed for any of the eleven color traits in the five regional samples large enough for statistical testing. Thus, these data indicate that no population of the *interlineatus-pleurostigma* group displays sexual dichromatism.

Only two color traits (HeadMid, DlatSt) were invariant within any regional samples. No color trait was uniform across all regional samples. IngSpt was present in all individuals of the Mon, Tanintharyi, and Borneo samples, and was present in most individuals in each of the other samples; however, this spot was absent in a few individuals. Further, it was of variable size in most samples, and the white outer edge was also of variable distinctiveness. This latter variation can result from variable quality of preservation and time in preservative, although it appears to exist in living individuals from the same population. The dorsal head stripe (HeadMid) was absent in all Borneo individuals and most Philippine frogs; otherwise it occurred at about a 50 % frequency in the other samples (Table 2). DlatSt occurred as a bold stripe in all Mon frogs, and as a distinct or bold stripe in individuals of all other samples, except the Philippines where it was more commonly indistinct or absent.

Distinct parasagittal head stripes (HeadPsag) occurred in less than 50 % of the individuals in all samples. Presence-absence frequency is more variable for DorsNap. The nape stripe was present in the majority of individuals of the Tanintharyi and Philippines samples, rarely occurred in Mon and Borneo frogs, and present in about a third of the northern Myanmar and Thai-Indochina samples. The parasagittal stripes (DorsPsag) occurred in 50 % of Mon and Tanintharyi individuals, about a third of northern Myanmar and Philippines ones, and rarely in Tanintharyi and Borneo. Face coloration (Loreal) is typically darker than the top of head, but the degree of darkness beneath the distinct dark canthal ridge is variable and difficult, at times, to discriminate between character states 1 and 2; nonetheless, my data indicate that most individuals in the Tanintharyi, Thai-Indochina, and Borneo samples have uniformly dark faces. Lateral trunk coloration from fore- to hindlimbs (LatTrnk) is dark in most individuals in all samples. Barring or banding of the upper surface of the thigh (HndlBr) is present in the majority of the Tanintharyi, Thai-Indochina, and Philippine samples, in about a third of the individuals of Mon and Borneo samples, and rare in northern Myanmar frogs. Half or more individuals in all samples, except Borneo, have distinct chin markings; most Borneo frogs have dusky throats without markings. Chest markings (Chest) are less common in all samples and nearly absent in Mon, Borneo, and Philippine samples.

No single coloration trait uniquely delimits any population with the possible exception of the nape-anterior trunk hourglass blotch in *K. pleurostigma*. The few *K. pleurostigma* examined prevents an unequivocal declaration to the uniqueness of this pattern. Additionally, few color traits are invariant within a sample or population. As noted above, only the presence of inguinal spots (IngSpt) was invariant in the Mon, Tanintharyi, and Borneo samples, absence of middorsal head stripe (HeadMid) was invariant in the Borneo sample, and presence of distinct dorsolateral trunk stripes (DlatSt) was invariant in the Mon sample. The variation in the two largest samples (Borneo, Philippines) is no greater or less than the variation in the smaller samples, thereby indicating that small samples of eight or more individuals encompass most coloration variation.

Taxonomic Discussion and Conclusions

Not surprising, the pan-Asian concept of *Kalophrynus pleurostigma* is incorrect. Matsui and associates (1996) began the current recognition of multiple species by elevating the two subspecies (*K. pleurostigma pleurostigma*, *K. pleurostigma interlineatus*) to specific status. Their concept of the two taxa was based primarily on the morphology of north-central Thai and Borneo specimens and the difference in call structure of these two populations. They did not examine the holotypes of either taxon. The proposed distributions of the two taxa from their map (Matsui et al. 1996: fig. 3) placed *K. interlineatus* as a northern Southeast Asian species and *K. pleurostigma* as a southern species from southern Thailand, Malaysia and Sumatra eastward into the Philippines. This paradigm was the one with which I began my study of the Burmese populations of *Kalophrynus*. This paradigm was also the one that led me to conceptualize the larger *Kalophrynus* species as the *pleurostigma* species group and a clade. Once I began a thorough review of the literature, I discovered that the earliest molecular phylogeny (Matsui et al. 2011) did not support the monophyly of this species group. I will discuss the genetic relationships later, but first, a discussion of my analysis of the morphology of the larger members of the *interlineatus-pleurostigma* populations

Kalophrynus pleurostigma and *K. interlineatus* and the earlier inclusive *K. pleurostigma* (i.e., pre-Matsui et al., 1996) have been variously mentioned in diagnoses of new *Kalophrynus* species, but the first analysis of geographic variation awaited Ohler and Grosjean's (2005) analysis of the advertisement call structure of a Vietnamese population of *K. interlineatus*. They demonstrated that the call of their Vietnamese population differed little from that of the Thai population analyzed by Matsui et al. (1996). They interpreted this similarity to indicate that the two populations were conspecific. They (Ohler and Grosjean 2005) also examined coloration, noting that variation occurred in the reverse V-striped dorsal pattern, although it usually remained recognizably distinct from the dorsal pattern of *pleurostigma* sensu Matsui et al. With their coloration data, they compared type specimens of *Kalophrynus stellatus* Stejneger (Basilan, Philippines) and *Calophrynus pleurostigma* var. *Sinensis* Peters (correcting the type locality to Mindanao, Philippines) and concluded that the names were synonyms of and available for the Philippine populations of *K. pleurostigma* sensu Matsui et al. 1996. They also considered that the description of *K. orangensis* did not sufficiently differentiate it from *K. interlineatus* and proposed it as a synonym of the latter, even though they performed no analysis to support their decision. Matsui and colleagues (2009, 2011, 2012) continued to recognize *K. orangensis*.

Ohler and Grosjean (2005) suggested that the dorsal reverse-V pattern (my DorsNap character) of northern Vietnam-China displayed differences from that of Thai individuals. Further, in their discussion of dorsal color pattern of Southeast Asian *pleurostigma*, they emphasized constancy of pattern at a local intrapopulation level and interpopulation differences on a broader geographic scale. My observations indicate a higher level of intrapopulation variation. Relative to the presence of the reverse V-stripe, it is present in the majority (> 80 %) of the Philippine and Tanintharyi samples, and usually absent in the Borneo and Mon samples, and roughly half of the other samples. It is important to note that my coding and scoring of this trait differ from their evaluation owing to their consideration of the 'wholeness' and fragmentation of the arms of the stripe; furthermore, my Thai-Indochina sample contains individuals from both eastern and western localities. Ohler and Grosjean's recognition of pattern difference between northern Vietnam and Thailand is suggestive of regional differentiation even though they found no differences in the structure of Thai and Vietnamese vocalizations. My Thai-Indochina sample combines these areas and the variation within characters is no greater than the geographically more restricted samples of the Philippines, Borneo, and Tanintharyi, suggesting, although not verifying, the presence of a single species in this area.

Do the Thai-Indochina sample and the Tanintharyi one represent a single species? Given that there are no striking differences in coloration (Table 2) and morphology (Table 1), I propose that they represent the same species. The decision on the specific status of populations in peninsular Myanmar is less certain, although I propose that the Mon and the Tanintharyi populations represent the same species. The most striking difference is the relative hindlimb length (HndIL/SVL; Table 1) between these two samples; however because the former sample is composed entirely of juveniles and the latter of adults, I interpret this difference as an ontogenetic one. Accepting them as representatives of a single species attaches the name *Kalophrynus interlineatus* (Blyth 1855) to the peninsular Myanmar population and further to the populations of Thailand, Laos, Vietnam, Cambodia, and southern China (composition of my Thai-Indochina sample). I do not have a sample representing the Peninsular Malaysia and Singapore populations; however, Chan et al. (2014) recognized the uncertainty of the distribution of *K. palmatissimus* and *K. interlineatus* (= their *pleurostigma*) and gave their characters for differentiation of these two. They demonstrated that *K. interlineatus* occurred widely through central and southern Peninsular Malaysia and that *K. palmatissimus* occurred at only three locations and sympatric with *K. interlineatus* at only one locality. Their Malaysian *interlineatus* localities are the ones mapped in Fig. 4.

The preceding morphological analysis of *Kalophrynus* specimens reveals modest regional differentiation of populations. Although modest, I interpret the differences to indicate speciation and propose the recognition of multiple species within the *interlineatus-pleurostigma* populations. Molecular data and analyses for the postulation of phylogenetic relationships among *Kalophrynus* species are accumulating slowly and largely as “out-group” taxa for the examination of relationships of other microhylid genera or species complexes. This situation handicaps the interpretation of relationship based on DNA sequence data because of the incomplete representation of *Kalophrynus* species. Four studies (Kurabayashi et al. 2011; Matsui et al. 2011; de Sa et al. 2012; Vassilieva et al. 2014) provide information on relationships, and all four demonstrate that *Kalophrynus* populations are a monophyletic group. This monophyly is the only information that can be drawn from the Kurabayashi group’s results as their two *Kalophrynus* samples derive from pet-trade specimens with questionable locality data. The phylogeny of Matsui and collaborators is more useful in portraying interpopulational relationships. Their samples represent eight different taxa (each a single individual) with broad geographic coverage. The resulting phylogenetic analysis identifies the Sumatran sample (*pleurostigma*) as the basal branch of the *Kalophrynus* phylogeny. The Philippine sample is the next branch and without a close relative. Subsequent branching has the Southeast Asian *K. interlineatus* embedded in a cluster of the smaller West Malaysian species and the northern Myanmar (Chatthin) individual shows sister relationships to the Borneo *K. heterochirus*. In an analysis of American microhylids, de Sa and associates had four *Kalophrynus* samples and similarly place the Sumatran sample as basal on the *Kalophrynus* tree. The northern Myanmar sample is sister group to two Thai *K. interlineatus*, one of which is a Kurabayashi pet-trade specimen. The phylogeny of Vassilieva and colleagues (2014) was generated specifically to examine relationships among Vietnamese *Kalophrynus* (a third of their genetic sample) and those with other *Kalophrynus* taxa. Their two new species and the Vietnamese, southern China, and northern Myanmar *interlineatus* form a clade as the final branch in their phylogram. The northern Myanmar individual is the basal branch in the latter clade. The other *interlineatus-pleurostigma* populations/species are distributed elsewhere throughout the phylogram. Their *pleurostigma* clade includes a Borneo specimen as a sister group to a Sumatra-West Malaysia pair. The Philippine sample is a pet-trade specimen without reliable locality data.

I interpret the preceding molecular data as demonstrating: 1) monophyly of the *Kalophrynus* species; 2) polyphyly of a *interlineatus-pleurostigma* group; 3) genetic uniqueness of northern

Myanmar population; 4) strong indication that the Sumatran *pleurostigma* and the Philippine *sinensis* are each distinct genetic entities.

In summary, I propose that the morphological differences support the recognition of six species in the polyphyletic *interlineatus-pleurostigma* species group. I recommend the continuing recognition of *K. orangensis*. Ohler and Grosjean (2005) correctly observed that the proposed diagnostic features of this taxon were inadequate to differentiate the Assam population from other *pleurostigma* group populations; however, comparison of the Assam sample to its closest geographic congener identifies some differences. Adult *K. orangensis* are smaller than the northern Myanmar population, and they display no sexual dimorphism of SVL. The largest female *orangensis* is 3.0 mm smaller (SVL) than the smallest mature Myanmar female. The northern Myanmar population differs in several traits from the peninsular Myanmar populations of *K. interlineatus* as well as being distantly geographically isolated from the latter. Our current distributional data indicates that *K. interlineatus* is widespread throughout Southeast Asia although with a spotty occurrence. Sumatran specimens of *Kalophrynus* are rare; the few available ones demonstrate some striking morphological differences and support the uniqueness of this island's *Kalophrynus*. The large size and other features emphasize the distinctiveness of the Borneo "*pleurostigma*" populations. Similarly, the "*pleurostigma*" populations of the Philippines differ morphologically from the Borneo and other populations thus also represent a separate species, *K. sinensis*. The following section provides a detailed taxonomic and nomenclatural summary of my conclusions.

TAXONOMY OF *KALOPHRYNUS*

Species are arranged alphabetically. The two new species described herein are *Kalophrynus anya* from northern Myanmar and *K. meizon* from Borneo. Those two taxa and the members of *interlineatus-pleurostigma* group of populations (i.e., *K. interlineatus*, *K. pleurostigma*, *K. sinensis*; Fig. 4) have more detailed descriptive synopses than the other species in order to present the morphological details from the preceding analysis. Morphological details for the remainder (and majority) of the *Kalophrynus* species derive entirely from published information, as I examine no types or other specimens of these taxa. Measurements and proportions are for adults unless noted otherwise. NA indicates that data were not available in any published studies.

***Kalophrynus* Tschudi, 1838**

Sticky Frogs

Type species: *Kalophrynus pleurostigma* Tschudi, 1838.

DEFINITION.— Small to medium-sized microhylid frogs (adults, 17–60 mm SVL) with deltoid to ovate dorsal body outline, narrowest anteriorly, and well-developed, moderate-length fore- and hindlimbs. Dorsal skin thick, surface typically granular, often spiny, and strongly glandular.

Skull with prevomer divided and postchoanal portion absent; palatine absent; ethmoids small or absent. Pectoral girdle with well-developed clavicles and procoracoids reaching ventral midline cartilage and laterally the scapulae; omosternum small, cartilaginous; sternum large, cartilaginous. Terminal phalanges T-shaped.

Pupil round to slightly horizontal elliptical. Tongue oblong to obovate, posterior edge blunt to rounded, and half to two-thirds free. Palate with two to three transverse ridges or folds, anterior one (vomerine) smooth, usually medially interrupted, and adenticulate just behind choanae, middle one (postorbital) smooth and adenticulate between posterior edges of orbits, and posterior one (buccal) variably segmented and adenticulate lying about halfway between rear of orbits and epiglottis.

TABLE 3. Select characteristic of currently recognized species of *Kalophrynus*.

Species	Range of adult SVL		Inguinal spots		Ocellus	Forefoot digit formula	Hindfoot webbing
	Females	Males	Present	color			
<i>Kalophrynus anya</i> sp nov. ¹ North Myanmar	36-47	34-41	yes, occasionally absent	black	light-edged	3>2 >4	at base
<i>Kalophrynus batuensis</i> ² Borneo	to 47	to 36	yes	yellow	None or dark brown-edged	3>2 >4	at base or slightly beyond
<i>Kalophrynus baroensis</i> ³ Borneo	21	18-20	yes	black	none	3>2 >4	at base or slightly beyond
<i>Kalophrynus bungaranus</i> ⁴ Great Natuna Isl.	25-27	22-23	yes	black	none	3>2 >4	at base
<i>Kalophrynus calciphilus</i> ⁵ Borneo	35-39	29-30	no	none	none	3>2 >4	at base
<i>Kalophrynus cryptophonus</i> ⁶ Vietnam	23	28-30	yes	black	none	3>2>4 >1	at base
<i>Kalophrynus cok</i> ⁷ Borneo	?	26	no	none	none	3>2 >4	at base
<i>Kalophrynus heterochirus</i> ⁸ Borneo	30-33	24-27	yes	bluish-white	none	3>2 >4	one-third
<i>Kalophrynus honbaensis</i> ⁹ Vietnam	?	27-37	yes	black	light-edged	3>2>4 >1	one-third
<i>Kalophrynus interlineatus</i> ¹⁰ SE Asia	35-46	34-45	yes, occasionally absent	black	light-edged	3>2 >4	one-third
<i>Kalophrynus intermedius</i> ¹¹ Borneo	38-41	?	no	none	none	3>2 >4	~ two-thirds
<i>Kalophrynus timboolaiti</i> ¹² West Malaysia	?	26-29	yes	dark	none	3>2 >4	at base or slightly beyond

<i>Kalophrynus meizon</i> sp. nov. ¹³	35–60	37–50	yes	black	light-edged	3>2≥1≥4	one half to two-thirds
Borneo							
<i>Kalophrynus menglienicus</i> ¹⁴	?	20–23	yes	none	none	3>4>2>1	slight to none
China							
<i>Kalophrynus minusculus</i> ¹⁵	to 35	to 25	no	none	none	?	?
Java & Sumatra							
<i>Kalophrynus nubicola</i> ¹⁶	21–24	19–20	no	none	none	3>2>1>4	~ one-third
Borneo							
<i>Kalophrynus orangensis</i> ¹⁷	35–38	36–38	yes	black	light-edged	3>2>1>4	at base
NE India							
<i>Kalophrynus palmatissimus</i> ¹⁸	31–39	31–39	no	none	none	3>2>1=4	two-thirds
West Malaysia							
<i>Kalophrynus pleurostigma</i> ¹⁹	34–35	?	yes	black	light-edged	3>2≥1>4	~ one-third
Sumatra							
<i>Kalophrynus punctatus</i> ²⁰	?	22–27	no	none	none	3>2>1>4	at base
Borneo							
<i>Kalophrynus robinsoni</i> ²¹	18+	17–18	no	none	none	3>2>1>4	one-third
West Malaysia							
<i>Kalophrynus sinensis</i> ²²	39–46	35–42	yes, occasionally absent	black	light-edged	3>2>1>4	variable, one-third to two-thirds
Philippines							
<i>Kalophrynus subterrestris</i> ²³	26–27	21–23	yes, occasionally absent	black	none	3>2>1>4	one-third
Borneo							
<i>Kalophrynus tiomanensis</i> ²⁴	25–26	26	yes	dark brown	yes	3>2≥1>4	at base or slightly beyond
West Malaysia							
<i>Kalophrynus yongyi</i> ²⁵	?	29–31	yes	black	none	3>2>1>4	at base
West Malaysia							

DATA RESOURCES. 1, this study; 2, Kiew, 1984b, Malkmus et al., 2002; 3, Matsui & Nishikawa, 2011; 4, Günther, 1895, Inger, 1966; 5, Dehling, 2011, Inger, 1966; 6, Das & Haas, 2003; 7, Vassilieva et al., 2014; 8, Boulenger, 1900, Inger, 1966; 9, Vassilieva et al., 2014; 10, this study; 11, Inger, 1966; 12, Matsui et al., 2012; 13, this study, Inger, 1966; 14, Yang & Su, 1980, Fei et al., 1999, Fei et al., 2010; 15, Iskandar, 1998; 16, Dring, 1983; 17, Dutta et al., 2000; 18, Dehling, 2011, Kiew, 1984a; 19, this study; 20, Inger, 1966; 21, Dehling, 2011, Smith, 1922; 22, this study, Inger, 1954, Taylor, 1921; 23, Inger, 1966; 24, Chan et al., 2011; 25, Matsui, 2009.

A “?” denotes that datum is not available.

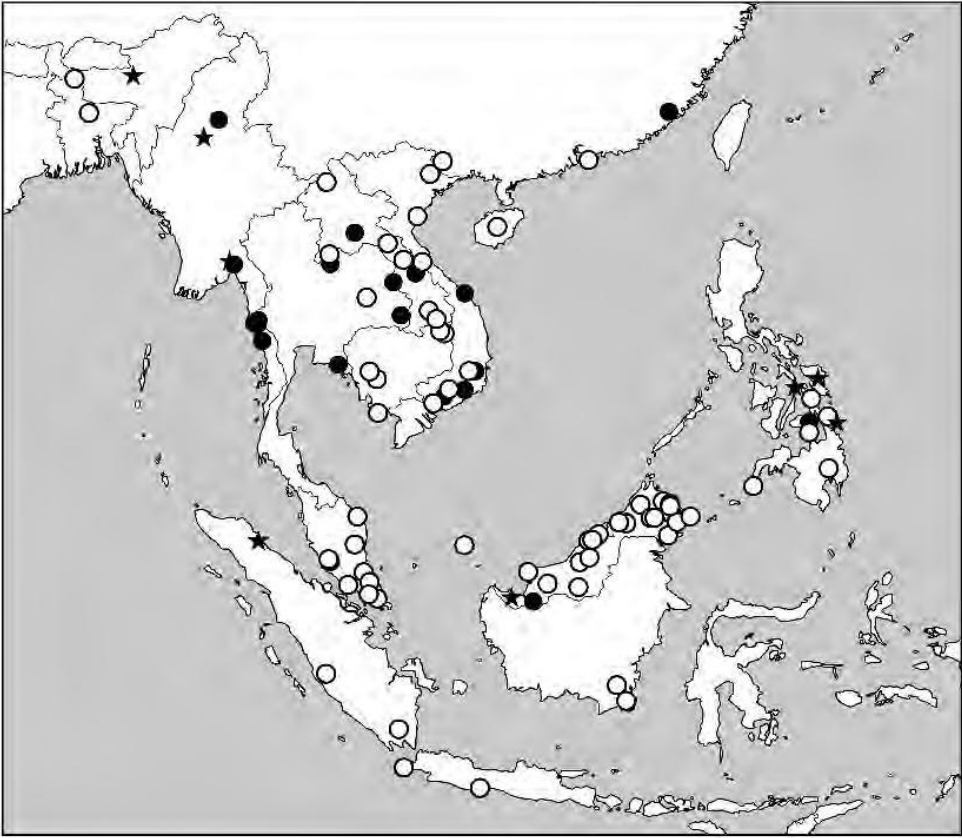


FIGURE 4. General distribution of the *Kalophrynus interlineatus-pleurostigma* group. Solid circles denote specimens examined in this study; open circles are literature records and museum records of specimens not seen; stars represent type localities of available names. Source of the locality records are in Appendix Specimens examined section.

Tympanum always visible, although posterodorsal edge often partially overlapped by edge of thick glandular dorsal skin. Digit well-developed and not expanded distally. Forefoot usually without webbing or slight basal webbing, basal to moderate webbing on hindfoot. Both fore- and hindfeet with numerous subarticular tubercles. Commonly, snout with short, pointed proboscis.

CONTENT.— Twenty-five species (Table 3) with the greatest diversity in Borneo (ten endemic species).

DISTRIBUTION.— Northeast India (Assam, West Bengal) and northern Bangladesh (Rajshahi), north-central Myanmar (Sagaing, Kachin), peninsular Myanmar (Mon, Tanintharyi), Southeast Asia (Laos, Thailand, Vietnam, Cambodia), southern China (Yunnan, Guangxi, Hainan, Guangdong, Fujian), Sumatra, Java, Borneo (Kalimantan, Sarawak, Brunei, Sabah), and Philippines (southeastern islands). See Fig. 4.

***Kalophrynus anya* Zug, sp. nov.**

Northern Burmese Sticky Frog

Figure 5, 11A–B.

TYPE MATERIAL.— HOLOTYPE: USNM 537420, adult male from Chatthin Wildlife Sanctuary, San Maung Camp (~23°35'57"N, 95°31'13"E) elevation ~200 m, approximately 2 km WNW of Chatthin (town), Sagaing Division, Myanmar, collected 5 September 1998 by Htun Win.

PARATYPES: CAS 232488, Moenyini, Indawgyi Wildlife Sanctuary headquarters (24°44'55.7"N 96°20'52.6"E) elevation 799 ft [~242 m], Kachin State, Myanmar; USNM 520321, 523964–965 locality same as holotype; USNM 523966 Chatthin Wildlife Sanctuary, approximately 5 km WNW (~23°36'06"N, 95°31'13"E) of Chatthin (town), Sagaing Division, Myanmar; USNM 537419, 537421–422 locality same as holotype.

DEFINITION.— Adult *K. anya* can be distinguished from all congeners by the following combination of characters: no size dimorphism, adults 34–47 mm SVL; HeadL/SVL 30–32 %; tympanum about equal eye diameter, Tymp/EyeD 72–100 %; moderate short hindlimbs, HndLL/SVL 132–147 %; short hindfoot, HndfL/ThghL 85–91 %; dimorphism of SnEye/HeadL (35–43 %) and EyeD/HeadL (31–37 %) with females smaller; strong supratympanic ridge dorsoposteriorly overhanging tympanic annulus; paired vomerine folds, each broad, smoothly undulatory with modest medial separation; single postorbital fold with five or six undulatory lobes; single broad buccal fold comprised of ten or more abutting rectangular lobes; forefeet without webbing; hindfeet webbed at base, highest between 3rd and 4rd toe, usually to base of 2nd subarticular tubercle of 4rd toe; head pattern variably with HeadMid 50 % present and DorsNap 33 % present; chin usually with paired, broad longitudinal bars; hindlimbs (HndlBr) seldom barred.

DESCRIPTION OF HOLOTYPE.— Moderately robust-bodied male (39.7 mm SVL) with well-developed, moderate-length fore- and hindlimbs (45 % ForarmL+HandL/SVL, 119 % HndLL/SVL); head ovate (25 % HeadL/SVL, 30 % HeadW/SVL) and continuous with body (no apparent constriction or enlargement at juncture of head and trunk). Body measurements are: HeadL 10.1 mm; HeadW 11.8 mm; SnEye 4.3 mm; NarEye 2.3 mm; EyeD 3.5 mm; Tymp 3.1 mm; ForarmL 9.8 mm; HandL 8.1 mm; ThghL 14.4 mm; CrusL 13.0 mm; TarsL 7.5 mm; HndfL 12.8 mm. Eye distinctly larger than tympanum (89 % Tymp/EyeD).

Skin strongly glandular with dorsal skin thickened and cloak-like extending from nape to posterior end of trunk, smooth surface, thickest anteriorly forming distinct supratympanic fold over dorsal and posterior edge of tympanic annulus and swollen mass above axilla; posteriorly glandular cloak merges imperceptibly into lateral trunk skin; limbs without enlarged glandular folds; chest and abdominal skin glandular and pebble-like with scattered unpigmented 'pebbles' on chest. Tongue large, elliptical, posterior two-thirds free. No vomerine teeth. Three sets of palatal folds on roof of mouth: vomerine paired, each long with smooth undulatory free edge and distinctly separated medially; postorbital single, indistinct, and free-edge undulatory; buccal, single continuous fold of 15 to 16 rectangular, abutting lobes, medial lobes larger than lateral ones. Fingers and toes well-developed and tips bluntly rounded; hand web free; foot basally webbed (WebIII.2 = 1, WebIV.1 = 0.5). Subarticular tubercles well developed on hand and foot (Fig. 2A–B); large, nearly circular palmar tubercle with small tubercle at base of each finger and only third finger with tubercle of free portion of digit; no nuptial pads or asperities evident; paired moderate-sized, circular metatarsal tubercles on edges, inner slightly smaller than outer; each toe with basal subarticular tubercle; third toe with single tubercle on free portion of digit, fourth with two tubercles, and fifth with one (hence total of two tubercles on fifth toe). Digital length formulae, hand 3>2≈4=1, foot 4>3>5>2>1.

COLORATION IN PRESERVATIVE.— Dorsum from tip of snout to thigh medium rufous brown with faded brown middorsal stripe on head, bifurcating at nape into diagonally diverging stripes; parasagittal stripes from nape to trunk also diagonal; laterally neck and trunk dark brown, fading ventrally; narrow white dorsolateral stripe evident only on neck and shoulder; face (loreal) dark brown at canthus rostralis, lighter brown to mouth; vague banding on dorsal of thighs. Venter dark brown to nearly black on chin to mid throat, fading gradually thereafter to creamy white in prepubic area; vague lighter longitudinal stripe from chin to anterior chest.



DESCRIPTION AND INTRAPOPULATIONAL VARIATION.— Moderate-sized adults, not sexually dimorphic although females average larger (mean 41.6, 36.4–47.1 mm SVL) than males (40.7, 34.0–41.3 mm). These differences are reflected in the other measurements: HeadL 9.9–13.8 mm ♀♀, 9.6–10.7 mm ♂♂; HeadW 10.5–14.8 mm ♀♀, 10.3–12.0 mm ♂♂; SnEye 3.7–5.0 mm ♀♀, 3.8–4.4 mm ♂♂; NarEye 2.2–3.5 mm ♀♀, 2.2–2.7 mm ♂♂; EyeD 3.3–4.6 mm ♀♀, 3.2–4.0 mm ♂♂; Tymp 2.0–3.9 mm ♀♀, 2.5–3.3 mm ♂♂; ForarmL 9.3–12.1 mm ♀♀, 9.0–10.6 mm ♂♂; HandL 7.0–10.7 mm ♀♀, 8.1–9.1 mm ♂♂; ThghL 13.1–17.8 mm ♀♀, 11.7–15.5 mm ♂♂; CrusL 11.7–15.8 mm ♀♀, 12.1–13.3 mm ♂♂; TarsL 7.0–10.5 mm ♀♀, 6.9–8.4 mm ♂♂; HndfL 11.3–14.9 mm ♀♀, 10.3–13.4 mm ♂♂. Body proportions differ between females and males, although not greatly so (all values are percent): HeadL/SVL 25–32 ♀♀, 25–28 ♂♂; HeadW/HeadL 97–118 ♀♀, 105–117 ♂♂; SnEye/HeadL 35–41 ♀♀, 40–43 ♂♂; NarEye/SnEye 56–65 ♀♀, 50–61 ♂♂; EyeD/HeadL 31–33 ♀♀, 34–37 ♂♂; Tymp/EyeD 61–93 ♀♀, 78–89 ♂♂; Forarm/SVL 24–26 ♀♀, 22–26 ♂♂; Forarm/CrusL 73–85 ♀♀, 69–80 ♂♂; HndfL/SVL 110–125 ♀♀, 119–122 ♂♂; CrusL/SVL 30–32 ♀♀, 32–33 ♂♂; CrusL/ThghL 81–96 ♀♀, 86–103 ♂♂; TarsL/ThghL 52–62 ♀♀, 52–59 ♂♂; HndfL/SVL 27–32 ♀♀, 30–32 ♂♂; HndfL/ThghL 79–96 ♀♀, 82–88 ♂♂.

Tongue large, obovate, posterior half to two-thirds free. Vomerine teeth absent. Palatal fold morphology is moderately variable although these data are not quantified. The vomerine folds range from smooth-edged, undulatory folds to folds with broad lobular appearance (USNM 523964, 537419, 537422); usually folds moderately separated on midline, rarely narrowly separated. Postorbital folds are usually well developed and higher than buccal folds; also most variable of three palatal folds and usually continuous although uncommonly narrow separated at midline; fold free edge ranges from smooth, undulatory to broad, round-edged lobes. Buccal fold is low, continuous with ten to 14 smooth-edged rectangular lobes.

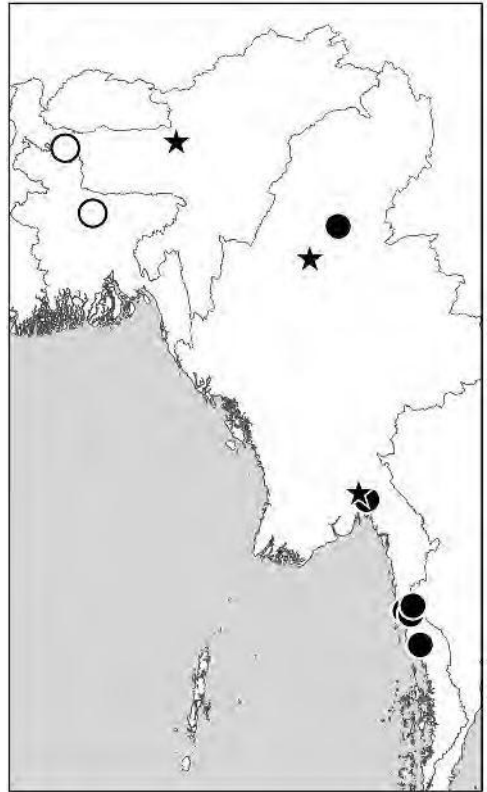
Fingers lack webbing. Both finger and toe tips are bluntly rounded. Subarticular tubercles are well developed on digits; only third finger bears subarticular tubercle on free portion of digit (low on fifth); all fingers have a tubercle at their base and another row between a large, usually circular (rarely elliptical), nearly medial outer palmar tubercle. Nuptial pads not present. For hindfoot, each toe has a basal subarticular tubercle, third and fifth toes have an additional tubercle on free portion of digit, two tubercles on fourth toe (fifth toe of USNM 523965 lacks tubercles). Inner and outer metatarsal tubercles are present; inner is small to moderate-sized, nearly circular to elliptical; outer moderate-sized, circular to elliptical; inner and outer tubercles equal-sized to outer larger than inner. Toes lightly webbed WebIII2 median 1.0 (0.5–1.0), WebIV1 1.0 (0.5–1.0). Digit lengths nearly constant for fore- and hindfeet; finger formula $3>1\approx 2>4$; toe formula $4>3>5>2>1$.

Color pattern variation statistics for adults are (median and range): HeadMid 1, 0–2; HeadPsag 1, 0–2; DorsNap 1, 0–2; DorsPsag 1, 0–2; IngSpt 2, 0–2; HndfBr 0, 0–2; DlatSt 2, 1–2; Loreal 1, 0–2; LatTrnk 2, 0–2; Chin 1, 0–2; Chest 1, 0–2. *Kalophrynus anya* is highly variable, commonly with distinct middorsal stripe and faded parasagittal stripes on head, faded to distinct nape stripe in most individuals and bifurcating and quickly fragmenting or disappearing; inguinal spot almost always present and usually as ocelli, dorsolateral narrow white stripe rarely absent or indistinct, hindlimbs uncommonly barred, loreal area and lateral trunk usually uniformly dark, chin and throat always dusky and often with pair of darker longitudinal bars, and chest commonly dusky.

ETYMOLOGY.— All readers of Burmese cultural history are familiar with the country's division into Upper and Lower Burma. This species occurs in the more northern portion of Upper Burma, and the Burmese *a-nya tha* refers to the human inhabitants of Upper Burma (*auk tha*,

FIGURE 5 (left). Images of holotype of *Kalophrynus anya* (USNM 537420, male, 39.7 mm SVL) in (A) dorsal, (B) lateral, and (C) ventral views [photographer, J.A. Poindexter].

FIGURE 6. Burmese distribution of voucher specimens of *Kalophrynus anya* sp. nov. in northern Myanmar and *K. interlineatus* in southern and peninsular Myanmar. The three reported localities of *K. orangensis* are also shown; all lie within the Brahmaputra river valley. Solid circles denote specimens examined in this study; open circles are literature or unexamined museum records; and stars represent type localities of available names.



Lower Burma inhabitants). Because *tha* references human populations, I have taken the liberty of subverting the meaning of *a-nya* to the region of Upper Burma, hence the name for this Upper Burma endemic species.

DISTRIBUTION.— Myanmar. *Kalophrynus anya* is presently known from recent vouchers in east-central Sagaing Division (Chatthin) and south-central Kachin State (Indawgyi) (Fig. 6). Bourret (1942) reported specimens from Bhamo and Teinzo in Upper Burma. I have not located the source of these records; see discussion in the distribution section of the *K. interlineatus* account.

NATURAL HISTORY.— Many authors (e.g., Fei et al. 2010, Ohler and Grosjean 2005) report *K. interlineatus* and *K. pleurostigma* as a common frog and regularly calling in choruses. Our (MHS teams) observations found *K. anya* an uncommon species, and we heard no choruses. Our assessment is that it is an uncommon species. We found individuals in open In (*Dipterocarpus tuberculatus*) forest with slight to moderate ground vegetation (grass), seasonally with heavy leaf litter.

Kalophrynus baluensis Kiew, 1984

Balu Sticky Frog

Kalophrynus baluensis Kiew, 1984a, *Malayan Nature Journal* 38:152 [type locality: “Kamborangoh at 7,200 feet, Mount Kinabalu”, Sabah, Malaysia].

TYPE MATERIAL.— HOLOTYPE: BMNH 1929. 12. 22. 51, by original designation.

DEFINITION.— Small, adult females 24.7–25.8* mm SVL ($n = 2$), adult males 25.8– 26.3* mm SVL ($n = 2$) [*see Comments]; head moderately long 31–33 % HeadL/SVL; head slightly wider than long 104–106 % HeadW/HeadL; naris closer to snout than to eye 59–72 % NarEye/SnEye; eye moderately large 36–37 % EyeD/HeadL; tympanum visible and smaller than eye 77–79 % Tymp/EyeD; slender moderately long forelimb 29–31 % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb moderately long NA % HndIL/SVL, 39–40 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth absence; palatal fold morphology not reported; tongue size and shape not reported.

Fingers no webbing; lengths $3 > 2 > 1 > 4$; tips rounded and slightly dilated; subarticular tubercles present, shape and numbers on digits not reported; fleshy palmar tubercle, size and shape not reported. Toes moderately webbed, web extending to distal subarticular tubercle of toe 3 and

between proximal and middle tubercle of toe 4, lengths $4 > 3 > 5 > 2 > 1$; tips rounded, not dilated; sub-articular tubercles present, number and shapes not reported; oval inner and round outer metatarsal tubercles poorly developed.

Color in life not known; dorsum brown with darker brown hour-glass mark from between eyes to mid-trunk with broad brown stripes radiating rearward, no inguinal ocelli (see Comments); loris dark brown; dark brown dorsolateral stripe from above eye to anterior trunk; sides of trunk dark spotted; venter tannish with numerous small dark spots from chin to pelvis.

ETYMOLOGY.— The name *baluensis* derives from the frog's origin in the high montane forest of Mount Kinabalu.

DISTRIBUTION.— Sabah, Borneo. Known only from upper slopes of Mount Kinabalu.

NATURAL HISTORY.— *Kalophrynus baluensis* is a high-elevation, forest-floor frog living in the leaf-litter of oak-chestnut forest between 1400–1800m a.s.l. It calls predominantly at night and typically from burrows or forms. It appears to have a unique handstand defensive posture.

COMMENTS.— Preceding information extracted from Kiew (1984a). The description of this species in Malkmus et al. (2002) differs substantially from Kiew's original description, and the former's characterization is summarized below. I accept their characterization as mostly correct and attribute the differences to Kiew's data as a result of Kiew having juveniles and their examination of a larger series of adults.

Moderate-sized, adult females to 47 mm SVL, adult males to 36 mm SVL; head wider than long; tympanum smaller than eye 50–75 % Tymp/EyeD, supratympanic fold present (their fig. 114); tips of fingers round, not dilated, finger length $3 > 2 > 1 > 4$; hindlimbs moderately long 39–45 % CrusL/SVL; toes webbed at base; subarticular and metatarsal tubercles weakly developed; one to two yellow inguinal “ocelli” (not clear whether just spots or dark-edged spots).

Kalophrynus barioensis Matsui and Nishikawa, 2011

Bario Sticky Frog

Kalophrynus barioensis Matsui and Nishikawa, 2011, *Current Herpetology* 30:146 [type locality: “Jln. Arul Dalan trail to New Dam, Bario, State of Sarawak, Malaysia (03°45'N, 115°26'E, 1141 m asl)”].

TYPE MATERIAL.— HOLOTYPE: Sarawak Museum MU455.16, by original designation. PARATYPE: Kyoto University Graduate School 53128–129, 5371.

DEFINITION.— Small, adult female 20.5 mm SVL ($n = 1$), adult males 17.5–19.8 mm SVL ($n = 5$); head moderately long 33–36 % HeadL/SVL; head width equals length 33–36 % HeadW/SVL; naris closer to snout than to eye 15–21 % NarEye/SVL; eye moderately large 15–20 % EyeD/SVL; tympanum visible and about equal to eye 60–140 % Tymp/EyeD; slender moderately long forelimb 56–63 % Forelimb/SVL; hindlimb moderately long 126–141 % HndIL/SVL, 42–47 % CrusL/SVL.

Vomerine teeth presence or absence not reported; palatal folds present, morphology not reported; tongue entire.

Fingers with slight basal web; lengths $3 > 2 > 1 > 4$, 4th very short; tips rounded and not dilated; subarticular tubercles round, indistinct, and one on digit 2, two on 3; outer palmar tubercle large, inner indistinct; no nuptial excrescences on fingers. Toes slightly webbed not extending beyond proximal subarticular tubercles of toe 4, lengths $4 > 3 > 2 > 5 > 1$; tips rounded, not dilated; subarticular tubercles indistinct and one on digit 2, two on 3, three on 4, and none on 1 and 5; oval inner and no outer metatarsal tubercles.

Color in life, dorsum orangish brown with faint brown hour-glass mark from between eyes to suprascapular area and largely immaculate from mid-trunk rearward; body; large black inguinal spot, no light edge; loris and temporal area to inguina dark brown, fading ventrally; yellowish

white oblique stripe from above eye to lower inguinal area; chin and chest dark brown with indistinct lighter bands, posterior chest and belly yellowish white with scattered black spots anteriorly.

ETYMOLOGY.— The name *barioensis* derives from the town of Bario in the Kelabit Highlands of Sarawak.

DISTRIBUTION.— Sarawak, Borneo. Presently, *K. barioensis* is known only from the vicinity of the type locality.

NATURAL HISTORY.— These frogs are ground-dwelling residents of broad-leaf and bamboo forest. All specimens were collected in mid August from the leaf litter along forest trails. Males, hidden beneath the leaf litter, were calling in scattered small chorus and chorused in late afternoon and early evening whether it rained or not.

COMMENTS.— The extreme variance of the Tymp/EyeD data suggest an error in the measurement of one individual.

Preceding information extracted from Matsui and Nishikawa (2011).

***Kalophrynus bunguranus* (Günther, 1895)**

Natuna Sticky Frog

Diplopelma bunguranum Günther, 1895, *Novitates Zoologicae* 2:501 [type locality: “Bunguran, or Great Natuna [Island]”, Indonesia].

TYPE MATERIAL.— SYNTYPES: number and deposition not noted in original publication, presumably BMNH; British Museum of Natural History 1947.2.11.38–41 (formerly 95.5.1.105–108) according to R. F. Inger (in Frost, 1985).

DEFINITION.— Small, adult females 25–27 mm SVL, adult males 22–23 mm SVL; head medium length 28 % HeadL/SVL; head slightly wider than long 113 % HeadW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large 45 % EyeD/HeadL; tympanum visible and smaller than eye 61 % Tymp/EyeD; slender moderately long forelimb 29–31 % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb moderately long HndIL/SVL, NA % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed 85 % HndfL/CrusL.

Vomerine teeth presences or absence not reported; palatal fold morphology not reported; tongue large, subelliptical and entire behind.

Fingers without web; lengths $3 > 2 \approx 1 > 4$ (nub-like); tips rounded; subarticular tubercles not reported; palmar tubercle not reported; spiny nuptial excrescences dorsally on base of fingers 1 to 3 and adjacent hand of males (fide Parker; see comment). Toes weakly webbed, lengths $4 > 3 > 5 > 2 > 1$; tips rounded, not dilated; subarticular tubercles indistinct, numbers on toes not reported; indistinct inner and outer metatarsal tubercles.

Color in life unknown. Dorsum purplish brown, no mark mentioned; large dark brown, oval black inguinal spot without light border; loris edged with reddish rose that extends posteriorly above eye and onto and widening on trunk to inguina and hindlimbs; loris, chin to anterior chest black fading to yellowish.

ETYMOLOGY.— Great Natuna Island is also called Bunguran, whence the name of the species as a resident of Bunguran.

DISTRIBUTION.— Great Natuna Island.

NATURAL HISTORY.— Günther considered it a common frog owing to its abundance in collections.

COMMENTS.— Preceding information extracted from Günther (1895) and Parker (1934). Parker considered *C. heterochirus* Boulenger as a synonym of *K. bunguranus* and may have included traits of the former in the description of the latter. Parker reported nuptial pads on dorsum of fingers; Inger (1966: table 16) specifically noted their absence.

Kalophrynus calciphilus* Dehling, 2011*Limestone Sticky Frog**

Kalophrynus calciphilus Dehling, 2011, *Zootaxa* 2737:51 [type locality: “close to the northern entrance of Gua Bulansusu (Moonmilk Cave) on Batu Bungan, ca. 200 m a.s.l., Gunung Mulu National Park, Sarawak, Malaysia”].

TYPE MATERIAL.— HOLOTYPE: Naturhistorisches Museum der Burgergemeinde Bern 1056261. PARATYPES: BMNH 1978.1611–1615, FMNH 171777, NMBE 1056262–263. All by original designation.

DEFINITION.— Small, adult females 35.5–38.8 mm SVL ($n = 2$), adult males 29.7–30.1 mm SVL ($n = 2$); head moderately long 31 % HeadL/SVL; head wider than long 119 % HeadW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large 38 % EyeD/HeadL; tympanum visible and distinctly smaller than eye 54 % Tymp/EyeD; slender moderately long forelimb NA % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb slender and long 183 % HndLL/SVL, 43 % CrusL/SVL, and 96 % CrusL/ThghL; hindfoot well developed 84 % HndfL/CrusL. Proportions from holotype only.

Vomerine teeth absence; vomerine fold paired and crenulated, condition of other palatal fold morphology not reported; tongue broad and not bifurcated. Adult males with series of spiny tubercles on rear half of mandible.

Fingers with slight basal web; lengths 3>2>1>4; tips rounded and not dilated; subarticular tubercles distinct, round, and one on digits 1, 2, 4, and two on 3; one large palmar tubercle on outer half of palm, bordered distally by four small, round tubercles. No nuptial pad or asperities present. Toes modestly webbed not extending to proximal subarticular tubercle of toe 4, lengths 4>3>5>2>1; tips rounded, slightly dilated; subarticular tubercles large, round and one on digits 1, 2, two on 3, three on 4, none on 5; large, elongate inner and small, round outer metatarsal tubercles.

In life and at night, dorsum and sides of head and body black from tip of snout to end of trunk; narrow white oblique stripe from tip of snout, passing above eye and tympanum to lower inguinal area; venter from chin to anterior belly fading to dusky thereafter; chest and anterior belly with scattered white spots. During day, dorsum and sides lighten to a medium brown.

ETYMOLOGY.— The specific name derives from the Latin *calx* for limestone and the Latinized Greek suffix *philus* for “who is attracted to” combined to denote this species affinity to karst forest.

DISTRIBUTION.— Sarawak, Borneo. Known only from the karst forest in Gunung Mulu National Park, Sarawak.

NATURAL HISTORY.— *Kalophrynus calciphilus* is a terrestrial species, apparently confined to karst forest. It calls day and night from the entrance of small burrows in the soil and owing to the absent of standing water in the karst forest, it is hypothesized that eggs are laid in these burrows and possibly “guarded” by the male.

COMMENTS.— Preceding information extracted from Dehling (2011).

Kalophrynus cryptophonus* Vassilieva, Galoyan, Gogoleva, and Poyarkov, 2014*Lam Dong Bamboo Sticky Frog**

Kalophrynus cryptophonus Vassilieva, Galoyan, Gogoleva, and Poyarkov, 2014, *Zootaxa* 3769(3):410 [type locality: “Loc Bao, Lam Dong Province, Vietnam (coordinates 11°44'17"N, 107°42'25"E, elevation 800 m a.s.l.)”].

TYPE MATERIAL.— HOLOTYPE: Zoological Museum of the Lomonosov Moscow University (ZMMU) A-4944. PARATYPES: ZMMU A-4858–59. Original designations.

DEFINITION.— Small, adult female 23.4 mm SVL ($n = 1$), adult males 27.9–30.4 mm SVL ($n = 5$); head moderately long 28–32 % HeadL/SVL; head wider than long 105–122 % HeadW/HeadL; naris closer to snout than to eye 59–68 % NarEye/SnEye; eye moderately large 35–42 % EyeD/HeadL; tympanum visible and smaller than eye 55–77 % Tymp/EyeD; slender moderately long forelimb NA % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb slender and moderate length 129–140 % HndLL/SVL, 40–43 % CrusL/SVL, and 89–98 % CrusL/ThghL; hindfoot well developed 77–96 % HndfL/CrusL.

Vomerine teeth absence; three palatal folds, vomerine one continuous, postorbital short and low, buccal continuous and crenulated; tongue rounded free end. Skin on margin of mandible with longitudinal series of short triangular spines in males.

Fingers rudimentary webbing; lengths 3>2>4>1; tips rounded and not dilated; subarticular subarticular tubercles distinct, round, and one on digits 1, 2, 4, and two on 3; one large oval palmar tubercle on outer half of palm, bordered distally by four small, round tubercles; smooth nuptial excrescences on base of fingers 2 and 3; fine-spined asperities dorsally covering fingers 2, 3, and 4 from base to end of penultimate phalanx. Toes modestly webbed not extending beyond proximal subarticular tubercles of toe 4, lengths 4>3>5>2>1; tips rounded, not dilated; subarticular tubercles moderate, oval and one on digits 1, 2, two on 3, three on 4, two on 5 (only distal one prominent); moderate oval inner and small, round outer metatarsal tubercles.

In life, dorsum ranging from dark brown at night to diurnal pinkish beige with faint darker reticulation from between eyes to end of trunk and reverse Y-mark with base on crown and nape and arms extending to rear of trunk; body; narrow, orangish dorsolateral stripe from tip of snout and edge of canthus rostralis above eye running diagonally to mid inguina, bordered below by dark brown that fades ventrolaterally; small round, black inguinal spot, not light edged; venter pale yellowish-pink, chin to mid chest with dark marking, belly largely immaculate.

ETYMOLOGY.— Because this species was only discovered by the males' vocalization from hollow bamboo stems, the authors highlight this behavior with Greek *cryptos* for hidden or mystery and *phonus*, voice, thus hidden voice.

DISTRIBUTION.— Vietnam. *Kalophrynus cryptophonus* is known only from the vicinity of the type locality.

NATURAL HISTORY.— This sticky frog lives in a mid-montane evergreen tropical forest (secondary) with abundant bamboo clumps. It was discovered in mid April by the males' vocalization from inside cut bamboo stems. The water inside the bamboo stems serve as egg-deposition and larval development sites (phytotelm breeding).

COMMENTS.— Preceding information extracted from the original description by Vassilieva and colleagues (2014).

Kalophrynus eok Das and Haas, 2003

Eok Sticky Frog

Kalophrynus eok Das and Haas, 2003, *Raffles Bulletin of Zoology* 51:110 [type locality: "Long Re (03°42'2"N; 115°32'06"E), east of Bario along forest trail to Kalimantan border, Sarawak, East Malaysia (Borneo)"].

TYPE MATERIAL.— HOLOTYPE: Sarawak Biodiversity Centre Zoological Museum A.00310, by original designation.

DEFINITION.— Small, known from single adult male 26.3 mm SVL; head moderate length 20 % HeadL/SVL; head wider than long 132 % HeadW/HeadL; naris closer to snout than to eye 78 % NarEye/SnEye; eye large 55 % EyeD/HeadL; tympanum visible and smaller than eye 62 % Tymp/EyeD; with exception of CrusL, limb measurements not reported, 44.8 % CrusL/SVL.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue size and shape not reported.

Fingers with slight basal web; lengths 3>2>1>4; tips rounded and not dilated; subarticular tubercles distinct, round, and one on digits 1, 2, 4, and two on 3; one large palmar tubercle on outer half of palm, bordered distally by four small, round tubercles; smooth nuptial pad on base of fingers 2 and 3. Toes lightly webbed not extending beyond proximal subarticular tubercles of toe 4, lengths 4>3>5>2>1; tips rounded, not dilated; subarticular tubercles large, round and one on digits 1, 2, two on 3, 5, and three on 4; round inner and outer metatarsal tubercles.

In life, dorsum brick-red with brown interorbital bar, brown inverted V-shaped mark on posterior head to suprascapular area, and brown traverse bar at midbody; no inguinal ocelli; lores and temporal area to axilla dark brown, trunk side reddish brown; venter pinkish white, sides of throat light red, scattered white spots of chest and anterior belly.

ETYMOLOGY.— This small frog lives in the Kelabit language area of Borneo, and the Kelabit word *eok* meaning tiny.

DISTRIBUTION.— Borneo, Sarawak. This species is known currently only from the vicinity of the type locality.

NATURAL HISTORY.— The only known specimen is a male that was discovered calling from a water-filled node of a fallen bamboo trunk in primary submontane evergreen forest.

COMMENTS.— Preceding information extracted from Das and Haas (2003) and Frost (2014).

Kalophrynus heterochirus Boulenger, 1900

Short-fingered Sticky Frog

Calophrynus heterochirus Boulenger, 1900, *Proceedings of the Zoological Society, London* 1900:186 [type locality: “Borneo (no precise locality)”].

TYPE MATERIAL.— HOLOTYPE: Sarawak Museum according to the original description. Parker (1934) reported BMNH 1909.8.18.6–7 (now 1947.2.11.38–41) as syntypes; see Comments.

DEFINITION.— Small to medium size, adult females 30.5–32.9 mm SVL ($n = 6$), adult males 24.1–27.2 mm SVL ($n = 10$); head moderately long NA % HeadL/SVL; head slightly wider than long NA % HeadW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible and smaller than eye ~50 % Tymp/EyeD; slender forelimb NA % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb moderately slender NA % HndIL/SVL, NA % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth presence or absence not reported; vomerine fold transverse interrupted medially, morphology of others not reported; tongue large and ovate.

Fingers not webbed; lengths 3>2>1>4, fourth nub-like; tips rounded and not dilated; subarticular tubercles present, shape and numbers on digits not reported; fleshy palmar tubercle, size and shape not reported. Toes one-third webbed, web extending to distal subarticular tubercle of toe 3, lengths 4>3>5>2>1; tips rounded, not dilated; subarticular tubercles present, number and shapes not reported, except none of fifth; inner and outer metatarsal tubercles poorly developed.

Color in life, dorsum purplish brown and largely immaculate, no inguinal ocelli, rather one or more bluish white spots; narrow white stripe extending from canthus rostralis above eye and tympanum diagonally to mid inguina; venter whitish immaculate or variously dusky on throat and anterior chest.

ETYMOLOGY.— Boulenger did not explain his selection of *heterochirus*. The Greek *heteros* for other or different and *cheir* for hand, i.e., different hand, likely to highlight the small, nub-like fourth finger of this species.

DISTRIBUTION.— Borneo. Inger (1966) reports it from western Sarawak and northeastern West Kalimantan.

NATURAL HISTORY.— All *K. heterochirus* have been found on the floor of hilly primary forest.

COMMENTS.— Preceding information extracted from Boulenger (1900), Smith (1922), and Inger (1966). Parker's (1934) listing of syntypes in The Natural History Museum, London (= BMNH) is in error. Boulenger (1900) specifically stated "Type in Sarawak Museum." thereby indicating only a single type. Additionally, no one has demonstrated that the type and other specimens were transferred from Sarawak to London.

***Kalophrynus honbaensis* Vassilieva, Galoyan, Gogoleva, and Poyarkov, 2014**

Hon Bao Sticky Frog

Kalophrynus honbaensis Vassilieva, Galoyan, Gogoleva, and Poyarkov, 2014, *Zootaxa* 3769(3):422 [type locality: "vicinity of the Yersin station on Hon Ba Mountain, Hon Ba Nature Reserve, Cam Lam District, Khanh Hoa Province, Vietnam (coordinates 12°07'16"N, 108°56'55"E, elevation 1500 m a.s.l.)"].

TYPE MATERIAL.— HOLOTYPE: Zoological Museum of the Lomonosov Moscow University (ZMMU) A-4941. PARATYPE: ZMMU A-4943.

DEFINITION.— Small to medium size, adult males 26.7–36.8 mm SVL ($n = 2$); head moderately long 30–32 % HeadL/SVL; head wider than long 122–129 % HeadW/HeadL; naris closer to snout than to eye 62–71 % NarEye/SnEye; eye moderately large 34–37 % EyeD/HeadL; tympanum visible and smaller than eye 76–78 % Tymp/EyeD; slender moderately long forelimb NA % Forarm/SVL and forearm to crus length NA % Forarm/ CrusL; hindlimb slender, moderately long 129–135 % HndLL/SVL, 39 % CrusL/SVL, and 95–97 % CrusL/ThghL; hindfoot well developed 86–99 % HndfL/ CrusL.

Vomerine teeth absence; three palatal folds, vomerine one indistinct, postorbital small and smooth, buccal continuous and crenulated; tongue with rounded free end. Skin on margin of mandible smooth in males.

Fingers basal webbing; lengths 3>2>4>1; tips rounded and not dilated; subarticular tubercles prominent, round, and one on digits 1, 2, 4, and two on 3; one small oval palmar tubercle on outer half of palm, bordered distally by four small, round tubercles; smooth nuptial excrescences on base of fingers 2 and 3; no nuptial pad on dorsal surface of hand. Toes modestly webbed not extending beyond proximal subarticular tubercles of toe 4, lengths 4>3>5>2>1; tips rounded, slightly dilated; subarticular tubercles moderate, oval and one on digits 1, 2, two on 3, three on 4, two on 5 (only distal one prominent); moderate oval inner and small, round outer metatarsal tubercles.

In life, dorsum orangish yellow and immaculate, except for inguinal spot; body; dark brown laterally from snout through loris above tympanum onto trunk narrowing at midtrunk and ending before inguina; ventrolaterally fading to yellowish pink of venter; small round, black inguinal spot with faint light border; venter pale yellowish-pink, chin to mid chest dusky, belly largely immaculate.

ETYMOLOGY.— The specific name derives from its presence in the Hon Ba Mountains.

DISTRIBUTION.— Vietnam. Known only from the type locality.

NATURAL HISTORY.— *Kalophrynus honbaensis* was found on the ground in a small patch of montane evergreen forest.

COMMENTS.— Preceding information extracted from Vassilieva et al. (2014).

Kalophrynus interlineatus* (Blyth, 1855)*Striped Sticky Frog**

Figures 7, 11C.

Engystoma (?) *interlineatum* Blyth, 1855, *Journal of the Asiatic Society of Bengal* [1854] 23:732 [type locality: "Pegu", Myanmar; see Comments below].

TYPE MATERIAL.—LECTOTYPE: Natural History Museum United Kingdom, formerly British Museum of Natural History 68.4.3.128, recataloged as 1947.2.31.26. PARALECTOTYPE: NHMUK/BMNH 68.4.3. 129, recataloged as 1947.2.31. 27. See discussion on the assignment of type specimens in the Comments section below.

DESCRIPTION AND INTRAPOPULATIONAL VARIATION. Moderate-sized adults, not sexually dimorphic although females average larger (mean 41.5, 35.0–46.4 mm SVL) than males (39.2, 33.7–44.6 mm). These differences are reflected in the other measurements: HeadL 11.2–15.3 mm ♀♀, 10.3–13.4 mm ♂♂; HeadW 12.7–15.1 mm ♀♀, 11.3–13.5 mm ♂♂; SnEye 4.3–5.7 mm ♀♀, 3.8–5.3 mm ♂♂; NarEye 2.8–3.7 mm ♀♀, 2.3–3.8 mm ♂♂; EyeD 3.6–4.5 mm ♀♀, 3.4–4.5 mm ♂♂; Tymp 3.1–3.8 mm ♀♀, 2.6–3.5 mm ♂♂; ForarmL 9.0–13.2 mm ♀♀, 8.7–12.2 mm ♂♂; HandL 8.4–11.3 mm ♀♀, 7.7–10.0 mm ♂♂; ThghL 13.7–18.6 mm ♀♀, 14.1–17.7 mm ♂♂; CrusL 13.0–16.2 mm ♀♀, 12.0–15.6 mm ♂♂; TarsL 8.5–10.4 mm ♀♀, 7.9–10.8 mm ♂♂; HndfL 13.0–16.6 mm ♀♀, 11.7–15.8 mm ♂♂. Body proportion means differ between females and males, although not greatly so (all values are percent): HeadL/SVL 29–36 ♀♀, 28–31 ♂♂; HeadW/SVL 31–36 ♀♀, 29–36 ♂♂; HeadW/HeadL 95–11 ♀♀, 95–116 ♂♂; SnEye/HeadL 36–41 ♀♀, 36–45 ♂♂; NarEye/SnEye 56–66 ♀♀, 54–78 ♂♂; EyeD/HeadL 28–36 ♀♀, 30–37 ♂♂; Tymp/EyeD 72–100 ♀♀, 71–79 ♂♂; Forarm/SVL 25–31 ♀♀, 24–31 ♂♂; Forarm/CrusL 69–83 ♀♀, 65–86 ♂♂; HndfL/SVL 127–147 ♀♀, 122–148 ♂♂; CrusL/SVL 34–40 ♀♀, 30–39 ♂♂; CrusL/ThghL 83–95 ♀♀, 81–96 ♂♂; TarsL/ThghL 51–62 ♀♀, 53–63 ♂♂; HndfL/SVL 30–40 ♀♀, 30–40 ♂♂; HndfL/ThghL 84–95 ♀♀, 80–93 ♂♂.

I noted earlier in the Morphometric section that the Tanintharyi sample displayed no significant sexual dimorphism and that females were significantly larger in the SE Asia sample. When the samples are combined, the overall size dimorphism declines, although a few traits remain dimorphic. Females have larger heads than males; HeadL, HeadW, and SnEye average larger, but none of the other head metrics do, and there are no proportional differences in the head or body metrics. There is strong dimorphism in ForarmL and HndfL with females being larger in both.

In their amphibian atlas, Fei et al. (2010) reported Chinese males as 32–38 mm SVL and females to 40 mm. These adult lengths are smaller, likely significantly so, than my sample which is comprised of frogs from more southern locations. Karsen et al. (1986) did not give a range or mean for Hong Kong *K. interlineatus* and his “up to 6 cm long”, contrasts sharply with Fei’s lengths and is much larger than the maximum SVL in our sample or that reported for this species elsewhere. Bourret (1942) gave single value adult sizes of 38 mm SVL for males and 44 mm for females. Berry (1975) gave total lengths of Peninsular Malaysia *K. interlineatus* as 47–58 mm. I interpret his total length as SVL, hence his size data are greater than the range for my Tanintharyi and Thai-Indochina samples and more closely match the size of *K. meizon*. Although I do not reject his data, I am uncertain how to interpret it and have not included his values in Table 3. Manthey and Grossmann (1997), in contrast, gave 35–41 mm SVL for males and 38–46 mm for females from Peninsular Malaysia, matching my adult size range for the Tanintharyi and Thai-Indochina samples. A more recent study of Malaysian *K. interlineatus* (Chan et al, 2011) reported 33.7–38.1 mm SVL for adult males ($n = 7$) and 41.1–47.3 mm SVL for adult females ($n = 10$); these values also match my values for the more northern Thai-Indochinese sample.

Tongue is broadly obovate, posterior edge smooth; vomerine teeth are absent; palatal fold mor-

phology appears relatively uniform among individuals although these data are not quantified. Vomerine folds are smooth-edged flaps, one adjacent to each choanae and widely separated from its opposite. Postorbital folds are more variable; in *Tanintharyi* frogs, a pair of folds is separated on the midline, and each side has two or three. Variation in the Thai and Indochina frogs is described in the morphology section. Buccal fold is a continuous lobular fold with abutting lobes and each lobe a low, round-edged rectangle. See Fei et al. (2005) for an illustration of the buccal cavity of a Chinese *K. interlineatus*.

Fingers lack webbing. Both finger and toe tips are bluntly rounded. Subarticular tubercle are well developed on the digits; only third finger bears a subarticular tubercle on free portion of digit; all fingers have a tubercle at their base and another row between a large, circular, nearly medial outer palmar tubercle. For the hindfoot, each toe has a basal subarticular tubercle, third and fifth toes have an addition tubercle on free portion of digit, two tubercles on fourth toe. Inner and outer metatarsal tubercles are present; inner is large, nearly circular to elliptical; outer small to nearly absent and circular. Toes modestly webbed WebIII2 median 2.0 (1.0–3.0), WebIV1 1.0 (0.5–2.0). Digit lengths nearly constant for fore- and hindfeet; finger formula $3>2\approx 1>4$; toe formula $4>3>5>2>1$.

Color pattern variation statistics for entire sample of juve-

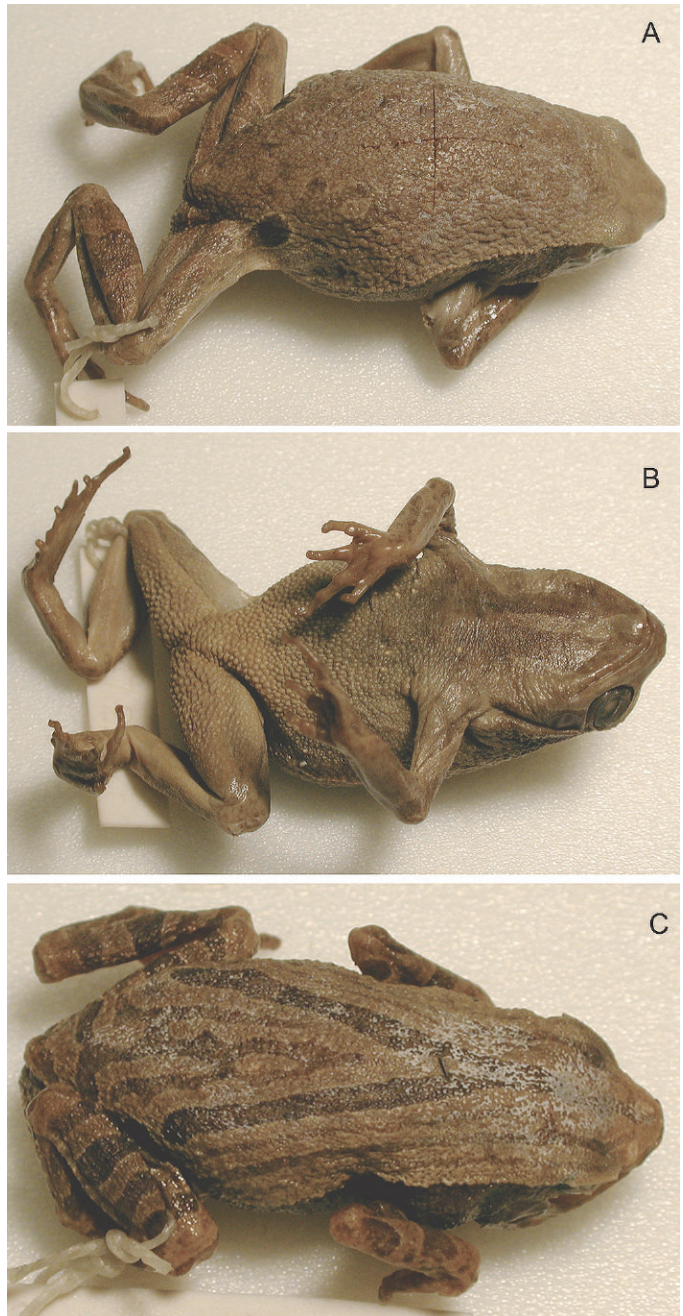


FIGURE 7. Images of lectotype of *Kalophrynus interlineatus* (NHMUK/BMNH 1947. 2.31.26, female) in (A) dorsal and (B) ventral views, and of paralectotype (NHMUK/BMNH 1947. 2.31.27, male) in (C) dorsal view [photographer G.R. Zug].

nile and adults are (median and range): HeadMid 1, 0–2; HeadPsag 0, 0–2; DorsNap 1, 0–2; DorsPsag 1, 0–2; IngSpt 2, 0–2; HndlBr 2, 0–2; DlatSt 2, 1–2; Loreal 2, 0–2; LatTrnk 2, 0–2; Chin 2, 0–2; Chest 1, 0–2. In summary, *K. interlineatus* usually has a faded to distinct middorsal stripe and no parasagittal stripes on head, distinct nape stripe in about half of the individuals continuing into bilateral (parasagittal) stripes, inguinal spot almost always present and usually as ocelli, dorsolateral narrow white stripe rarely absent or indistinct, hindlimbs almost always distinctly barred, loreal area and lateral trunk usually uniformly dark, chin and throat always dusky and usually with pair of darker longitudinal bars, and chest commonly dusky. Dorsal ground color is variable, ranging from a light beige or tan to medium or rufous brown, occasional individuals are rose to pink; sides from lore to inguinal are usually shades of medium to dark brown.

Fei et al. (2010) provided color images of five living individuals whose dorsal coloration ranged from unicolor [$n = 1$ individual] to strongly patterned with all six of my dorsal pattern characters strongly developed [$n = 5$]. The dorsal stripe pattern of Chinese *K. interlineatus* has the same layout/arrangement; however, the stripes differ markedly in being broader with strongly scalloped edges and fragmented, especially the DorsPsag ones. Karsen et al. (1986) pictured a Hong Kong striped individual that matched those of Fei et al. Additionally Fei's photographs showed well-developed white dorsolateral stripes that were strongly speculate in all individuals. The single individual depicted for Cambodia (Thy and Holden 2008) had a well-developed dorsal pattern similar to the western populations, although the white dorsolateral stripe was narrow and appeared interrupted. Ohler and Grosjean (2005) reported distinct pattern difference between "western" and Vietnamese frogs. The former depicted by a Laos individual (O&G 2005: figs. 1a,c,e) has straight-edged dorsal stripes, the latter (2005: figs. 1b,d,f) has the scalloped and fragmented stripes of the Chinese individuals. The preceding summary confirms Ohler's and Grosjean's observations of color pattern differences between west (Thailand) and east (Vietnam) and, as they noted, hints at the possibility of speciation between eastern and western populations. Chan and collaborators (2011) noted that half of their sample of Malaysian *K. interlineatus* (= their *pleurostigma*) lacked inguinal spots on one or both sides and concluded that "populations in Peninsular Malaysia are not conspecific" with mainland Asia populations. Their interpretation may be correct, although I suspect that there is no genetic discontinuity between these Malaysian population and those of peninsular Myanmar and Thailand.

ETYMOLOGY.— Blyth (1855) offered no explanation for his name, presumably using *interlineatus* to note the longitudinal lines on the dorsum, hence a derivation from the Latin *inter*, between, and *lineatus*, from Latin *lineo*, drawing lines, and *linearis*, *lineatus*, of a line, linear.

DISTRIBUTION.— *Kalophrynus interlineatus* as here defined has the broadest geographic range of the *pleurostigma* group, extending eastward from northern-most Peninsular Myanmar, eastward through northern Thailand, Laos, Cambodia, and Vietnam, southward through Peninsula Malaysia, and also in southern China from southeastern Yunnan to Hong Kong and adjacent Guangdong.

Bourret's (1942) concept of *K. interlineatus* was as a subspecies with a northern distribution from Myanmar through northern Thailand to Vietnam and adjacent China to Hong Kong. He had only a single male specimen (38 mm SVL) of questionable locality (probably Tonkin, Vietnam) in Indochina. He listed four Burmese localities: Bhamo, Teinzo, Palon, Toungo (credited to Oates [Toungo] and Fea [diverse localities]). The first two records are potential localities for *K. anya*, the latter two are potential localities for *K. interlineatus*. Toungo (= Taungo, 20°56'N 95°24'E) is in the upper Sittaung River valley. MNHN 1893.492 is identified as *Kalophrynus interlineatus* from Palon; I did not examine this specimen to confirm its presence or identification. Palon (7°41'N 97°31'E), Kayin State, is identified as a Pegu locality in the British natural history museum spec-

imen register but represented by only one gecko and one *Micryletta inornata*. This record highlights the broad geographic concept of Pegu by the British in late 19th century.

Thy and Holden (2008) stated that *K. interlineatus* was a common frog and suggested that it occurred throughout Cambodia.

NATURAL HISTORY.— In Cambodia, Thy and Holden (2008) reported it as a common species living in grassland, scrub forest adjacent to villages, and deciduous forest. The recent Burmese individuals derived from the soil surface in mixed deciduous-evergreen secondary growth forest (Mon) and from evergreen forest abutting a clear-cut (weedy) pipeline (Tanintharyi).

COMMENTS.— The type locality “Pegu” is commonly interpreted by biologists as equivalent to the present Myanmar division of Bago (formerly called Pegu). Nineteenth century Pegu encompassed a much broader area than the present political division. The older Pegu encompassed the area from the Arkan (roughly equivalent to the present state of Rakhine) eastward to the Sittang River drainage. This broad Pegu likely encompassed northernmost Mon State, hence my placement of the type locality straddling the Bago-Mon border. This broad Pegu is emphasized by a NHMUK/BMNH specimen from Palon, Kayin state, that was geographically labeled as Pegu.

Ohler and Grosjean (2005) reported examining the holotype of *Engystoma interlineatum* Blyth, a specimen (ZSI 9853) from Mergui, Myanmar. The British Museum has two specimens (NHMUK/BMNH 68.4.3.128–129, recataloged as 1947.2.31.26–27, an adult female and male, respectively) collected by Theobald in Pegu. I believe that the latter two Pegu specimens of Theobald’s (Fig. 7) are the individuals on which Blyth based his description of *interlineatum*, and they were subsequently sent to London. The precision of ZSI locality indicates that someone arbitrarily selected a *Kalophrynus* specimen and designated it as a ZSI holotype. Mergui was never recognized as part of Pegu and is in Tenasserim. Because both Blyth (1855:720) and Theobald (1882:192) specifically noted having two specimens, I recommend recognizing one of them as a lectotype and select BMNH 1947.2.31.26, the female, because this specimen is presently in the best physical condition. BMNH 1947.2.31.27 is then a paralectotype. Because Pegu is not sufficiently delimited, I recommend a more precise, yet not overly restrictive, type locality: Bago Division-Mon State border in the lower Sittaung River valley, Myanmar (~17°35’24”N 96°53’33”E).

Kalophrynus intermedius Inger, 1966

Mengiong Sticky Frog

Kalophrynus intermedius Inger, 1966, *Fieldiana, Zoology* 52:131 [type locality: “Nanga Tekalit, Mengiong River, Third Division, Sarawak”, Malaysia (Borneo)].

TYPE MATERIAL.— HOLOTYPE: Field Museum of Natural History 139348. PARATYPES: FMNH 138070, 144298. By original designation.

DEFINITION.— Medium size, adult females 37.9–40.5 mm SVL ($n = 2$), no males known; head moderately long NA % HeadL/SVL; head wider than long NA % HeadW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible and smaller than eye ~66 % Tymp/EyeD; slender moderately long forelimb NA % Forarm/SVL and forearm to crus length NA % Forarm/ CrusL; hindlimb moderately long NA % HndIL/SVL, 38–41 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/ CrusL.

Vomerine teeth, presence or absence not reported; palatal fold morphology, vomerine fold not described, postorbital fold short and notched medially, and buccal fold long and crenulated; tongue size and shape not reported.

Fingers not webbed; lengths 3>2>1>4, fourth nub-like; tips rounded, not dilated; subarticular tubercles present, shape and numbers on digits not reported; fleshy palmar tubercle, size and shape

not reported. Toes two-thirds webbed, web extending to distal subarticular tubercle of toe 3 and between proximal and middle tubercle of toe 4, lengths $4 > 3 > 5 > 2 > 1$; tips rounded, not dilated; subarticular tubercles present, number and shapes not reported, distinct on toes 1–4, barely visible on 5; inner and outer metatarsal tubercles poorly developed.

Color in life not known; dorsum brown to purplish brown with obscure darker markings on back, no inguinal ocelli; sides cream or yellow; venter cream, pinkish on throat and pair of dark bars on throat and scattered small dark spots on chest.

ETYMOLOGY.— The choice of the name *intermedius* was not stated, presumably it is in reference to this frog's size between that of two smaller Bornean *Kalophrynus heterochirus*, *punctatus*, and *subterrestris* and the larger *K. "pleurostigma"*.

DISTRIBUTION.— Borneo, Sarawak. Known only from the type locality.

NATURAL HISTORY.— The three known specimens were collected on the floor of primary rain forest at less than 300 m a.s.l.

COMMENTS.— Preceding information extracted from Inger (1966).

***Kalophrynus limbooliati* Matsui, Nishikawa, Belabut, Ahmad, and Yong, 2012**

Johor Tiny Sticky Frog

Kalophrynus limbooliati Matsui, Nishikawa, Belabut, Ahmad, and Yong, 2012, *Zootaxa* 3155:39 [type locality: "Gunung (= Mt.) Pulai, Kpg. (Kampung = village) Sri, Kulai, State of Johor, Peninsular Malaysia (01°36'N, 103°32'E, 457 m a.s.l.)"].

TYPE MATERIAL.— HOLOTYPE: Universiti Kebangsaan Malaysia Herpetological Collection 705. PARATYPES: Kyoto University Health & Environment 53314–315, 52061. All by original designation

DEFINITION.— Small, no adult females, adult male 26.2–28.7 mm SVL ($n = 3$); head long 32 % HeadL/SVL; head width subequal length 32–34 % HeadW/SVL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large 13–17 % EyeD/SVL; tympanum visible and smaller than eye 8–9 % Tympl/SVL; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long 129–136 % HndIL/SVL, 41–42 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed 33–36 % HndfL/SVL.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue entire, i.e., presumably end rounded and not notched.

Fingers with slight basal web; lengths $3 > 2 > 1 > 4$; tips rounded and not dilated; subarticular tubercles large, round, and two on digits 1, 2, 4, and three on 3; outer palmar tubercle fleshy and large, inner indistinct; asperities (nuptial pad) absent on hand. Toes lightly webbed to below level of proximal subarticular tubercles of toe 4, lengths $4 > 3 > 5 > 2 > 1$; tips rounded; subarticular tubercles variously developed, none on digit 5, one on 1, 2, two on 3, and three on 4, tubercles prominent only on fourth toe (distal and middle one); large, oval inner metatarsal tubercle, indistinct outer tubercle.

In life, dorsum variable from light orange brown to dark brown with obscure darker hourglass mark from interorbital to shoulders and scattered small dark spots posteriorly on trunk; light colored narrow stripe from tip of snout above eye and tympanum, then diagonally to mid inguina; dark inguinal spot without light border; loris and temporal area to axilla dark brown, trunk side as dorsum; venter pinkish gray with scattered white spots.

ETYMOLOGY.— The specific name honors Dr. Lim Boo Liat, a pioneer of field zoology in Malaysia.

DISTRIBUTION.— Southern Peninsular Malaysia (Johor, Negeri Sembilan, and possibly Pahang but unconfirmed) and Singapore.

NATURAL HISTORY.— *Kalophrynus limbooliati* is a forest-floor resident in a variety of forests, secondary broad-leaved and bamboo. Males call from beneath leaf litter.

COMMENTS.— Preceding information extracted from Matsui et al. (2012).

***Kalophrynus meizon* Zug, sp. nov.**

Borneo Big Sticky Frog

Figures 8, 11D.

TYPE MATERIAL.— **HOLOTYPE:** Field Museum of Natural History 267881, adult male from Samarakan Nursery (2°56'N 113°05'E), Bintulu Division, Sarawak, collected by Robert F. Inger on 29 Nov 2004 (Fig. 8). **PARATYPES:** FMNH 267873, 267875–880, same locality as holotype; FMNH 269668–670, 269673, 269675 Sg Mina, Kakus District, Sarawak; 273260–262 same locality as holotype; FMNH 273264, 273266 Penyaria, Bintulu Division, Sarawak; USNM 197671 (formerly FMNH 157676) Tabua Camp on Sungei Pesu, Bintulu District, Sarawak.

DEFINITION.— Adult *K. meizon* can be distinguished from all congeners by the following combination of characters: size dimorphic, adults female 48–60 mm, males 44–50 mm SVL; proportion not dimorphic (except for TarsL/ThghL and HndIL/SVL; females smaller), HeadL/SVL 29–35 %; tympanum about equal eye diameter, Tymp/EyeD 84–112 %; moderately long hindlimbs, HndIL/SVL 136–157 %; short hindfoot, HndfL/ThghL 71–87 %; strong supratympanic ridge dorsoposteriorly overhanging tympanic annulus; paired vomerine folds, each broad smoothly undulatory with narrow medial separation; single postorbital fold of broad undulatory lobes; single broad buccal fold comprised of numerous abutting short blunt lobes; forefeet without webbing; hindfeet moderately webbed, highest between 3rd and 4th toe, usually to base of 2nd subarticular tubercle of 4th toe; head without median head stripe (HeadMid 0 %) uncommonly with parasagittal ones (HeadPsg 11 % present) and DorsNap (11 % present); chin seldom with paired, broad longitudinal bars; hindlimbs (HndlBr) weakly or inconspicuously barred (50 %) and commonly (>50 %) with light horizontal stripe on rear of thighs.

DESCRIPTION OF THE HOLOTYPE.— Moderately robust-bodied male (47.5 mm SVL) with well-developed, moderate-length fore- and hindlimbs (51 % ForarmL+HandL/SVL, 147 % HndIL/SVL); head ovate (33 % HeadL/SVL, 30 % HeadW/SVL) and continuous with body (no apparent constriction or enlargement at juncture of head and trunk). Body measurements are: HeadL 15.8 mm; HeadW 14.2 mm; SnEye 6.2 mm; NarEye 3.4 mm; EyeD 4.1 mm; Tymp 3.7 mm; ForarmL 13.2 mm; HandL 11.0 mm; ThghL 22.7 mm; CrusL 17.9 mm; TarsL 11.9 mm; HndfL 17.2 mm. Eye distinctly larger than tympanum.

Skin strongly glandular with dorsal skin thickened and cloak-like extending from nape to posterior end of trunk, surface with numerous small white conical spines in adult males; skin thickest anteriorly forming distinct supratympanic fold over dorsal and posterior edge of tympanic annulus and swollen mass above axilla; distinct diagonal dorsolateral ridge from eye to inguina, below cloak merges imperceptibly into lateral trunk skin; limbs without enlarged glandular areas and surface mostly smooth; chest skin smooth, abdominal skin glandular and pebble-like; chest without small unpigmented glands. Nuptial pad of dense fine spines on bases second and third fingers. Tongue large, spatulate, posterior one half free. Vomerine teeth absent. Three sets of palatal folds on roof of mouth: vomerine paired, each long with low smooth free edge and narrowly separated medially; postorbital single, continuous, composed of 10 to 12 rectangular lobes; buccal slightly lower than postorbital and single continuous fold of 15 to 16 rectangular, abutting lobes, medial lobes larger than lateral ones. Fingers and toes well-developed and tips bluntly rounded; hand web

free; asperities dorsally on base of second and third fingers; foot moderately webbed (WebIII.2 = 2.5, WebIV.1 = 1.5). Subarticular tubercles well-developed on hand and foot; large, elliptical palmar tubercle with moderately large tubercle at base of each finger and only third finger with tubercle of free portion of digit; on foot, paired moderate-sized, elliptical metatarsal tubercles on edges, inner slightly smaller than outer; each toe with basal subarticular tubercle; third toe with single tubercle on free portion of digit, fourth with two tubercles, and fifth with one (hence total of two tubercles on fifth toe, both low). Digital length formulae, hand $3 > 1 \approx 2 \approx 4$, foot $4 > 3 > 5 > 2 > 1$.

Coloration in preservative (Fig. 8). Dorsum from tip of snout to between eyes uniform light brown thereafter to end of body dusky brown; dorsum largely without marking aside from numerous white spine; distinct dark centered ocelli in light brown inguinal pocket; dorsolateral ridge light brown bordered immediately below by narrow 'stripe' of dark brown quickly fading to medium brown ventrolaterally; face (loreal) dark brown at canthus rostralis, lighter brown to mouth; no banding on dorsal of thighs although light brown horizontal stripe from vent to behind knees. Venter light brown from chin to thighs, somewhat dusky from chin to base of throat; no stripes or bars on venter.

DESCRIPTION AND INTRA-POPULATIONAL VARIATION.— Large adults, strongly sexually

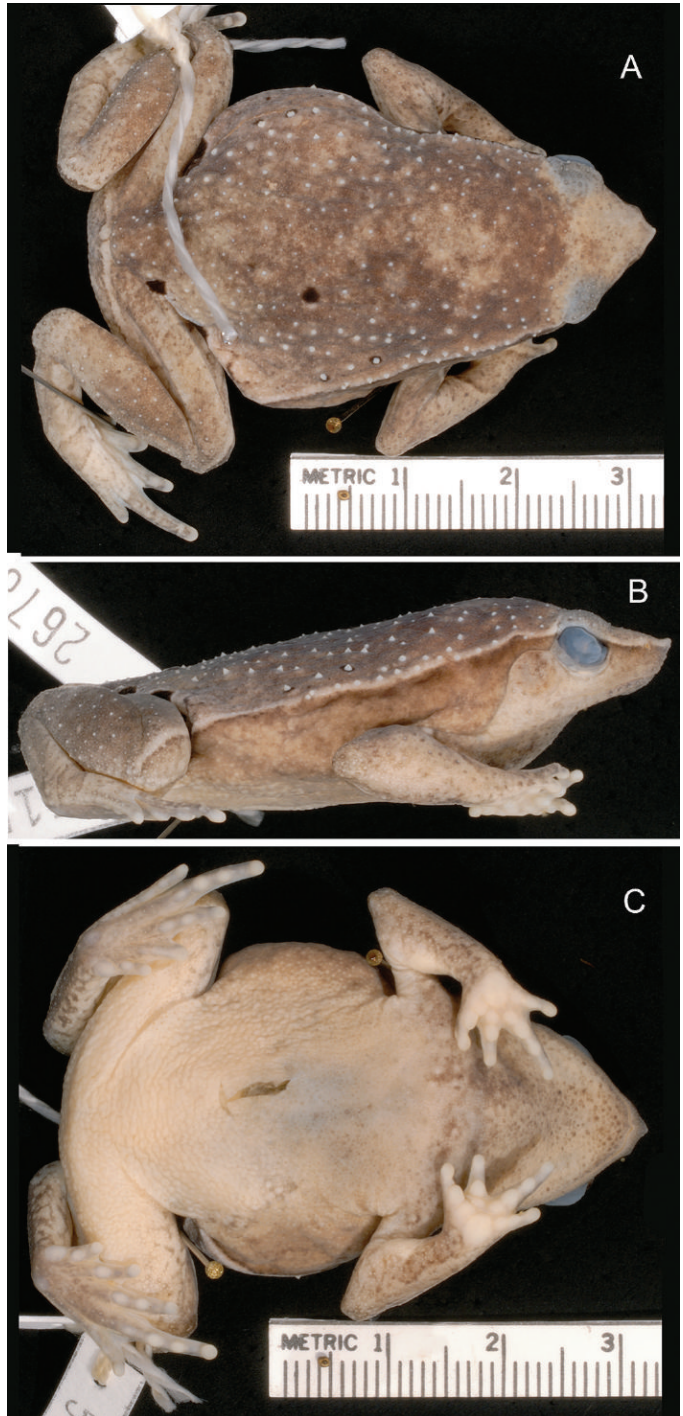


FIGURE 8. Images of holotype of *Kalophrynus meizon* (FMNH 267881, male, 47.5 mm SVL) in (A) dorsal, (B) lateral, and (C) ventral views [photographer, J.A. Poindexter].

dimorphic with females averaging larger (54.8 mm, 48.2–60.2 mm SVL) than males (45.6 mm, 44.1–47.5 mm). These size differences occur in all other measurements: HeadL 16.0–19.2 mm ♀♀, 13.4–15.8 mm ♂♂; HeadW 16.3–21.1 mm ♀♀, 14.1–16.9 mm ♂♂; SnEye 6.4–8.4 mm ♀♀, 5.1–6.2 mm ♂♂; NarEye 3.5–4.8 mm ♀♀, 5.1–6.2 mm ♂♂; EyeD 3.5–4.8 mm ♀♀, 4.0–4.9 mm ♂♂; Tymp 4.4–5.6 mm ♀♀, 3.7–4.6 mm ♂♂; ForarmL 14.9–18.3 mm ♀♀, 12.4–14.3 mm ♂♂; HandL 11.3–13.4 mm ♀♀, 10.0–11.9 mm ♂♂; ThghL 21.6–27.1 mm ♀♀, 19.8–22.7 mm ♂♂; CrusL 19.5–23.1 mm ♀♀, 17.9–19.7 mm ♂♂; TarsL 12.1–14.9 mm ♀♀, 11.4–12.5 mm ♂♂; HndfL 17.1–19.8 mm ♀♀, 15.4–18.0 mm ♂♂. Body proportions do not differ between females and males, except for TarsL/ThghL and HndfL/SVL (all values are percent): HeadL/SVL 29–35 ♀♀, 30–34 ♂♂; HeadW/SVL 31–36 ♀♀, 30–36 ♂♂; HeadW/HeadL 97–117 ♀♀, 90–108 ♂♂; SnEye/HeadL 36–46 ♀♀, 36–45 ♂♂; NarEye/SnEye 52–62 ♀♀, 53–67 ♂♂; EyeD/HeadL 27–30 ♀♀, 26–31 ♂♂; Tymp/EyeD 90–112 ♀♀, 84–105 ♂♂; Forarm/SVL 26–32 ♀♀, 26–32 ♂♂; Forarm/CrusL 66–76 ♀♀, 66–76 ♂♂; HndfL/SVL 136–157 ♀♀, 144–156 ♂♂; CrusL/SVL 38–43 ♀♀, 38–43 ♂♂; CrusL/ThghL 85–91 ♀♀, 79–93 ♂♂; TarsL/ThghL 51–59 ♀♀, 52–62 ♂♂; HndfL/SVL 31–38 ♀♀, 35–39 ♂♂; HndfL/ThghL 71–87 ♀♀, 76–83 ♂♂. The dimorphism between TarsL/ThghL and HndfL/SVL indicates that the tarsus is longer in males than in females, although the differences are significant, the proportions strongly overlap.

All individuals dorsally with thick cloak of glandular skin from behind eyes to vent; unlike other *pleurostigma* group members surface texture and dorsolateral ridge/fold are sexually dimorphic, latter distinctly elevated in males; surface dimorphic, smoothly rugose in females, spiny rugose in males. Most males, perhaps sexually active ones, have numerous small white, sharp-tipped, conical spines from nape to vent, spines more numerous on posterior third of males' trunks; in females, most individuals are spine free, when present, spines rounded (dome-shaped) and widely scattered on posterior third of trunk. Ventrally, males and females have similar surface morphology, smoothly rugose from chin to chest, abdomen large, pebble-like rugose. All adult males have asperities on bases of second and third finger, but of variable development.

Oral morphology is relatively uniform among individuals although these data are not quantified. Tongue broadly ovate, about ½ free. No vomerine teeth. Vomerine folds are elongate smooth-edged flaps, nearly in contact on midline. Postorbital folds are well developed and continuous across midline and consist of six to eight abutting rectangular lobes. Buccal fold is low continuous fold with low abutting rectangular lobes.

Fingers lack webbing. Both finger and toe tips are bluntly rounded. Subarticular tubercle are well developed on the digits; only third finger bears a subarticular tubercle on free portion of digit; all fingers have a tubercle at their base and another row between a large, elliptical to oblong, nearly medial outer palmar tubercle. Second and third fingers bear asperities on dorsal surface of distal end of the metacarpal and first phalanx. For the hindfoot, each toe has a basal subarticular tubercle, third toe with addition tubercle on free portion of digit, two tubercles on free portion of fourth toe, and fifth toe with basal and midlevel tubercles often poorly developed to nearly absent. Inner and outer metatarsal tubercles are present; inner is large, nearly circular to elliptical; outer circular and small to nearly absent. Toes moderately webbed WebIII2 median 2.0 (2.0–2.5), WebIV1 1.0 (1.0–2.0). Digit lengths nearly constant for fore- and hindfeet; finger formula 3>1≈2≈4; toe formula 4>3>5>2>1.

Color pattern variation statistics for adults are (median and range): HeadMid 0, 0–0; HeadPsag 0, 0–2; DorsNap 0, 0–1; DorsPsag 0, 0–2; IngSpt 2, 2–2; HndlBr 1, 0–2; DlatSt 2, 1–2; Loreal 1, 1–2; LatTrnk 1, 1–2; Chin 0, 0–1; Chest 0, 0–1. In preservative, most *K. meizon* are dull, muddy colored (light to moderate grayish brown) frogs from dorsal view. Most individuals are unicolor dorsally or with few widely scattered, small, dark brown spots. Dorsolateral white stripe is

well developed in all individuals and extends from snout tip above orbit to inguina, bordered below by dark brown fading to light brown ventrally. Inguinal dark-centered ocelli present in all individuals and uncommonly unilateral, smaller ocellus posteromedial to main ocellus. Venter is typically without pattern, dusky from chin through chest and light brown to cream on abdomen. Hindlimb commonly lack thigh banding and about half of individuals with horizontal light stripe continuously across rear of thighs. One individual (FMNH 267879) possesses the hourglass dorsal pattern of neotype of *K. pleurostigma*; pattern is outlined by narrow cream edge.

ETYMOLOGY.— Of the twenty-one species of *Kalophrynus*, this species has the largest average size, and the Greek adjective *meizon* for larger or greater denotes this feature.

DISTRIBUTION.— *Kalophrynus meizon* is potentially widespread in Borneo; however, the specimens or records available to me, of which I can confidently identify, indicate a predominantly northern Borneo distribution (Fig. 9) extending from northern West Kalimantan to northeastern Sabah with outlying occurrence in southern South Kalimantan.

NATURAL HISTORY.— In the Mt. Kinabalu area (Malkmus et al. 2002), this Sticky Frog occurs on the floor of primary dipterocarp forest between 500 to 800 m. Breeding males commonly vocalized from body pits beneath leaf litter or at edge of shallow, ephemeral, forest pools. Eggs are deposited in clusters and develop quickly with metamorphosis in about 16 days. Diet is principally ants although other small invertebrates are eaten.

Earlier, Inger (1966) observed that individuals occurred on the forest floor of primary forest and mainly beneath leaves. He also confirms small pools in logs and road ruts as breeding sites. Between 1984 and 2005, Inger (field data – *in litt.*, August 2013) observed more than 125 *K. meizon* at 11 field sites (340–700 m asl) in Sabah and Sarawak. The following is my summary of his data sheets. The majority (>75 %) of the frogs were found on midstream bars or tree snags in intermittent streams in primary forest. During morning searching, he and his team found ~30 % of the total frogs observed and all but few were beneath dry to moist leaf litter or other forest litter; at night, the frogs were exposed and most were sitting on the surface of the leaf litter. A few (4; ~3 % of total observations) were sitting on vegetation hanging over the stream bed, one individual at 8 m, the others at ~2 m.

COMMENTS.— Inger (1966: table 6) gave a smaller adult size for both the female (35 mm) and male (37 mm) *K. pleurostigma* from northern Borneo. It is unclear how he sexed his specimens (I suspect externally through darkened throats in male and egg-swollen abdomens in females). Although his maturity identifications are likely correct, I have retained the minimum adult size as determined by my examination of the gonads for the specimens available to me for this account, but use his broader range of sizes in Table 3.

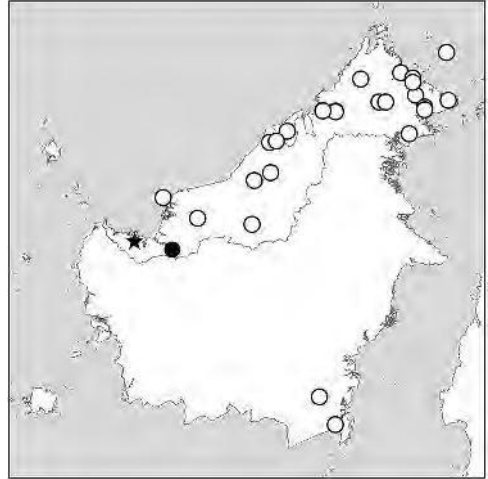


FIGURE 9. Distribution of *Kalophrynus meizon* (Borneo). Solid circle denote specimens examined in this study; open circles are literature records and museum records of specimens not examined.

Kalophrynus menglienicus* Yang and Su, 1980*Menglien Dwarf Sticky Frog**

Kalophrynus menglienicus Yang and Su, 1980, *Zoological Research, Kunming* 1:257 [type locality: “Menglien, Yunnan, altitude 1040 m”, China.]

TYPE MATERIAL.— HOLOTYPE: Kunming Institute of Zoology 751377. PARATYPES: KIZ, 32 males without number. All by original designation.

DEFINITION.— Small, no adult females, adult males 19.7– 23.4 mm SVL ($n = 16$); head long 31–33 % HeadL/SVL; head width subequal length NA % HeadW/SVL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large 14 % EyeD/SVL; tympanum visible and subequal to eye 14 % Tymp/SVL; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long 133–134 % HndIL/SVL, 44–45 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed 44–46 % HndfL/SVL.

Vomerine teeth absence; palatal fold morphology diagrammatically illustrated; tongue moderately large, oblong and rounded posteriorly.

Fingers not webbed; lengths $3 > 4 > 2 > 1$; tips rounded and not dilated; subarticular tubercles apparently present, shape and numbers on digits not reported; fleshy palmar tubercle, size and shape not reported. Toes not webbed, lengths $4 > 3 \approx 5 > 2 > 1$, first toe nub-like; tips rounded, not dilated; subarticular tubercles presence, number and shapes not reported; inner and outer metatarsal tubercles not reported.

Coloration not described. A color illustration is presented in Fei’s (1999:305) field guide to Chinese amphibians.

ETYMOLOGY.— This frog takes its specific name from its origin at Menglien.

DISTRIBUTION.— Known only from the vicinity of its type locality.

NATURAL HISTORY.— Not reported; however, I note that it is a high elevation frog.

COMMENTS.— Preceding information extracted from Yang and Su (1980). Mensural data from their table; however, owing to the column headings in Chinese, I may have misinterpreted the data.

Kalophrynus minusculus* Iskandar, 1998*Dwarf Sticky Frog**

Kalophrynus minusculus Iskandar, 1998, *The Amphibians of Java and Bali* p.53 [type locality: “Cigeunteur, Ujung Kulon, West Java”, Indonesia].

TYPE MATERIAL.— HOLOTYPE: Museum Zoologicum Bogoriense 367. PARATYPES: MZB 265–66, 375–76, MZB 2339, MZB 2924, and possibly ten other specimens not designated by museum number. All specimens by original designation.

DEFINITION.— Small, adult females to 35 mm SVL ($n = 1$), adult males to 25 mm SVL ($n = 10$); head modest length NA % HeadL/SVL; head wider than long NA % HeadW/HeadL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible and smaller than eye NA % Tymp/EyeD; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long NA % HndIL/SVL, NA % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL; limb measurements not reported.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue morphology not reported.

Hand and foot morphology not reported.

In life, dorsum brownish black with darker bands and stripes.

ETYMOLOGY.— The specific epithet *minusculus* refers to small size of adults relative to the larger *K. interlineatus-pleurostigma* frogs.

DISTRIBUTION.— This species appears to be fairly common on Peucang Island and on the mainland of Ujung Kulon National Park, Java. It is also reported to occur in southern Sumatra (Lampung Province).

NATURAL HISTORY.— *Kalophrynus minisculus* occurs only in forest at low altitudes in West Java. Females bear 30 to 50 eggs which hatch into nonfeeding tadpoles.

COMMENTS.— Preceding information extracted from Iskander (1998).

***Kalophrynus nubicola* Dring, 1983**

Blue-spotted Sticky Frog

Kalophrynus nubicola Dring, 1983, *Amphibia-Reptilia* 4:103 [type locality: “camp four 1800 m, Gunung Mulu [National Park], Fourth Division, Sarawak”, Malaysia, Borneo].

TYPE MATERIAL.— HOLOTYPE: British Museum of Natural History 1978.69. PARATYPES: BMNH 1978.66–68, 1978.1553–1558; Sarawak Museum not numbered/tagged. All by original designation.

DEFINITION.— Small, adult females 21.4–24.1 mm SVL ($n = 3$) adult male 19.3–20.1 mm SVL, sexually dimorphic in size but proportions do not differ; head modest length 30 % HeadL/SVL; head wider than long 37 % HeadW/SVL; snout moderately broad 9 % SnW/SVL; naris closer to snout than to eye 5 % NarEye/SVL; eye moderately large 12 % EyeD/SVL; tympanum indistinct and smaller than eye 40 % Tymp/EyeD; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long NA % NA % HndIL/SVL, 40 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndFL/CrusL.

Vomerine teeth presence or absence not reported; vomerine fold not reported, postorbital fold short and crenulated, buccal fold bony with fleshy crenulated edge; tongue size and shape not reported.

Fingers with weak fleshy web extending along edge of fingers as ridge; lengths $3 > 2 > 1 > 4$, fourth nub-like; tips rounded and slightly flatten; subarticular tubercles indistinct or absent; palmar tubercle indistinct or absent; no nuptial pad on hand. Toes about one-third webbed, lengths $4 > 3 \approx 5 > 2 > 1$; tips not reported; subarticular tubercles absent or single flesh pad covering length of toe; large oval inner metatarsal tubercle, outer absent.

In life, dorsum brown with faint dark mottling, yellow chevron edged with dark brown on snout in some individuals; no inguinal ocelli, occasionally with yellowish patches in groin; lores and temporal area not darker than dorsum; ventrally throat and chest orange with dark brown mottling, posteriorly belly and underside of thighs with light blue spots on brown background.

ETYMOLOGY.— The specific epithet derives from the Latin *nubicolus* for sky-dwelling and refers to its high elevation occurrence.

DISTRIBUTION.— This species occurs widely in upper slopes of Gunung Mulu, Sarawak.

NATURAL HISTORY.— *Kalophrynus nubicola* is a terrestrial frog of the high-elevation forest, oak-laurel or ericaceous. It appears to chorus only during the day.

COMMENTS.— Preceding information extracted from Dring (1983).

***Kalophrynus orangensis* Dutta, Ahmed, and Das, 2000**

Indian Striped Sticky Frog

Figure 6.

Kalophrynus orangensis Dutta, Ahmed, and Das, 2000, *Hamadryad* 25:68 [type locality: “Orang National Park (26°30'N; 92°15'E), Darrang District, Assam, north-eastern India”].

TYPE MATERIAL.— HOLOTYPE: Zoological Survey of India, Kolkata A9087. PARATYPES: ZSI A9088–91. All specimens by original designation.

DEFINITION.— Medium-sized, adult females to 35–38 mm SVL ($n = 3$), adult males 36–38 mm SVL ($n = 2$); head modest length NA % HeadL/SVL; head wider than long 118–133 % HeadW/SVL; snout moderately broad ?38–43 % SnW/HeadL; naris closer to snout than to eye NA ?72–80 % NarEye/SnEye; eye moderate ?42–44 % EyeD/HeadL; tympanum visible and nearly as large as eye ?83–94 % Tymp/SVL; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long NA % HndIL/SVL, NA % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL; limb measurements not reported. Question marks preceding data indicate uncertainty of original data.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue elongate with rounded tip.

Fingers not webbed; lengths 3>2>1>4; tips rounded and not dilated; subarticular tubercles round, one beneath fingers 1, 2 and 4, two beneath finger 3; fleshy palmar tubercle, size and shape not reported. Toes webbed at base, lengths 4>3>5>2>1; tips rounded, not dilated; large round subarticular tubercles, one of 1 and 2, two on 3 and 5, and 3 on 4; small, round inner and outer metatarsal tubercles.

In life, dorsum reddish brown to cream with dark brown reverse-Y shaped mark with base between eyes, bifurcating on nape and limbs extending diagonally to top of hindlimbs, distinct narrow white stripe from above eyes to shoulder and extending diagonally to mid inguina; black white-edged inguinal ocellus. Venter yellowish cream with black speckled throat and anterior chest.

ETYMOLOGY.— The specific name derives from the type locality, Orang National Park.

DISTRIBUTION.— (Fig. 6) Presently known from the type locality in Orang National Park (26°30'N, 92°15'E) in central Assam, India, and two other localities: West Bengal, India (Paul et al. 2007); Mymensingh, Bangladesh (Mahony and Ali Reza 2007). All three localities are within the lower middle portion of the Brahmaputra River drainage.

NATURAL HISTORY.— The individuals from the type series were found on the ground [litter] in grassland adjacent to dry deciduous forest [secondary] or among trees at forest edging on grassland. Breeding occurred in this area in June with females depositing eggs in small puddles; males called beneath vegetation overhanging these puddles. The West Bengal individual was found 60 cm high in a bush in a primary semi-evergreen forest. No habitat data are available for the Bangladesh specimen.

COMMENTS.— Preceding information extracted from Dutta et al. (2000). Question marks in the Definition indicate my uncertainty on the accuracy of the proportions.

K. orangensis is recently described and is based on five adult specimens, three females and two males. Because the variation in head striping and outer metatarsal tubercle size, the two major diagnostic features identified by Dutta et al. (2000), were encompassed in a wider sample of Thai and Vietnamese *K. interlineatus*, Ohler and Grosjean (2005) proposed that Assam and Indochinese specimens were conspecific; they thus considered *K. orangensis* a junior synonym of *K. interlineatus*. Matsui and colleagues (2009, 2011, 2012) continued to recognize *K. orangensis* as a valid species. An additional difficulty in evaluating the status of this species is presumed errors in the measurements of the head of the type series (Dutta et al. 2000: table 1; see comments in *Morphometric* subsection of the above *Morphology and Variation* section). I have not examined any specimens of this population, and even though, this taxon is poorly characterized in its original description, I hesitate to consider it a synonym without a thorough comparison. Additionally, recent molecular analyses have demonstrated considerable genetic diversity in *Kalophrynus*, hence the geographic isolation of the Indian populations likely will be matched by their genetic uniqueness.

Kalophrynus palmatissimus* Kiew, 1984*Web-footed Sticky Frog**

Kalophrynus palmatissimus Kiew, 1984b, *Malayan Nature Journal* 37:146 [type locality: “lowland dipterocarp forest at about 75 m a.s.l. at the Pasoh Forest Reserve in Negeri Sembilan”, Malaysia (Malaya).

TYPE MATERIAL.— HOLOTYPE: British Museum of Natural History 1982.1508. PARATYPES: BMNH 1982.1509–1523, FMNH two unnumbered (now 216461–462), University of Malaysia one unnumbered. All by original designation.

DEFINITION.— Medium-sized, adults 31.2–38.3 mm SVL ($n = 19$, not sexed); head moderately large 29–34 % HeadL/SVL; head slightly broader than long 102–116 % HeadW/HeadL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large 36–48 % EyeD/HeadL; tympanum visible and smaller than eye 55–70 % Tymp/EyeD; moderate length forelimb 24–28 % Forarm/SVL and forearm shorter than crus length 56–66 % Forarm/CrusL; hindlimb moderate NA % HndL/SVL, crus moderate length 41–46 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue elongate with rounded tip.

Fingers without web; lengths 3>2>1=4; tips rounded and not dilated; subarticular tubercles prominent, number beneath each finger not reported; palmar tubercle not reported. Toes strongly although not fully webbed, web between toes 3 and four to tip of 3, toe lengths 4>3>5>2>1; tips rounded; subarticular tubercles prominent on digits 1, 2, 3, 4, none beneath 5; oval inner and small indistinct outer metatarsal tubercles.

In life, dorsum light brown to reddish brown with darker brown blotch extending from between eyes and extending posteriorly and breaking into patches on trunk; no inguinal ocelli; lores and temporal area to axilla dark brown, trunk side reddish brown; venter yellowish with two faint longitudinal dusky bars on throat and gray mottling on sides and posterior of abdomen.

ETYMOLOGY.— The specific epithet *palmatissimus* refers to the strongly webbed hindfeet, the greatest amount of webbing seen in the genus *Kalophrynus*.

DISTRIBUTION.— This species is a resident of southern Peninsular Malaysia and presently known from only three localities in the provinces of Selangor, Negri Sembilan, and Johor.

NATURAL HISTORY.— *Kalophrynus palmatissimus* is a terrestrial frog of lowland dipterocarp forests. Kiew (1984) provides details on breeding and tadpole development and morphology.

COMMENTS.— Preceding information extracted from Kiew (1984), Chan et al. (2011), and Dehling (2011).

Kalophrynus pleurostigma* Tschudi, 1838*Rufous-sided Sticky Frogs**

Figures 10, 11F.

Kalophrynus pleurostigma Tschudi, 1838, *Classification der Batrachier; . . . Abteilung der Reptilien*: 86 [type locality: “Sumatra”, Indonesia]

TYPE MATERIAL.— NEOTYPE: United States National Museum 36645, an adult female from “Aru Bay, East Sumatra”, collected by Dr. W.L. Abbott on 9 December 1905. This Indonesia, Sumatra locality was identified by Lyon (1908) as “about longitude 98°15′ East, and latitude 4°10′ N”, which places it in present-day Sumatera Utara province, on the island Pulau Sembilan, NNW of Medan.

DEFINITION.— Definition is based on two specimens, a 34.5 mm SVL adult female (neotype) and a 25.4 mm juvenile male; both collected prior to 1934 and both from northeastern Sumatera Utara. Moderate sized *Kalophrynus*, adults estimated 30–36 mm SVL, sexual dimorphism unknown. Additional information is available below in the description; data for the juvenile (MCZ

A22499) are in brackets when different from neotype. *K. pleurostigma* is the smallest member of the *interlineatus-pleurostigma* group and differs from other members by the morphology of its oral folds, proportionately longer hindlimbs yet proportionately smaller hindfeet, and coloration

DESCRIPTION OF NEOTYPE.—Moderately robust-bodied female frog with well-developed, moderate-length fore- and hindlimbs; head ovate and continuous with body (no apparent constriction or enlargement at juncture of head and trunk). Body measurements are: SVL 34.5 [25.4]; HeadL 9.9 mm [8.1 mm]; HeadW 10.1 mm [7.9 mm]; SnEye 4.1 mm [3.2 mm]; NarEye 2.3 mm [2.0 mm]; EyeD 2.9 mm [2.6 mm]; Tymp 2.6 mm [2.3 mm]; ForarmL 8.9 mm, [7.1 mm]; HandL 8.5 mm [6.4 mm]; ThghL 14.7 mm [12.0 mm]; CrusL 12.7 mm [12.3 mm]; TarsL 8.3 mm [8.1 mm]; HndfL 13.2 mm [8.7]. Body proportions are (all values are percent): HeadL/SVL 29 [31]; HeadW/SVL 29 [30]; HeadW/HeadL 102 [96]; SnEye/HeadL 41 [41]; NarEye/HeadL 23 [25]; NarEye/SnEye 56 [63]; NarEye/SnEye 56 [63]; EyeD/HeadL 29 [33]; Tymp/EyeD 90 [89]; Forarm/SVL 28 [28]; Forarm/CrusL 67 [58]; HndfL/SVL 152 [162]; CrusL/SVL 41 [48]; CrusL/ThghL 81 [103]; TarsL/ThghL 52 [68]; HndfL/SVL 34 [34]; HndfL/ThghL 66 [73].

No vomerine teeth present. Tongue obovate and about half free. Palatal fold morphology is similar for the two specimens. Vomerine folds are smooth, straight-edged flaps behind choanae, each extending from labial edge of mouth to near midline, separated by short gap from its opposite fold. Postorbital fold is single, medial smooth edged fold, closely followed by broad buccal fold; this latter fold is strongly serrate. Each serration has shape of tri-crowned tooth, but there is no evidence of dentine or enamel on these closely packed ‘denticles.’

Fingers lack webbing. Both finger and toe tips are bluntly rounded. Subarticular tubercle are well developed on digits; all digits bear subarticular tubercle on proximal phalanx, third finger also with subarticular tubercle on second phalanx; large, oblong to ovate, nearly medial outer palmar tubercle; digital formula $3>2\approx 1>4$. On hindfoot, each toe has one or more subarticular tubercles, one each on first, second and fifth toes, on proximal phalanx of first two toes, on penultimate phalanx of fifth toe; two tubercles on third toe, three on fourth toe (first low and elongate). Inner and outer metatarsal tubercles are present; inner is largest, nearly circular to oval; outer small (neotype) to nearly absent (juvenile) and circular. Toes moderately webbed WebIII2 1.5 [2.5], WebIV1 1.0 [1.5]. Digit lengths for hand differ for neotype and MCZ juvenile, toe lengths same in both, formula $4>3>5>2>1$.

Skin strongly glandular with dorsal skin thickened and cloak-like extending from nape to posterior end of trunk, light granular surface, thickest anteriorly forming distinct supratympanic fold over dorsal and posterior edge of tympanic annulus and swollen mass above axilla; posteriorly glandular cloak merges imperceptibly into lateral trunk skin; limbs without enlarged glandular folds; chest and abdominal skin glandular and pebble-like with scattered unpigmented ‘pebbles’ on chest.

Coloration in both is faded to near medium brown dorsum and tan venter. Juvenile (MCZ 22495) is nearly unicolor; dark inguinal spots persist with light encircling border; portions of narrow, light dorsolateral stripes remain, and face or loreal area appears nearly uniformly dark brown. Pattern is more evident in neotype (USNM 36645) although faded and does not match the longitudinal dorsal striping of other members of *interlineatus-pleurostigma* group, presumably owing to preservative induced fading. Dark centered inguinal ocelli and uniformly dark loreal area persist. Dorsally, head is unicolor; dorsally double vague hourglass-shape pattern extends from behind eyes to shoulder then repeated and more elongate from shoulders to mid-ilial area. Diagonal dorsolateral stripe and pattern on dorsal surface of hindlimbs are not evident. Venter is uniformly light grayish brown from tip of chin to end of body.

For color in life see Fig. 11F of an individual recently collected in western Sumatra; dorsum

light brown to tannish yellow, faint nape hourglass-shaped blotch, distinct white “dorsolateral stripe from tip of snout to inguinal, tan to yellow side of face, lemon yellow side of trunk, and no dark bars on top of thighs.

ETYMOLOGY.— Tschudi did not explain his choice of *pleurostigma*, although it likely refers to the inguinal or lateral (from Greek *pleura* for side, from *pleuron* for rib) spot (Greek *stigma*, for mark, brand or spot).

DISTRIBUTION.— Presently known from northeastern coastal (Sumatera Utar) and west central (Jambi) Sumatra. I assume that the GenBank *K. pleurostigma* sample (MZB A.15298) from Lampung is the same taxon as the northern populations, thus giving this species a Sumatra-wide distribution.

NATURAL HISTORY.— Not reported.

COMMENTS.— Specimens of *K. pleurostigma* are rare in collections. *K. pleurostigma* survives in Sumatra, although their abundance and actual distribution are unknown.

I tentatively identify the Javan populations as *K. pleurostigma* owing to their nearness to Sumatra, although I suspect that they represent a distinct species. The Javan occurrence relies on a single specimen from Nusa Kambangan Island (Iskandar 1998) and the report of it being a common species in Ujung Kulon National Park (Crampton 1990). Crampton

(1990) further noted that it was an abundant frog in leaf litter near water throughout Ujung Kulon, Java; the individuals observed were SVL to 35 mm. Crampton may have mistaken *K. minusculus* for *K. pleurostigma* as both have adults in the same size range.

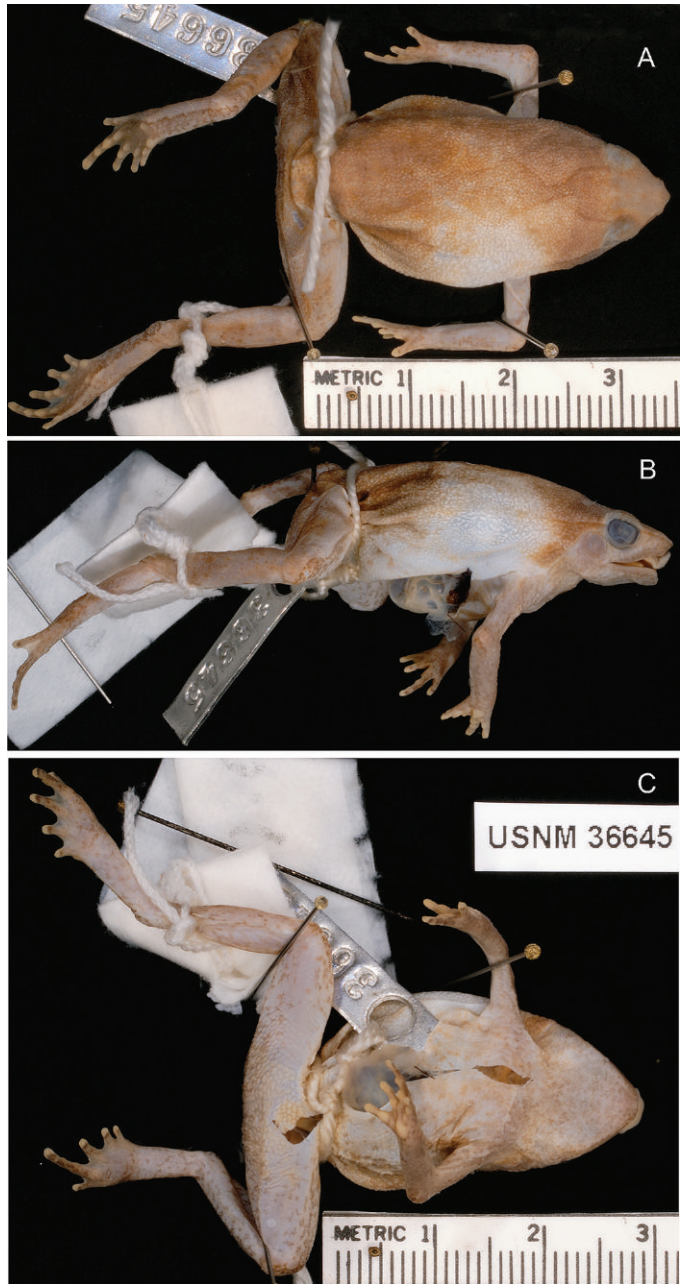


FIGURE 10. Images of neotype of *Kalophrynus pleurostigma* (USNM 36645, female, 34.5 mm SVL) in (A) dorsal, (B) lateral, and (C) ventral views [photographer, J.A. Poindexter].

Kalophrynus punctatus* Peters, 1871*Spotted Sticky Frog**

Calophrynus punctatus Peters, 1871, *Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin* 1871:579 [type locality: "Sarawak", East Malaysia (Borneo)].

TYPE MATERIAL.— HOLOTYPE: Museo Civico di Storia Naturale di Genova 29130, according to *Annali del Museo Civico di Storia Naturale di Genova*, ser. 2, 3, 69:219.

DEFINITION.— Small, adult males 22–27 mm SVL ($n = 2$); head modest length 26 % HeadL/SVL; head wider than long NA % HeadW/HeadL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible but obscured by skin and smaller than eye 50 % Tymp/EyeD; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long 137 % HndIL/SVL, NA % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue shape and size not reported.

Fingers without web; lengths $3 > 2 \approx 1 > 4$; tips rounded and not dilated; subarticular tubercles prominent, number of tubercle on each finger not reported; fleshy palmar tubercle. No asperities on dorsum of fingers. Toes lightly webbed to below level of proximal subarticular tubercles of toe 4, lengths $4 > 3 \approx 5 > 2 > 1$; tips rounded, not dilated; subarticular tubercles prominent and four on 4, not reported for toes 1, 2, 3, 5; rounded inner metatarsal tubercle and no outer one.

Dorsum reddish brown, back with or without small black spots; side of head, neck and trunk dark brown; venter pale yellowish white, chin and anterior throat with dark band, scattered black spots posteriorly.

DISTRIBUTION.— Borneo (Kalimatan and Sarawak). See comment below.

NATURAL HISTORY.— Not reported.

COMMENTS.— Preceding information extracted from Peters (1871) and predominantly from Inger (1966). Peters' description is brief and incomplete for diagnostic purposes. Inger's account is detailed and includes a second adult male that he discovered in the Rijksmuseum in Leiden. The latter specimen also had specific locality information, "Semedum," which the holotype did not.

In a 1894 report on a small herpetological collection from one of the Mentawai Islands. Boulenger identified a juvenile specimen (23 mm SVL) and declared that it closely matched Peters' description of *K. punctatus*. I believe this identification is erroneous and highly unlikely for a Borneo frog to occur in the distant Mentawai Islands.

Kalophrynus robinsoni* Smith, 1922*Pahang Mountain Sticky Frog**

Kalophrynus robinsoni Smith, 1922, *Journal of the Federated Malay States Museums* 10:280 [type locality: "Wray's camp", Pahang, Malaysia].

TYPE MATERIAL.— Holotype. BMNH 1923.5.14.29, according to R.F. Inger in Frost, 1985:383.

DEFINITION.— Small, juveniles female 18 mm SVL, males 17–18 mm SVL ($n = NA$); head modest length NA % HeadL/SVL; head width, not reported NA % HeadW/HeadL; snout short and truncate NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible and smaller than eye 66 % Tymp/EyeD; moderate length forelimb NA % Forarm/SVL and NA % Forarm/CrusL; hindlimb moderate length NA % HndIL/SVL, NA % CrusL/SVL and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth presence or absence not reported; vomerine fold V-shaped and broadly sepa-

rated on the midline, condition of postorbital fold not reported, buccal fold strong and denticulate; tongue elliptical and entire.

Fingers presumably without basal web; lengths 3>2>1>4, first and second very short, fourth nub-like; presumably tips rounded and not dilated; subarticular tubercles low and indistinct; fleshy palmar tubercle; asperities on fingers 1–3. Toes one-third webbed, lengths 4>3>5>2=1; tips bluntly pointed; subarticular tubercles low and indistinct; small oval inner and larger round outer metatarsal tubercles.

Dorsum light brown with elongated X-shaped mark, anterior arms extend to eyelids, posterior arms to groin; no inguinal ocelli; loris through side of trunk dark brown, no light dorsolateral stripe; venter yellowish with spots and speckles of brown.

ETYMOLOGY.— Malcolm Smith named the frog for Mr. Herbert Robinson, director of the Federated Malaya States Museum in appreciation for his opportunity to examine the herpetological collection made in association with a meteorological survey.

DISTRIBUTION.— Western Malaysia on side of Gunung Tahang.

NATURAL HISTORY.— Not reported.

COMMENTS.— Preceding information extracted from Smith (1922) and Dehling (2011). Smith considers the specimens to be juveniles; Dehling noted the presence of asperities on at least one of the males, thereby suggesting sexual maturity.

Kalophrynus sinensis Peters, 1867

Philippine Sticky Frog

Figure 11E.

Calophrynus pleurostigma var. *Sinensis* Peters, 1867, *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin* 1867:33 [type locality: “Hongkong”; in error; actually “Dapa, Siargao [Island]”, 9°45'39.23"N, 126°03'26.27"E, Province Surigao del Norte, Philippines]. See Comment below.

Calophrynus acutirostris Boettger 1897, *Zoologischer Anzeiger* 20:165 [type locality: “Philippinen, entweder von Culion oder von Samar”].

Kalophrynus stellatus Stejneger, 1908, *Proceedings of the United States National Museum* 33:575 [type locality: “Basilan, Philippines Islands”].

TYPE MATERIAL.— HOLOTYPE: Museum für Naturkunde, Berlin 5696, see Comments on identity and assignment of holotype.

DESCRIPTION AND INTRAPOPULATIONAL VARIATION. The following characterization derives largely from my Bohol Island sample. Moderate-sized adults, sexually dimorphic with females averaging larger (42.4, 39.4–45.7 mm SVL) than males (37.9, 34.9–41.6 mm). These size differences are reflected in the other measurements: HeadL 12.0–14.1 mm ♀♀, 10.6–12.6 mm ♂♂; HeadW 13.0–14.0 mm ♀♀, 10.6–13.7 mm ♂♂; SnEye 4.8–5.6 mm ♀♀, 4.3–5.0 mm ♂♂; NarEye 2.7–3.6 mm ♀♀, 2.2–3.2 mm ♂♂; EyeD 3.9–4.8 mm ♀♀, 3.5–4.5 mm ♂♂; Tymp 2.3–4.8 mm ♀♀, 2.7–3.9 mm ♂♂; ForarmL 10.2–13.0 mm ♀♀, 9.6–11.5 mm ♂♂; HandL 10.2–11.9 mm ♀♀, 8.8–10.9 mm ♂♂; ThghL 14.8–21.3 mm ♀♀, 15.1–19.9 mm ♂♂; CrusL 16.0–19.0 mm ♀♀, 14.9–17.8 mm ♂♂; TarsL 9.8–15.2 mm ♀♀, 9.3–11.4 mm ♂♂; HndfL 15.4–18.2 mm ♀♀, 13.2–18.6 mm ♂♂. Body proportions differences are not significantly different between adult females and males (all values are percent): HeadL/SVL 28–34 ♀♀, 29–32 ♂♂; HeadW/HeadL 98–120 ♀♀, 96–114 ♂♂; HeadW/SVL 31–35 ♀♀, 30–35 ♂♂; SnEye/HeadL 37–45 ♀♀, 37–44 ♂♂; NarEye/SnEye 52–69 ♀♀, 47–67 ♂♂; EyeD/HeadL 31–36 ♀♀, o-o ♂♂; Tymp/EyeD 55–104 ♀♀, 68–92 ♂♂; Forarm/SVL 24–30 ♀♀, 24–32 ♂♂; Forarm/CrusL 63–69 ♀♀, 55–77 ♂♂; HndfL/SVL 142–163 ♀♀, 150–170 ♂♂; CrusL/SVL 38–44 ♀♀, 39–46 ♂♂; CrusL/ThghL 77–100 ♀♀, 88–111 ♂♂; TarsL/ThghL 52–73 ♀♀, 53–74 ♂♂; HndfL/SVL 36–43 ♀♀, 37–51 ♂♂; HndfL/ThghL 80–104 ♀♀, 79–123 ♂♂.

Dorsal skin forms thick, glandular cloak from behind eyes to vent; dorsolateral ridge on trunk variously defined from smooth transition to sides to distinct ridge or fold from shoulder to inguina. Dorsal surface lightly rugose to granular rugose, latter rugosity especially evident on posterior third of trunk; no spiny tubercles although lightly pigmented dome-like tubercles common on posterior third of trunk. Ventrally surface is lightly rugose from chin to chest, abdomen large pebbly rugose; some females with numerous unpigmented short tubercles on base of neck and chest.

Vomerine teeth absent. Tongue is moderate to large, usually oblong, and posterior half to two-thirds free. Palatal fold morphology appears relatively uniform although these data are not quantified. Pair of low vomerine folds nearly in contact on midline, free edge, smooth edged and lightly undulatory; postorbital folds short, low and continuous across midline, composed of four to eight irregular width lobes; buccal fold long, medium height, continuous with 14 to 18 abutting rectangular lobes.

Fingers lack webbing. Both finger and toe tips are bluntly rounded. Subarticular tubercles are well developed on the digits; only third finger bears a subarticular tubercle on free portion of digit; all fingers have a tubercle at their base and another row between a large, circular to elliptical, nearly medial outer palmar tubercle. Second and third fingers bear asperities on dorsal surface of distal end of the metacarpal and first phalanx. For the hindfoot, each toe has a basal subarticular tubercle although often poorly developed and low on fourth toe, low or absent on fifth toe; third and fifth toes with addition tubercle on free portion of digit, two tubercles on free portion of fourth toe. Inner and outer metatarsal tubercles are present; inner is large, nearly circular to elliptical; outer small to nearly absent and circular. Toes modestly webbed WebIII2 median 2.5 (1.0–3.0), WebIV1 2.0 (1.0–3.0). Digit lengths nearly constant for fore- and hindfeet; finger formula $3 > 2 \approx 1 > 4$; toe formula $4 > 3 > 5 > 2 > 1$.

Color pattern variation statistics for entire sample of juvenile and adults are (median and range): HeadMid 0 0–1, HeadPsag 0 0–2, DorsNap 1 0–2, DorsPsag 1 0–2, IngSpt 2 0–2, HndlBr 1 0–2, DlatSt 1 0–2, Loreal 1 0–2, LatTrnk 1 0–2, Chin 1 0–2, Chest 0 0–1. In preservatives, *K. sinensis* varies from dorsally uniformly colored to well-marked pattern of longitudinal stripes. Some striped individuals have a middorsal stripe extending from snout to neck, there bifurcating; most lack middorsal snout stripe, instead have pair of medially converging diagonal stripes or reverse triangle mark on rear of head; on rear of neck stripe of triangle bifurcates as pair of narrow (usually), diverging trunk stripes; latter stripes rarely fragmented although of variable sharpness; parasagittal trunk stripes regularly present although faded; narrow, light-colored dorsolateral trunk stripe usually present, regularly faded, and narrowly edged below from eye to mid trunk by dark brown border; inguinal ocelli rarely absent, occasionally with smaller ocellus (unilateral) to rear of main ocellus. Thigh banding evident in majority of individuals. Venter in majority is light brown or tan, uniform from chin to thighs, except most individual show pair of broad, dark, longitudinal stripes on throat (usually faded, but visible).

ETYMOLOGY.— Although a Philippine species, the original (holotype) was thought to derive from China. Peters designated the species as Chinese, hence *sinensis* derives from the Latin *Sinae*, the Chinese, and used broadly in English as the prefix Sino- in the sense of Chinese or of/from China.

DISTRIBUTION.— *Kalophrynus sinensis* occurs in the southern islands of Samar, Leyte, Dinagat, Siargao, Bohol, Camiguin, Mindanao, and Basilan.

NATURAL HISTORY.— This species is a forest floor and dry stream bed denizen, hiding under the leaf and other litter during the day and foraging on the surface at night. It also breeds in small, shallow pools of water.

COMMENTS.— Bauer et al. (1996) identified a single specimen in the Berlin collection as the



FIGURE 11. Coloration of living representatives of *pleurostigma-interlineatus* group. (A) Dorsolateral view of a *K. anya* (USNM 520321) from the Chatthin Wildlife Sanctuary, Sagaing, Myanmar [photographer, C. Hansen]; (B) dorsolateral view of a *K. anya* (USNM 523966) from the Chatthin Wildlife Sanctuary, Sagaing, Myanmar [photographer, G.R. Zug]; (C) dorsolateral view of a *K. interlineatus* (CAS) from the Tanintharyi National Park, Tanintharyi, Myanmar [photographer, J.V. Vindum]; (D) dorsolateral view of a *K. meizon* (FMNH 242796) from Poring Station, Mt. Kinabulu Park, Ranau District, Sabah [photographer, R.F. Inger]; (E) dorsolateral view of a *K. sinensis* (UK 333148) from Agusan del Norte, Mindanao, Philippines [photographer, R.M. Brown]; (F) dorsolateral view of a *K. pleurostigma* (UK 333148) from Gunung Kunyit, Jambi, Sumatra [photographer, E.N. Smith].

syntype of *K. sinensis* and, based on W. Peters' handwritten note in the ZMB catalog identifying the specimen as the type and corrected the locality to "Dapa, Siargao". Ohler and Grosjean (2005) accepted the existence of two syntypes and identified the type locality as Mindanao, Philippines, based on a bottle label of a supposed syntype in the Vienna collection. I accept the interpretation of a single specimen, and it being the Berlin specimen. Either way, the correction of the syntypic

locality makes *sinensis* the senior synonym for the Philippine populations. Inger (1954) noted that the type locality of *C. acutirostris* is most likely Samar.

This study does not examine the possibility of multiple species in the Philippine Islands. Inger (1954) noted differences in toe webbing of males in samples from Basilan and Mindanao; however, a statistical test did not reveal the differences to be significant. Taylor (1921) accepted the specific status of the Basilian species *stellatus* (using his Mindanao sample for his detailed description) and Boettger's description of the Samar species *acutirostris*. He noted: "It is not improbable that *Kalophrynus stellatus* and *K. acutirostris* are merely variations of the same species."

Stejneger (1908) reported that the buccal fold was strong denticulate in his description of *K. stellatus*. My examination of the Basilian specimens available to him showed the lobes to be mostly blunt rectangular, occasionally with an irregular free edge.

Kalophrynus subterrestris Inger, 1966

Labang Sticky Frog

Kalophrynus subterrestris Inger, 1966, *Fieldiana, Zoology* 52:137 [type locality: "Sungei Seran, Labang, Bintulu District, Fourth Division, Sarawak", East Malaysia (Borneo)].

TYPE MATERIAL.— HOLOTYPE: Field Museum of Natural History 150421. PARATYPES: FMNH 140238, 154022–026, 157652–656. All by original designation.

DEFINITION.— Small, adult females 25.8–27.0 mm SVL ($n = 4$), adult males 21.0–23.4 mm SVL ($n = 6$); head moderately long NA % HeadL/SVL; head slightly wider than long NA % HeadW/HeadL; snout moderately broad NA % SnW/HeadL; naris closer to snout than to eye NA % NarEye/SnEye; eye moderately large NA % EyeD/HeadL; tympanum visible and smaller than eye 50–66 % Tymp/EyeD; moderate length forelimb NA % Forarm/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long NA % HndIL/SVL, 40–45 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed 85 % HndfL/CrusL.

Vomerine teeth presence or absence not reported; palatal fold morphology, vomerine fold not reported, postorbital fold angular and strongly notched, buccal fold crenulated; tongue size and shape not reported.

Fingers with slight basal web; lengths 3>2>1>4, fourth nub-like; tips rounded and not dilated; single subarticular tubercle between palmar tubercle and tip of finger 4, number of subarticular tubercles not reported for other fingers; fleshy palmar tubercle. Toes lightly webbed to center of distal subarticular tubercles of toe 3, lengths 4>3>5>2>1; tips rounded; conspicuous subarticular tubercles on first four toes, number not reported, none on toe 5; low inner and outer metatarsal tubercles.

In life, dorsum dark gray without darker or lighter markings; usually no light diagonal line of side or dorsolaterally on head; inguinal region with or without a dark spot, if present without light border; side of body orange in groin; venter dusky mottling anteriorly, white belly.

ETYMOLOGY.— The name *subterrestris* was selected because two individuals were discovered in burrows.

DISTRIBUTION.— This species occur broadly, if not commonly in northern Borneo (Sarawak and Sabah).

NATURAL HISTORY.— Most individuals of this species derived from the floor of primary rain forest in hillside situations, and most were found beneath the floor litter and two in long burrows.

COMMENTS.— Preceding information extracted from Inger (1966).

Kalophrynus tiomanensis* Chan, Grismer, and Grismer, 2011*Tioman Sticky Frog**

Kalophrynus tiomanensis Chan, Grismer, and Grismer, 2011, *Zootaxa*, 3123:62 [type locality: “outside Gua Tengkok Air (= Tengkok Air Cave), Gunung Kajang, Tioman Island, Pahang at 810 m elevation (2°46' 12.22"N 104°9'15.75"E)”, Western Malaysia].

TYPE MATERIAL.— HOLOTYPE: La Sierra University Herpetological Collection 5024. PARATYPES: LSUHC 4682, 5154, 5558, 6147. All by original designation.

DEFINITION.— Small, adult females 24.7–25.8 mm SVL ($n = 2$), adult males 25.8–26.3 mm SVL ($n = 2$); head moderately long 31–33 % HeadL/SVL; head slightly wider than long 104–106 % HeadW/HeadL; naris closer to snout than to eye 59–72 % NarEye/SnEye; eye moderately large 36–37 % EyeD/HeadL; tympanum visible and smaller than eye 77–79 % Tymp/EyeD; slender moderately long forelimb 29–31 % Forarm/SVL and forearm to crus length NA % Forarm/CrusL; hindlimb moderately long and forearm to crus length NA % Forarm/CrusL; hindlimb moderately long NA % HndIL/SVL, 39–40 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed NA % HndfL/CrusL.

Vomerine teeth absence; palatal fold morphology not reported; tongue size and shape not reported.

Fingers with slight basal web; lengths $3 > 2 \approx 1 > 4$; tips rounded and slightly dilated; subarticular tubercles distinct, round, and one on digits 1, 2, 4, and two on 3; one large palmar tubercle on outer half of palm, bordered distally by four small, round tubercles; smooth nuptial excrescences on base of fingers 2 and 3. Toes modestly webbed not extending to proximal subarticular tubercles of toe 4, lengths $4 > 3 > 5 > 2 > 1$; tips rounded, slightly dilated; subarticular tubercles large, round and one on digits 1, 2, two on 3, three on 4, none on 5; oval inner and no outer metatarsal tubercles.

Dorsum yellowish brown with dark brown hour-glass mark from between eyes to suprascapular area and small dark brown irregularly shaped spots from mid-trunk rearward; body; large dark brown, white-edged inguinal ocelli; loris and temporal area to axilla dark brown, fading to tan ventrally; yellowish white oblique stripe from above eye to lower inguinal area; venter light brown, chest and belly with scattered white spots.

ETYMOLOGY.— The specific epithet derives from this species type locality on Tioman Island.

DISTRIBUTION.— *Kalophrynus tiomanensis* has been found only on Gunung Kajang, Tioman Island, West Malaysia.

NATURAL HISTORY.— Like most other species of *Kalophrynus*, *K. tiomanensis* is a terrestrial frog, living mostly beneath leaf litter and foraging on the latter's surface in hill dipterocarp forests.

COMMENTS.— Preceding information extracted from Chan et al. (2011).

Kalophrynus yongi* Matsui, 2009*Cameroon Highland Sticky Frog**

Kalophrynus yongi Matsui, 2009, *Zoological Science* 26:580 [Type locality “near the top of Gunung Brinchang, 04°51'N, 101°38'E, 1954 m a.s.l., Cameron Highlands, Pahang, Peninsular Malaysia”].

TYPE MATERIAL.— HOLOTYPE: Kyoto University Humanities and Environment 15531. PARATYPES: KUHE 566, 52446. All by original designation.

DEFINITION.— Small to medium-sized, adult males 28.8–31.0 mm SVL ($n = 3$); head moderate length 29 % HeadL/SVL; head wider than long 32–33 % HeadW/SVL; snout moderately broad 7–8 % SnW/SVL; naris closer to snout than to eye 4–5 % SnNar/SVL; eye moderately large 13–14 % EyeD/SVL; tympanum visible and smaller than eye 8–9 % Tymp/SVL; moderately long and stout forelimb 65–67 % Foreleg/SVL and forearm equal crus length NA % Forarm/CrusL; hindlimb moderately long 135–148 % HndIL/SVL, 38–43 % CrusL/SVL, and NA % CrusL/ThghL; hindfoot well developed 43–47 % HndfL/SVL.

Vomerine teeth presence or absence not reported; palatal fold morphology not reported; tongue elongate with rounded tip.

Fingers with slight basal web; lengths $3 > 2 > 1 > 4$; tips rounded and not dilated; subarticular tubercles large, round, and one on digits 1, 4, two on 2, and three on 3; fleshy outer palmar tubercle and no inner one; nuptial pad with conical tubercles present; weakly developed but externally protruding spine on proximal end of humerus. Toes with weak basal webbing, lengths $4 > 3 \approx 5 > 2 > 1$; tips rounded; subarticular tubercles large, round and one on digits 1, 2, two on 3, 5, and three on 4; prominent round inner and indistinct round outer metatarsal tubercles.

In life, dorsum changes from light orangish brown to dark brown; in lighter phase, ill-defined darker stripe from tip of snout to transverse interorbital bar, obscure shoulder chevrons and transverse bars on trunk; black spot in inguina without light border; laterally from loris to inguina darker than dorsum and demarcated from latter by a narrow darker dorsolateral stripe; dusky cream venter with darker throat and scattering of small spots on limbs.

ETYMOLOGY.— This species was named to honor Dr. Yong Hoi-Sen of the University of Malaya for his contributions to Malaysian zoology.

DISTRIBUTION.— Presently this species is known from only from the vicinity of the type locality on Gunung Brinchang, Cameron Highlands, Malaysia.

NATURAL HISTORY.— Eggs and larvae occurred on the internal walls of large pitcher plants. Males called from the inside of the pitchers as well. The pitcher plants and frogs live in the dense moss forests on the mountain side.

COMMENTS.— Preceding information extracted from Matsui (2009).

Diagnostic traits for the identification of adults of *Kalophrynus*

- 1a. Adult SVL equal or greater than 32 mm 2
- 1b. Adult SVL equal or less than 32 mm 14
- 2a. Moderate to large spot of contrasting color in inguinal area 6
- 2b. No moderate to large spot in inguinal area 3
- 3a. No light-colored diagonal dorsolateral stripes on trunk; adult size 37–41 mm SVL; subarticular tubercles beneath fingers and fourth finger nub-like; hindfoot two-thirds webbed with small indistinct inner and outer metatarsal tubercles [Borneo, Sarawak] *K. intermedius*
- 3b. Light-colored diagonal dorsolateral stripes on trunk 4
- 4a. Hindfoot strongly webbed, web extending half to two-thirds length of fourth toe; adult size 31–38 mm SVL; fingers with distinct subarticular tubercles; indistinct, flatten oval inner metatarsal tubercle, small indistinct outer tubercle [Peninsular Malaysia] *K. palmatissimus*
- 4b. Hindfoot webbed basally or one-third or less 5
- 5a. Moderately broad, light-colored diagonal dorsolateral stripes on trunk; adult size 29–39 mm SVL; large subarticular tubercles on all fingers, two beneath third, one beneath other three fingers; large oval inner and small round outer metatarsal tubercle [Borneo, Sarawak] *K. calciphilus*
- 5b. Presumed narrow, light-colored diagonal dorsolateral stripes on trunk; adult size 20–35 mm SVL; morphology of hand and hindfoot not described [Java]. *K. minusculus*
- 6a. Inguinal spot not dark brown or black, with or without a light border 7
- 6b. Inguinal spot dark, usually black, and light edged (ocellus) 8
- 7a. Inguinal spot bluish white and neither light or dark edged; adult size 24–33 mm SVL; distinct subarticular tubercles on all fingers, fourth finger nub-like; hindfeet about one-third webbed; inner and outer metatarsal tubercles weakly developed [Borneo, Kalimantan & Sarawak] *K. heterochirus*
- 7b. Inguinal spot yellow; adult size 36–47 mm SVL; finger morphology not reported; hindfeet webbed at base; inner and outer metatarsal tubercles poorly developed [Borneo, Sabah] *K. baluensis*
- 8a. Hindlimbs short, 110–125 % HndIL/SVL; adult size 34–47 mm SVL; distinct subarticular tubercles on all finger, two beneath third, one beneath other three fingers; hindfeet less than one-third webbed; moderate sized, round inner and outer metatarsal tubercles, outer often smaller; dorsal coloration variable, usually a dark nape stripe [northern Myanmar] *K. anya*
- 8b. Hindlimbs moderate length, 130–160 % HndIL/SVL; distinct subarticular tubercles on all finger, two beneath third, one beneath other three fingers 9
- 9a. Outer palmar tubercle small and oval; adult size 27–37 mm SVL; hindfeet modestly webbed, about one-third; medium-sized, oval inner metatarsal tubercle, outer small and round; dorsum immaculate except for inguinal ocelli [Vietnam] *K. honbaensis*
- 9b. Outer palmar tubercle moderate to large and round. 10
- 10a. Toes with only basal webbing; small round metatarsal tubercles; adult size 35–38 mm SVL; middorsal or parasagittal stripes always present on head [Bangladesh, NE India] *K. orangensis*
- 10b. Toes modestly webbed; moderate to large, oval or round outer metatarsal tubercle. 11
- 11a. Toes modestly webbed, one-third to one half between third and fourth toe; adult size 44–60 mm SVL; distinct subarticular tubercles on most toes, one beneath first and second fingers, two on third, three on fourth, one or two indistinct tubercles on fifth; never a middorsal head stripe, dorsum of trunk commonly unicolor [Borneo] *K. meizon*
- 11b. Toes modestly webbed, one-third or less between third and fourth toe; distinct subarticular tubercles beneath all toes 12
- 12a. Faint hour-glass mark on dorsum of nape and trunk; buccal fold continuous series of abutting denticulate-like lobes; adult size 34–35 mm SVL [Sumatra]. *K. pleurostigma*
- 12b. Dorsum from nape to at least midtrunk usually with whole or broken reverse Y-shaped mark, occasionally dorsum near immaculate; buccal fold continuous series of abutting abutting rectangular lobes. . 13
- 13a. Middorsal or parasagittal stripes on head of many individual; adult size 35–46 mm SVL [southern Myanmar, SE Asia] *K. interlineatus*

- 13b. No middorsal or parasagittal stripes on head; adult size 37–46 mm SVL [Philippines] *K. sinensis*
- 14a. Moderate to large spot of contrasting color in inguinal area 15
- 14b. No moderate to large spot of contrasting color in inguinal area; no spots or scattered small spots . . . 23
- 15a. Inguinal spot light colored and not contrastingly edged 16
- 15b. Inguinal spot dark, usually black, with or without a light border 17
- 16a. Inguinal spot yellow; adult size 24–26 mm SVL; finger morphology not reported; hindfeet moderately webbed, about one third; oval inner and round outer metatarsal tubercles poorly developed [Borneo, Sabah] *K. baluensis*
- 16b. Inguinal spot bluish-white without dark or lighter edge: adult size 24–33 mm SVL; distinct subarticular on all fingers, fourth finger nub-like; hindfeet about one-third webbed; inner and outer metatarsal tubercles weakly developed [Borneo, Kalimantan & Sarawak] *K. heterochirus*
- 17a. Black inguinal spot without light border (no ocellus) 19
- 17b. Dark inguinal spot with light border (ocellus) 18
- 18a. Outer palmar tubercle small and oval; adult size 27–37 mm SVL; hindfeet modestly webbed, about one-third; medium-sized, oval inner metatarsal tubercle, outer small and round; dorsum immaculate except for inguinal ocelli [Vietnam] *K. honbaensis*
- 18b. Dark brown inguinal spot with light border; adult size 24–26 mm SVL; subarticular tubercles on hand distinct, one on fingers 1, 2, 4 and two on 3; large outer palmar tubercle; feet modestly web, less than one third; oval inner metatarsal tubercle, no outer one [Peninsular Malaysia] *K. tiomanensis*
- 19a. Fourth finger very short and nub-like. 20
- 19b. Fourth finger short but not nub-like 22
- 20a. Toes modestly webbed, about one-third between third and fourth toes; adult size 21–27 mm SVL; toes with subarticular tubercles except fifth toe; inner and outer metatarsal tubercles present; diagonal, light dorsolateral stripe usually absent [Borneo, Sabah & Sarawak]. *K. subterrestris*
- 20b. Toes weakly webbed at base; subarticular tubercle variably present, occasionally indistinct. 21
- 21a. Tympanum size variable from smaller than eye to larger than eye 60–140 % Tymp/EyeD; faint hourglass mark on dorsum from eyes to suprascapular area; adult size 17–21 mm SVL; subarticular tubercle usually absent or indistinct on first and fifth toe [Borneo, Sarawak]. *K. barioensis*
- 21b. Tympanum always smaller than eye ~60 % Tymp/EyeD; dorsum usually immaculate; adult size 22–27 mm SVL [Great Natuna Isl.]. *K. bunguranus*
- 22a. Large subarticular tubercles on hand, two on first, second and fourth fingers and three on third; adult size 26–29 mm SVL; distinct subarticular tubercles on first through fourth toe, none of fifth; diffuse hourglass-shaped mark on dorsum between eyes and suprascapular area [West Malaysia] . . . *K. limbooliati*
- 22b. Distinctiveness of subarticular tubercles on all fingers variable, round and elevated to flat or absent 23
- 23a. Distinct subarticular tubercles on finger, one on first and fourth, two on second and three on third; adult size 28–31 mm SVL; hindfoot webbing slight, basally between all toes; modest round inner metatarsal tubercle, small round outer one; dorsally suprascapular area with dark chevron marks [West Malaysia] *K. yongi*
- 23b. Indistinct or absent subarticular tubercles on fingers. 24
- 24a. Distinct subarticular tubercles on fingers, one on first, second and fourth, two on third finger. 30
- 24b. Subarticular tubercles on fingers indistinct or condition not reported. 25
- 25a. Distinct to faded light diagonal dorsolateral stripe from behind head to inguina 26
- 25b. No light dorsolateral stripe on head and trunk; adult size 17–18 mm SVL; hand with short first and second fingers, third longest, fourth nub-like; subarticular tubercles of hand and feet weak and indistinct; dorsum brown with dark X-shaped mark on back of head to pelvis [West Malaysia] *K. robinsoni*
- 26a. Toes without webs; first toe very short, nub-like; adult size 19–23 mm SVL [China, Yunnan]. *K. mengliensis*
- 26b. Toes webbed, at least at base 27
- 27a. Hindfoot strongly webbed, web extending half to two-thirds length of fourth toe; adult size 31–38 mm

- SVL; fingers with distinct subarticular tubercles; indistinct, flatten oval inner metatarsal tubercle, small indistinct outer tubercle [Peninsular Malaysia] *K. palmatissimus*
- 27b. Toes weakly to modestly webbed, one-third or less between third and fourth toe 28
- 28a. Hands web free; subarticular tubercles absent on all toes except fourth with one tubercle; adult size 22–27 mm SVL; round inner metatarsal tubercle, no outer one; reddish brown dorsum with or without scattered black spots [Borneo, Kalimantan & Sarawak] *K. punctatus*
- 28b. Slight or shallow webbing between fingers 29
- 29a. Fourth finger of hand short, nub-like; adult size 19–24 mm SVL; subarticular tubercles on hand and palmar tubercle indistinct or absent; subarticular tubercles on toes indistinct or as single flattish pad extending length of toe [Borneo, Sarawak] *K. nubicola*
- 29b. Fourth finger short, but not nub-like; adult size 26 mm SVL; distinct round subarticular tubercles, one on first, second and fourth, two on third finger; distinct subarticular tubercles on all fingers; round inner and outer metatarsal tubercles [Borneo, Sarawak] *K. eok*
- 30a. Distinct subarticular tubercles on fingers, one on first, second and fourth, two on third; adult size 23–30 mm SVL; hindfoot webbing modest, less than quarter height between third and fourth toe; moderate-sized oval inner metatarsal tubercle, small round outer one; reverse Y-shaped pattern from back of head to midtrunk [Vietnam] *K. cryptophonus*
- 30b. Subarticular tubercles present on all toes, faint to strong 31
- 31a. Diagonal, light dorsolateral stripe usually absent; toes modestly webbed, about one-third between third and fourth toes; adult size 21–27 mm SVL; toes with subarticular tubercles except fifth toe; inner and outer metatarsal tubercles present; [Borneo, Sabah & Sarawak] *K. subterrestris*
- 31b. Light-colored diagonal dorsolateral stripes on trunk 32
- 32a. Presumed narrow, light-colored diagonal dorsolateral stripes on trunk; adult size 20–35 mm SVL; morphology of hand and hindfoot not described [Java]. *K. minusculus*
- 32b. Moderately broad, light-colored diagonal dorsolateral stripes on trunk; adult size 29–39 mm SVL; large subarticular tubercles on all fingers, two beneath third, one beneath other three fingers; large oval inner and small round outer metatarsal tubercle [Borneo, Sarawak] *K. calciphilus*

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Appendices

APPENDIX 1. Specimens examined

Kalophrynus anya: Myanmar, Kachin CAS 232488; Sagaing USNM 520321, 523964–966, 537419–422.

Kalophrynus interlineatus: Myanmar, Bago-Mon(“Pegu”) NHMUK/BMNH 1947.2.31.26–27; Mon CAS 240327–331; USNM 587070; Tanintharyi CAS 229825, 243687, 243749, 243927, 245699–5700, 255733, 245749, 245895, 245941, 246333–334, 246685, 247889, 247917, 247923, 247932, 247937, 247981, 247995, 249946. Cambodia FMNH 270637. China FMNH 176352. Laos FMNH 270357, NCSM 79833. Thailand FMNH 265845, 265847. NCSM 76409–410, 79833, USNM 103422, 103450. Vietnam CAS 115821, FMNH 261613, NCSM 80324–325.

Kalophrynus meizon: Borneo, Sarawak CAS-SU A23030, FMNH 267873, 267875–881, 269668–670, 269673, 269675, 273260–262, 273264, 273266, USNM 197671.

Kalophrynus pleurostigma: Indonesia, Sumatra, Sumatera Utara MCZ A22499, USNM 36645.

Kalophrynus sinensis: Philippines, Biliran USNM 318371; Bohol CAS 22063–078, 22080–083, 21967–969, 21972–973, 21980, 21982; Camiguin USNM 305724; Leyte USNM 160015–016.

Data for the maps derives from the preceding specimens. Additional distributional data were extracted from the electronic databases of CAS, FMNH, KU, MCZ, and MVZ. Literature records derive from Chan et al. (2011), Crampton (1990), Das and Hass (2003), Dutta et al. (2000), Fei (1999), Günther (1895), Iskandar (1998), Karsen et al. (1986), Mahony and Ali Reza (2007), Matsui et al. (2011), Ohler and Grosjean (2005), Parker (1934), Paul et al. 2007, and Vassilieva et al. (2014). Recent Sumatra voucher locality (Gunung Kunyit, Jambi Prov. @ 1242 m) is from A. Hamidy and E. N. Smith, University of Texas Arlington.

APPENDIX 2. Character definitions

MEASUREMENTS. [mm; all bilateral measurements recorded from right side.]

Crus length (CrusL): Straight-line distance from knee to ankle.

Eye diameter (EyeD): Horizontal diameter of eye [exposed surface] from anterior to posterior.

Hand length (HandL): Distance from base of palm (proximal edge of medial outer palmar tubercle) to tip of third finger.

Forearm length (ForarmL): Straight-line distance from elbow to wrist.

Head length (HeadL): Straight-line, horizontal distance from tip of snout to posterior corner of jaw.

Head width-posterior (HeadW): Straight-line, transverse distance from left to right edges of rear corner of jaws.

Hindfoot length (HndfL): Straight-line distance from heel to tip of fourth toe.

Hindlimb length (HndlL): Sum of ThghL, CrusL, TarsL, and HndfL.

Snout width or internarial distance (SnW): Distance between left and right nares.

Snout-eye distance (SnEye): Distance between tip of snout and anterior corner of orbit.

Snout-vent length (SVL): Distance from tip of snout to vent. Measurement is taken with frog’s venter adpressed against a flat, firm surface.

Naris-eye distance (NarEye): Distance between naris and anterior corner of orbit.

Tympanum diameter (Tymp): Horizontal diameter of tympanum from outer edge of annulus.

Thigh length (ThghL): Straight-line distance from vent to knee.

Tarsus or ankle length (TarsL): Straight-line distance from crus-ankle joint to heel.

MERISTIC.

Hindfoot webbing

Webbing is recorded only in halves and whole numbers using the subarticular tubercles as integers, e.g., basal tubercle is 1. Toes are identified by Roman numerals, and inner (anterior) and outer (posterior) edges by integers; for example, the inside edge of third toes is **III1**, its outside edge **III2**.

WebIII2: location at which web joins outside edge of third toe.

WebIV1: location at which web joins inside edge of fourth toe.

Subarticular tubercles

Fifth toe, number of (Toe5Sub): number of subarticular tubercles on fifth digit of hindfoot.

COLOR PATTERN. These traits are coded arbitrarily in a numerical sequence. All observations on color pattern derive from preserved specimens.

Dorsal Patterns

Head, middorsal stripe (HeadMid) three states: absent [0]; faded and/or fragmented [1]; sharply defined, often from tip of snout [2].

Head, parasagittal stripes (HeadPsag) three states: absent [0]; faded [1]; sharply defined, usually extend from supraorbital area onto trunk [2].

Dorsum, nape stripe (DorsNap), three states: absent [0]; single, faded [1] or bold [2] middorsal stripe, bifurcating on shoulders.

Dorsum, parasagittal stripes (DorsPsag), three states: absent [0]; indistinct, possibly fragmented, lacks narrow white borders [1]; bold, dark stripes with narrow white borders [2].

Inguinal spots (IngSpt) three states: absent [0]; small to large, without light border [1]; ocellus, narrow light encircling border [2].

Hindlimb barring (HndlBr): three states: absent [0]; indistinct, without light edging [1]; bold on thigh and crus, usually light edged [2].

Lateral Pattern

Dorsolateral stripe (DlatSt) three states: absent [0]; indistinct, narrow, faded light stripe, at least from supraorbital to mid trunk [1]; bold, narrow light stripe from snout to inguinal [2].

Loreal color (Loreal) three states: lightly shaded with or without thin dark subcanthal stripe [0]; broad dark subcanthal stripe, lighter below canthus stripe to upper lip [1]; dark from canthus to mouth [2].

Lateral trunk color (LatTrnk) three states: lightly shaded from supratympanic fold to inguinal [0]; dark from fold to mid trunk, faded thereafter [1]; dark from fold to inguinal [2].

Ventral Pattern

Chin & throat (Chin) three states: dusky without distinct markings [0]; dusky with ill-defined blotches or vague pair of longitudinal stripes [1]; pair of bold, dark longitudinal stripes, usually narrowly edged in white [2].

Chest (Chest): three states: dusky without markings [0]; dusky with vague dark spots or blotches [1]; dusky with distinct dark spots and blotches [2].