

Systematics of a widespread Southeast Asian frog, *Rana chalconota* (Amphibia: Anura: Ranidae)

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The abundant Sundaland forest frog, *Rana chalconota*, has long been considered a single widespread species, although some authors have recommended its division into regional subspecies. The discovery of co-occurring pairs of morphologically distinct populations in three widely separated parts of the range led to a morphological and molecular analysis of populations from all parts of the known range. The results suggest that *R. chalconota* consists of at least seven species from Thailand through Borneo and Java. Existing names are applied to three of these species, *R. chalconota* (Schlegel), *R. raniceps* (Peters) and *R. labialis* Boulenger. We describe four others as new species and suggest the existence of one or two additional, unnamed species. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, 155, 123–147.

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INTRODUCTION

Interest in the systematics of widely distributed Sundaland frogs usually assigned to the genus *Rana* has been generated in two contexts. One is their confused taxonomy. The phylogenetic relationships among these species are still unresolved and constitute a basic cause of taxonomic confusion. Dubois (1992) attempted a classification of the Ranidae and placed two of these widespread (occurring at least in Borneo, Sumatra and Peninsular Malaysia) species, *Rana chalconota* (Schlegel) and *R. hosii* Boulenger, in his newly created subgenus *Chalcorana*. Matsui *et al.* (2005) found *Chalcorana* not to be monophyletic and placed *R. hosii* in the genus *Odorrana*, a decision agreed upon by Cai *et al.* (2007). Dubois (1992) assigned the remainder of these species of *Rana* to his newly defined subgenus *Pulchrana*. *Pulchrana*, along with other of Dubois' (1992) subgenera, was established in the absence of knowledge of its phylogenetic

relationships (Inger, 1996) and Matsui *et al.* (2005) failed to find convincing support for the relationships among these taxa. Frost *et al.* (2006) placed *chalconota* in the genus *Hydrophylax*. That decision has a serious weakness, because they did not study the type species, *malabarica*. Given the uncertain phylogenetic status of the subgenera proposed by Dubois (1992), and doubts about application of the name *Hydrophylax*, we continue to use the generic name *Rana* for this group of species.

The second context for an interest in these widely distributed Sundaland frogs is the recent recognition (e.g. Brown & Guttman, 2002; Bain *et al.*, 2003; Stuart, Inger & Voris, 2006) that many of the nominal species of the entire Southeast Asian region are in fact clusters of similar species. This is the focus of our study. Our present study of one of these species, *Rana chalconota* (Schlegel), was initiated because two distinct, co-occurring morphotypes, both fitting general descriptions of *R. chalconota* in the literature (e.g. van Kampen, 1923), were discovered in the Padang area (0°53'S/100°28'E) of West Sumatra (Inger & Iskandar, 2005). These morphotypes differed sharply

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in size and in coloration of the webbing. We then encountered two forms, differing sharply in size, in a sample collected 40 years ago at Labang Forest Reserve (3°21'N/113°27'E) in Sarawak, Borneo. A molecular phylogenetic analysis (Stuart *et al.*, 2006) has shown that the members of these two sets of sympatric pairs are not each other's sister lineages and that there is also a pair of sympatric lineages in Peninsular Malaysia.

Rana chalconota (in the broad sense) is a Sundaland frog that breeds along streams of various sizes in lowland forests of various types, from hilly (but lowland) primary rain forest to swamp forest to secondary forest. It can be seen in low numbers during most nocturnal riparian searches, but exhibits pulses of breeding activity during which many individuals can be seen within a very narrow strip of stream bank (Inger, 1969). *Rana chalconota* is a slender, small to moderate-sized species (adults 30–60 mm snout–vent length). The tips of the digits, especially of the fingers, are distinctly enlarged and have circummarginal grooves. The webbing is extensive, reaching the distal subarticular tubercle of the fourth toe or slightly beyond. The general coloration is green above and white or cream-coloured below and the upper lip is usually distinctly lighter than the adjacent areas.

Described originally from Java, *Rana chalconota* is now reported from southern Thailand to Java, including Borneo and Sumatra (Iskandar & Colijn, 2000). References to this species in Sulawesi (e.g. van Kampen, 1923) almost certainly apply to *R. mocquardii* Werner (Iskandar & Colijn, 2000). Three names have been used for various Sundaland populations of this group: *Rana chalconota* (Schlegel), type locality Java; *Rana raniceps* (Peters), type locality Sarawak; and *Rana labialis* Boulenger, type locality Malacca, Peninsular Malaysia. Although originally Boulenger (1887) described *R. labialis* as a full species, he later (1920) placed it in the synonymy of *R. chalconota* (Schlegel). van Kampen (1923), however, maintained *R. labialis* as a valid species, although in a letter to Smith (1930) he changed his opinion. Smith (1930) also treated *R. labialis* as a synonym of *R. chalconota*. van Kampen (1923) placed *Polypedates raniceps* Peters under the heading of *Rana labialis* with a question mark. After examining several of the types of *R. raniceps* and *R. labialis*, Inger (1966) considered them to be indistinguishable and applied the name *Rana chalconota raniceps* (Peters) to the Bornean frogs that had been referred to *R. chalconota* and *R. labialis* by Boulenger (1920) and van Kampen (1923), respectively. Dubois (1992) elevated *R. raniceps* to full species status, without accompanying justification. Iskandar (1998) also used the name *Rana chalconota raniceps*, suggesting that the form occurred in Sumatra and Sulawesi, as well as in Borneo. Iskan-

dar & Colijn (2000) treated *R. raniceps* as a full species, noting that its distinction from *R. chalconota* needed confirmation.

We have obtained specimens (and associated tissues) of *chalconota*-like frogs from southern, peninsular Thailand and have been able to borrow additional specimens and tissue samples from peninsular Malaysia, Sumatra and Java and two tissues from Sulawesi. This material and specimens collected in the past from many localities in Borneo have enabled us to address several questions. How many distinct morphotypes of *R. chalconota* exist across the geographical range from Thailand to Java? Is there genetic support for these morphotypes? How are the various morphotypes related?

We have applied both morphological and molecular genetic data to an analysis of variation in these frogs. The molecular analysis reveals multiple, deeply divergent mitochondrial lineages that have a complex geographical pattern. The morphological part of the analysis is less clear, perhaps not surprisingly as all of these populations have been called *Rana chalconota* by a number of authors because of their general similarity. We have adopted a conservative operational criterion of recognizing as species those lineages that are diagnosable in more than one independent data set, in this case both morphology and mitochondrial DNA. Those lineages that are diagnosable in only one of these data sets are not designated as separate species in this study. Our argument for recognizing multiple species within *Rana chalconota* (in the broad sense) is strengthened by the finding that at three localities, two deeply divergent, phylogenetically unrelated mitochondrial lineages were found in sympatry and that, in the two of these cases in which we had reasonable sample sizes (i.e. $N > 3$), there are clear morphological criteria.

MATERIAL AND METHODS

SAMPLING

Voucher specimens (see species accounts below) and tissue samples ($N = 131$ individuals; Appendix) from a total of 42 localities across the ranges of the *R. chalconota* species complex (Fig. 1) were included in the study. Museum acronyms follow Leviton *et al.* (1980), with the addition of FRIM for Forest Research Institute Malaysia, THNHM for Thailand Natural History Museum, and ZRC for Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore.

MORPHOLOGICAL DATA

Six mensural features were used: snout–vent length (SVL), tibia length (T) measured with the limb flexed,

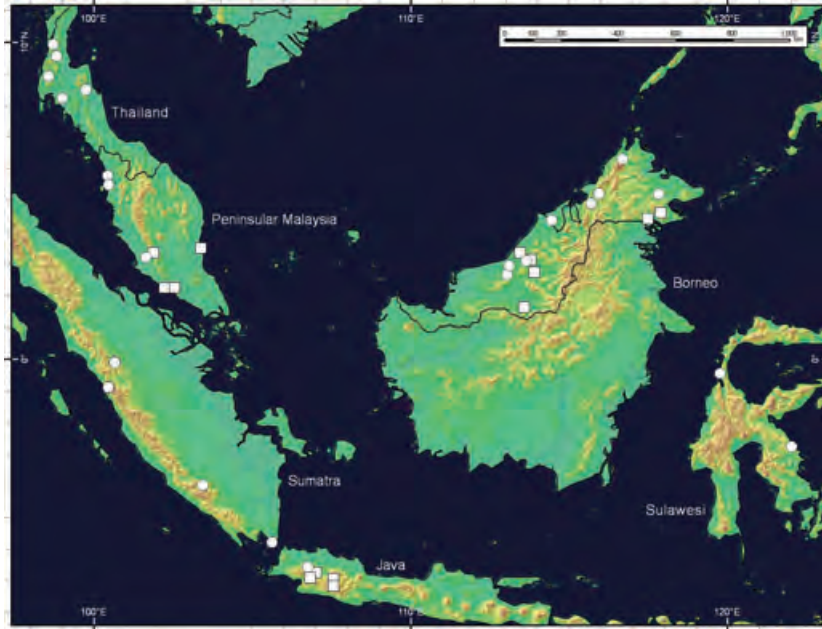


Figure 1. Map illustrating the provenance of specimens and tissues of the *Rana chalconota* species group used in this study. Squares represent specimens only, and circles represent both tissues and specimens.

head width (HW) measured at the rear of the head, head length (HL) from the rear of the jaws to the tip of the snout, horizontal diameter of tympanum (TYM) and width of the disc of the third finger (DF3). The last five measurements were converted into ratios of SVL. All measurements except the width of the finger disc were taken with a dial caliper graduated to 0.1 mm; the width of the finger disc was measured with an ocular micrometer at $\times 12$ magnification. For consistency, measurements were taken only by the senior author. SYSTAT9 was used for statistical analyses. Two qualitative characters that could be seen in preserved specimens were also used: black spots on the back (present or absent) and shape of the nuptial pad in males (constricted medially or not).

MOLECULAR DATA

Total genomic DNA was extracted from tissues using PureGene Animal Tissue DNA Isolation Protocol (Gentra Systems, Inc.). A fragment of mitochondrial (mt) DNA that encodes part of the cytochrome oxidase c subunit III gene, the complete tRNA glycine, the complete NADH dehydrogenase subunit 3 gene, and part of the tRNA arginine were amplified by PCR (94 °C, 45 s; 49 °C, 30 s; 72 °C 1 min) for 35 cycles using the primer pairs L-COXIII/Arg-HND3III (Stuart *et al.*, 2006) and either L-COXIIIext (5'-TACCAATGATGACGAGACGT-3')/H-GlyND3 (5'-AAGAAAATATGAGCCTCATCA-3') or L-COXIII5' (5'-CAAGCTCACGCTTTCCACATAGT-3')/H-GlyND3. A

fragment of mitochondrial DNA that encodes part of the 16S rRNA gene was amplified by PCR (94 °C, 45 s; 60 °C, 30 s; 72 °C 1 min) for 35 cycles using the primer pair L-16SRanaIII/H-16SRanaIII (Stuart *et al.*, 2006). PCR products were electrophoresed in a 1% low-melt agarose TALE gel stained with ethidium bromide and visualized under ultraviolet light. The bands containing DNA were excised and agarose was digested from bands using GELase (Epicentre Technologies). PCR products were sequenced in both directions by direct double strand cycle sequencing using Big Dye version 3 chemistry (Perkin Elmer) and the amplifying primers. Cycle sequencing products were precipitated with ethanol, 3 M sodium acetate, and 125 mM EDTA, and sequenced with a 3730 DNA Analyzer (ABI). Sequences were edited and aligned using Sequencher v. 4.1 (Genecodes). The aligned dataset contained 1635 mtDNA characters, consisting of 942 protein-coding, 615 rRNA and 78 tRNA characters. Sequences were deposited in GenBank under accession numbers DQ650353-650391, DQ650393-650431 and EF487354-487531 (Appendix).

Phylogenies were reconstructed using the maximum parsimony optimality criterion and mixed-model Bayesian inference. Identical haplotypes were removed from the alignment to facilitate phylogenetic computation. *Rana erythraea* and *R. nigrovittata* were used as outgroups following Frost *et al.* (2006).

Maximum parsimony analysis was performed using PAUP* 4.0b10 (Swofford, 2002). A heuristic search was performed with equal weighting of nucleotide

substitutions, stepwise addition with 10 000 random addition replicates and TBR branch swapping. Nodal support was evaluated with 1000 non-parametric bootstrap pseudoreplications (Felsenstein, 1985) using the heuristic search option with TBR branch swapping limited to 10 000 000 rearrangements per replicate.

Mixed-model Bayesian analysis was performed using MrBayes 3.1 (Ronquist & Huelsenbeck, 2003). The data were separated into first codon position, second codon position, third codon position, rRNA and tRNA data partitions. The model of sequence evolution that best described each of these five data partitions was inferred using the Akaike Information Criterion as implemented in Modeltest 3.7 (Posada & Crandall, 1998). The models selected were SYM + I + G for the first codon position partition, TVM + I + G for the second codon position partition, GTR + G for the third codon position partition, GTR + I + G for the rRNA partition and HKY + G for the tRNA partition. The SYM and TVM models are not implemented in MrBayes 3.1, and so the next more complex model available in the program (GTR) was used for those partitions. Four independent Bayesian analyses were performed. In each analysis, four chains were run for 10 000 000 generations using the default priors, trees were sampled every 2000 generations and the first 25% of trees were discarded as 'burn-in.' A 50% majority rule consensus of the sampled trees was constructed to calculate the posterior probabilities of the tree nodes.

RESULTS

MORPHOLOGY

SVL and all body proportions except HL/SVL showed statistically significant variation among locality samples (Table 1).

As recognition of the existence of co-occurring morphotypes at one locality in Sumatra and one in Sarawak was initially based on SVL, that character and geography were used to define provisional morphotypes: Borneo Large, Borneo Small, Java, Padang (West Sumatra) Large, Padang (West Sumatra) Small, Peninsular Malaysia and Thailand. Statistically significant differences among these seven in SVL and body proportions were pervasive (Tables 2 and 3), although the inter-taxa ranges of variation were not great except in SVL.

Frequency of frogs with black dorsal spots varied greatly from sample to sample. For example, all but two of 66 frogs from the area of Padang, West Sumatra, had black spots, whereas none of 39 from southern Thailand did. In a sample of 20 from Danum, Sabah (Borneo), half had black dorsal spots

Table 1. *P* values of morphological comparisons among locality samples of the *Rana chalconota* species complex

Character	Females	Males
	<i>N</i> samples = 221 <i>N</i> localities = 37	<i>N</i> samples = 220 <i>N</i> localities = 33
SVL	< 0.001	< 0.001
T/SVL	0.009	< 0.001
HW/SVL	0.002	0.008
HL/SVL	0.06	0.11
TYM/SVL	< 0.001	< 0.001
DF3/SVL	< 0.001	

ANOVA used for SVL, Kruskal–Wallis used for body proportions. Abbreviations are as defined in the Material and Methods.

and half did not. For the seven provisional morphotypes, the distribution (number with spots present/absent) was as follows: Borneo Large 31/151, Borneo Small 7/34, Padang Small 50/2, Padang Large 14/0, Peninsular Malaysia 26/14, Thailand 0/39, Java 11/13.

Frequency of constriction of the medial margin of the nuptial pad also varied in a complicated manner. For example, all males (*N* = 9) from Danum, Sabah, had constricted nuptial pads, whereas half of males (*N* = 12) from Mendolong, Sabah, did, and none of those (*N* = 20) from Padang, Sumatra did. For the seven provisional morphotypes, the frequency of constricted nuptial pads (given as constricted/non-constricted) was: Borneo Large 59/42, Borneo Small 10/1, Padang Small 0/13, Padang Large 0/7, Peninsular Malaysia 17/1, Thailand 19/3, Java 0/21.

MOLECULES

Sixty-three unique haplotypes were retained after pruning identical haplotypes from the alignment. Of the 1635 characters, 686 were variable and 589 were parsimony-informative. Uncorrected pairwise sequence divergences within the ingroup ranged from 0 to 19.36% (Table 4).

The heuristic search in the maximum parsimony analysis recovered 452 equally most parsimonious trees (*L* = 1927; *CI* = 0.503; *RI* = 0.813) and strict consensus showed that these trees differed only by the arrangement of individuals within clades.

The standard deviation of split frequencies among the four Bayesian runs was 0.003838, and trace plots of clade probabilities viewed using AWTY (Wilgenbusch, Warren & Swofford, 2004) were relatively stationary. These two measures suggest that the four

Table 2. Summary of mensural features of morphotypes of the *Rana chalconota* species complex

Population	SVL (mm)	T/SVL	HW/SVL	TYM/SVL	DF3/SVL
Males					
Selangor*	32.44 ± 0.48 (15)	0.556 (15)	0.296 (15)	0.105 (15)	0.051 (9)
Thailand	34.14 ± 0.39 (22)	0.590 (20)	0.310 (20)	0.108 (15)	0.058 (13)
Borneo Small	30.35 ± 0.93 (8)	0.542 (9)	0.304 (7)	0.112 (6)	–
Padang Small	32.39 ± 0.76 (13)	0.565 (13)	0.292 (13)	0.114 (13)	0.057 (10)
Borneo Large	39.21 ± 0.34 (113)	0.562 (96)	0.302 (71)	0.114 (76)	0.064 (52)
Padang Large	45.36 ± 0.51 (8)	0.560 (7)	0.297 (7)	0.105 (7)	0.064 (7)
Java	39.02 ± 0.47 (47)	0.526 (21)	0.309 (20)	0.114 (24)	0.050 (11)
Females					
Selangor	43.56 ± 0.64 (17)	0.576 (16)	0.290 (16)	0.078 (16)	0.052 (14)
Thailand	47.57 ± 0.96 (17)	0.580 (17)	0.308 (16)	0.087 (17)	0.060 (14)
Borneo Small	38.20 ± 0.48 (30)	0.553 (30)	0.294 (27)	0.083 (30)	0.060 (16)
Padang Small	41.54 ± 0.68 (15)	0.572 (13)	0.291 (13)	0.083 (13)	0.055 (8)
Borneo Large	53.66 ± 0.45 (115)	0.567 (98)	0.306 (61)	0.082 (80)	0.064 (51)
Padang Large	60.58 ± 1.55 (6)	0.556 (6)	0.303 (6)	0.068 (6)	0.062 (5)
Java	60.05 ± 1.23 (22)	0.558 (10)	0.310 (8)	0.076 (8)	0.050 (5)

Mean ± SE given for SVL, medians given for body proportions. Sample sizes are given in parentheses. Abbreviations are as defined in the Material and Methods.

*Representing the Peninsular Malaysia morphotype.

Table 3. *P* values of morphological comparisons among seven morphotypes (defined in the text) of the *Rana chalconota* species complex

Character	Females	Males
SVL	< 0.001	< 0.001
T/SVL	0.17	< 0.001
HW/SVL	< 0.001	0.02
HL/SVL	0.31	0.004
TYM/SVL	< 0.001	< 0.001
DF3/SVL	< 0.001	< 0.001

ANOVA used for SVL, Kruskal–Wallis used for body proportions. Abbreviations are as defined in the Material and Methods.

runs had sufficiently converged and that topologies were sampled in proportion to their true posterior probability distribution.

Ten major mitochondrial lineages were recovered, each supported with Bayesian posterior probabilities of 1.00 and bootstrap values ≥ 99 (Fig. 2). A lineage from Sulawesi (*R. mocquardii*) is the most basal member of the *R. chalconota* species complex. The remaining members of the *R. chalconota* species complex contain two major clades (A and B in Fig. 2). Clade A contains three lineages in Peninsular Malaysia, a lineage in Borneo (Borneo Large morphotype), a lineage in Thailand (Thailand morphotype) and a lineage in West Sumatra (Padang Small morphotype). Clade B contains a lineage in Borneo (Borneo Small

morphotype), a lineage in Java and South Sumatra (Java morphotype), and a lineage in West Sumatra (Padang Large morphotype). Two lineages are found in sympatry in Peninsular Malaysia, West Sumatra and Borneo, but in no case are sympatric lineages resolved as sister lineages. Two of the ten mitochondrial lineages contain significant genetic structure. The two samples representing the Sulawesi lineage have an uncorrected pairwise sequence divergence of 8.93%, and the two subclades within the Borneo Large lineage (representing samples from Sabah in one subclade and central Sarawak in the other) have a maximum uncorrected pairwise sequence divergence of 5.50% (Table 4). Uncorrected pairwise sequence divergences were relatively high between co-occurring lineages in Peninsular Malaysia (11.59–11.78%), West Sumatra (14.75–14.93%) and Borneo (13.11–13.97%; Tables 4 and 5).

The parsimony and Bayesian topologies differ only by relationships among the Padang Small, Thailand, and Peninsular Malaysia C and D clades (Fig. 2). The parsimony analysis resolves these clades as Peninsular Malaysia D [Peninsular Malaysia C (Thailand + Padang Small)], but without bootstrap support. The Bayesian analysis does not resolve relationships among these four clades (Fig. 2).

RELATIONSHIP BETWEEN MORPHOLOGICAL VARIATION AND MOLECULAR VARIATION

The molecular data corroborate the recognition of morphotypes Borneo Large, Borneo Small, Padang

Table 4. Uncorrected pairwise sequence divergences (%) within (diagonal) *R. mocquardii* from Sulawesi and seven morphotypes (defined in the text) of frogs in the *Rana chalconota* species complex

Morphotype	Borneo Small	Borneo Large	Padang Small	Padang Large	Thailand	Peninsular Malaysia	Java	<i>R. mocquardii</i>
Borneo Small	0.00–4.19							
Borneo Large	13.11–13.97	0.00–5.50						
Padang Small	12.81–14.28	7.30–8.28	0.00–3.71					
Padang Large	15.05–15.36	14.07–14.81	14.75–14.93	0.00				
Thailand	13.05–13.60	6.30–7.48	5.69–6.99	13.58–14.07	0.00–1.73			
Peninsular Malaysia	13.17–15.32	6.43–12.21	5.81–13.08	14.08–15.78	5.07–12.14	0.00–11.90		
Java	14.67–16.23	14.12–15.75	13.75–15.82	12.05–13.78	13.07–14.93	13.51–18.06	0.40–3.78	
<i>Rana mocquardii</i>	16.43–17.98	14.87–16.23	15.24–16.54	15.97–18.01	14.56–16.54	14.81–16.92	16.32–19.36	8.93

Large, Padang Small, Java and Thailand. However, the molecular phylogenetic analysis divides the Peninsular Malaysia morphotype into three clades (C, D and E in Fig. 2), one of which is phylogenetically unrelated to the other two. The taxonomic implications of that division are dealt with below. The molecular phylogenetic analysis does not group lineages with large body sizes and lineages with small body sizes; rather, both large and small body sizes are represented within both of the two major clades (A and B in Fig. 2).

Comparisons of the remaining clades (Fig. 2) revealed consistent significant differences in SVL (ANOVA $P < 0.001$ for both sexes), with 36 of the 42 possible pair-wise inter-clade comparisons showing statistically significant ($P \leq 0.04$) differences (Table 6). The only exceptions involved females of clades Padang Large and Java, males of Borneo Large and Java, males of Padang Small and Thailand, and males of Padang Small and Borneo Small. The only other mensural character that showed frequent inter-clade differences was TYM/SVL, with half of the pair-wise comparisons showing significant differences ($P \leq 0.04$). Clades Padang Small, Thailand and Padang Large showed the most frequent differences from other clades in pairwise comparisons.

The qualitative characters also showed frequent inter-clade differences. All except two individuals of Padang Small and Padang Large had black spots on the back, whereas none of the frogs in Thailand was spotted. None of the males of clades Padang Small, Padang Large and Java had constricted or divided nuptial pads, whereas all males of Thailand and all but one of Borneo Small did.

Among the co-occurring clades, Padang Small and Padang Large differ greatly in size, coloration of the web, in relative size of the tympanum and in relative size of the disc of the third finger. Clades Borneo Large and Borneo Small differ in size and, where they co-occur in Sarawak, they differ in frequency of constricted nuptial pads.

SPECIES ACCOUNTS

Species concepts and the criteria used to implement them are contentious and widely debated in the literature (e.g. de Queiroz, 1998; Wheeler & Meier, 2000). As noted above (Introduction) we have adopted a conservative operational criterion of recognizing as species those lineages that are diagnosable on the basis of both morphology and mitochondrial DNA. Those lineages that are diagnosable on the basis of only one of these data sets are not designated as species in this study. We note that the sympatric occurrences of morphologically distinct, genetically divergent mitochondrial lineages at localities in

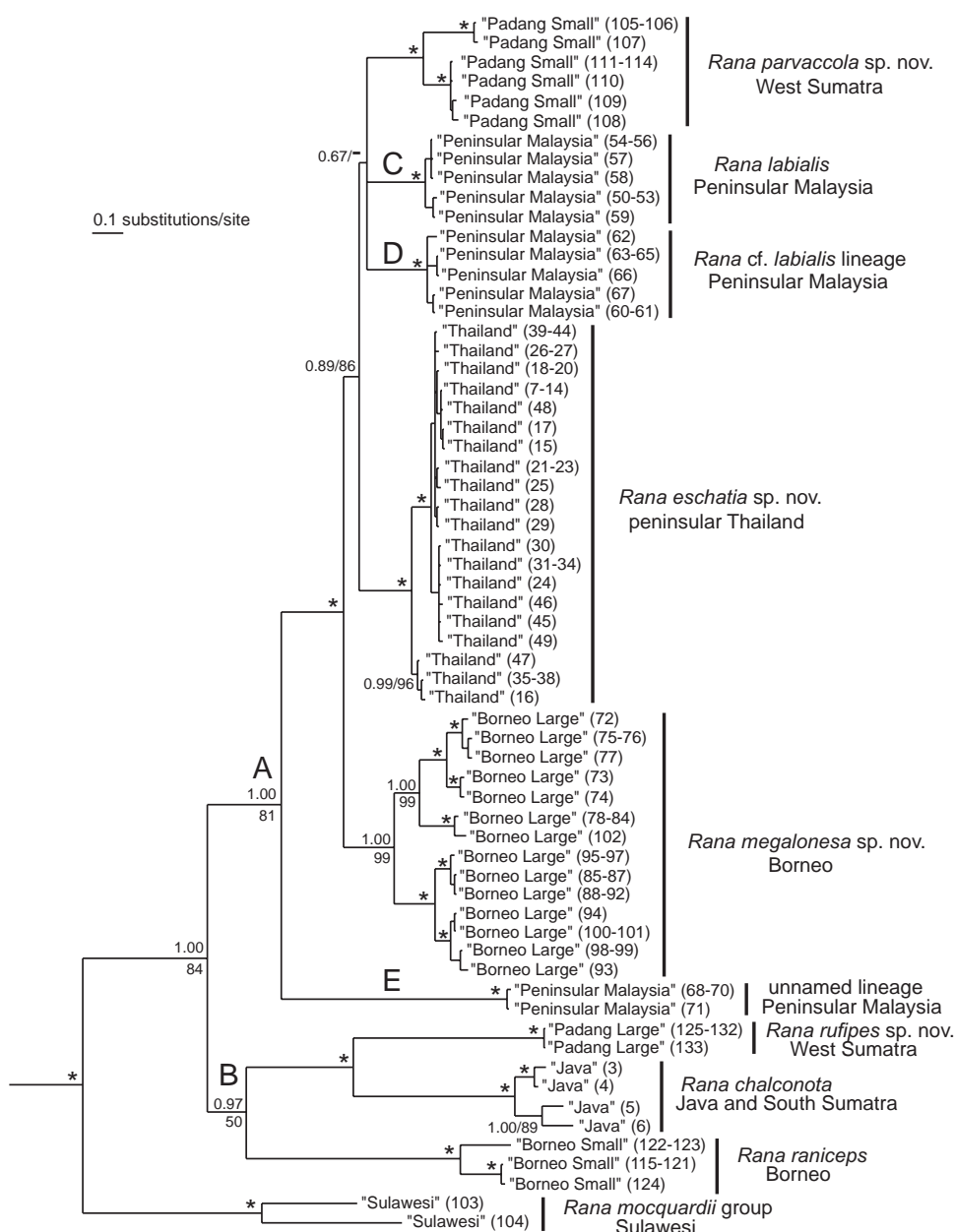


Figure 2. Fifty per cent majority-rule consensus phylogram resulting from mixed-model Bayesian analysis of mitochondrial DNA from frogs of the *Rana chalconota* species group. Trees were rooted with *R. erythraea* and *R. nigrovittata* (not shown). Numbers above and below nodes are Bayesian posterior probabilities and parsimony bootstrap values > 50 , respectively. An asterisk (*) indicates a Bayesian posterior probability of 1.00 and parsimony bootstrap value of 100. Maximum parsimony analysis resolved the clades Peninsular Malaysia D [Peninsular Malaysia C (Thailand + Padang Small)], but without bootstrap support.

Peninsular Malaysia, West Sumatra and Borneo lend strong support for these hypotheses. Genetic distances are provided as heuristic measures of evolutionary isolation, but are not used as criteria for recognizing species.

In this section morphological data apply only to adults, i.e. all females with convoluted oviducts and all males with nuptial pads.

RANA CHALCONOTA (SCHLEGEL, 1837)

(Previously referred to as Java morphotype)

Hyla chalconotus Schlegel, 1837: 24 – Java.

Rana chalconota Boulenger, 1882: 66 (part); Boulenger, 1920: 201 (part); van Kampen, 1923: 217 (part); Iskandar, 1998: 66; Iskandar & Colijn, 2000: 86 (part); Stuart *et al.*, 2006: 473.

Table 5. Uncorrected pairwise sequence divergences (%) within (diagonal) and between (below diagonal) molecular clades of frogs in the *Rana chalconota* species complex from Peninsular Malaysia

Molecular Clade	Peninsular Malaysia C	Peninsula Malaysia D	Peninsular Malaysia E
Peninsular Malaysia C	0.00–0.68		
Peninsular Malaysia D	4.94–5.56	0.00–0.87	
Peninsular Malaysia E	11.59–11.90	11.59–11.78	0.00–0.12

Clade letters refer to Figure 2. Clades D and E occur in sympatry.

Rana (Chalcorana) chalconota Dubois, 1992: 328.

Polypedates junghuhnii Bleeker, 1856 – Java.

The likely types are RMNH 4264, 5364 ('Java'). These are the only specimens collected early enough to have been sent to Schlegel by S. Müller. SVL of these types are: females 64.8, 67.7 mm, males 43.6–49.8 ($N = 3$).

Other specimens examined

Java: Bandung (6°57'S/107°34'E) FMNH 83623-41, 131052-62; Cibodas (6°45'S/107°01'E) FMNH 172352-61, 173623-37, ZRC 1.2755; Pengalengan (7°10'S/107°34'E) BM 96.1.23.26-27; Sukabumi (6°55'S/106°50'E) ZRC 1.6402-03, 1.6405, 1.6505; Desa Sukahami (6°34'S/106°45'E), near Bogor UTA 53665-66.

Sumatra: South Sumatra, Pagaralam (3°59'S/103°26'E) on road to Lahat UTA 53685; Lampung, S side of Gunung Rajabasa (5°47'S/105°38'E) UTA 53686. 'Java-Sumatra' in Figure 2.

Diagnosis

A large member of the *chalconota* group, SVL of females 49.3–73.1, mean 60.05 ± 1.23 ($N = 22$); males 33.8–49.8, mean 39.02 ± 0.47 ($N = 47$); leg relatively short for the group, T/SVL 0.50–0.60 (median 0.537, $N = 31$); nuptial pad in males not constricted; humeral gland in males large, protuberant and visible through skin. Back with (18) or without (15) dark spots. HW/SVL of females 0.30–0.33 (median 0.313, $N = 8$), of males 0.28–0.33 (median 0.309, $N = 21$); TYM/SVL of females 0.07–0.08 (median 0.075, $N = 8$); of males 0.088–0.129, median 0.113 ($N = 24$).

Descriptive notes

Head triangular; snout slightly projecting; tympanum slightly depressed relative to surface of temporal region; pineal body faintly visible, slightly anterior to or in line with front corners of upper eyelids; dorso-lateral fold narrow; skin of back granular in females, with many fine spinules in males; crossbars on hind limb visible in about half of preserved individuals; rear of thigh brown with obscure, rounded light markings.

Comparisons

Rana chalconota is one of the two largest members of this species complex (Table 2). Both sexes of this Javan species are larger (SVL) than the continental forms and the small species from Padang, Sumatra (*parvaccola*, see below). Females of *chalconota* are also larger than those of *raniceps* and of *megalonesa* (see below) from Borneo (Table 2). Males of *chalconota*, however, are smaller than those of the large form from Padang, Sumatra (*rufipes*, see below). *Rana chalconota* (both sexes) has a significantly wider head (HW/SVL) than *parvaccola* and *labialis* from Selangor. Females of *chalconota* have larger heads than those of *raniceps* and *rufipes*. Males of *chalconota* are the only ones in this complex that have conspicuously protruding humeral glands.

This species, and all the other members of the *Rana chalconota* group, differs from many Sundaland species of *Rana (Hylorana)*, *sensu* Boulenger (1920), by its green coloration; this is the case with respect to *Rana baramica* (Boettger), *R. cubitalis* Smith, *R. glandulosa* Boulenger, *R. laterimaculata* Barbour & Noble, *R. luctuosa* (Peters), *R. miopus* Boulenger, *R. nigrovittata* (Blyth), *R. picturata* Boulenger and *R. signata* (Günther). The *R. chalconota* group differs from *Rana crassiovis* Boulenger, *R. kampeni* Boulenger, *R. miopus* Boulenger and *Odorrana hosii* (Boulenger) in the presence, only in the *R. chalconota* group, of a distinct outer metatarsal tubercle. In all members of the *R. chalconota* group, the tips of the fingers are much enlarged and that of the third finger is equal to half (males) or almost two-thirds (females) the diameter of the tympanum. In contrast, the tip of the third finger is equal to or less than one-third the diameter of the tympanum in *Rana baramica*, *R. cubitalis*, *R. glandulosa*, *R. luctuosa*, *R. miopus* and *R. nigrovittata*.

RANA LABIALIS BOULENGER

(Previously referred to as Peninsular Malaysia morphotype)

Rana labialis Boulenger, 1887: 345 – Malacca; van Kampen, 1923: 220; Stuart *et al.*, 2006: 473.

Table 6. *P* values of morphological comparisons between clades of the *Rana chalconota* species complex

Clades	SVL	T/SVL	HW/SVL	HL/SVL	TYM/SVL	DF3/SVL
Males						
<i>labialis</i> vs. <i>eschatia</i>	0.01	0.04	0.02	0.02	0.10	0.02
<i>labialis</i> vs. <i>parvaccola</i>	0.20	0.20	0.30	0.30	0.002	–
<i>labialis</i> vs. <i>raniceps</i>	0.06	0.02	0.20	0.02	0.10	–
<i>labialis</i> vs. <i>megalonesa</i>	< 0.001	0.41	0.08	0.81	< 0.001	0.002
<i>labialis</i> vs. <i>rufipes</i>	< 0.001	0.75	0.44	0.03	0.72	–
<i>labialis</i> vs. <i>chalconota</i>	< 0.001	0.02	0.01	0.29	0.04	–
<i>parvaccola</i> vs. <i>eschatia</i>	0.056	0.039	0.01	0.42	0.018	0.80
<i>parvaccola</i> vs. <i>megalonesa</i>	< 0.001	0.72	0.26	0.43	0.19	0.005
<i>parvaccola</i> vs. <i>raniceps</i>	0.10	0.10	0.01	0.05	0.10	–
<i>parvaccola</i> vs. <i>rufipes</i>	< 0.001	0.87	0.43	0.043	0.003	0.002
<i>parvaccola</i> vs. <i>chalconota</i>	< 0.001	0.03	0.02	0.21	0.28	< 0.001
<i>eschatia</i> vs. <i>megalonesa</i>	< 0.001	0.002	0.03	0.11	0.49	0.002
<i>eschatia</i> vs. <i>raniceps</i>	0.001	0.002	0.10	0.10	0.01	–
<i>eschatia</i> vs. <i>rufipes</i>	< 0.001	0.03	0.04	< 0.001	0.03	0.002
<i>eschatia</i> vs. <i>chalconota</i>	< 0.001	< 0.001	0.68	0.009	0.29	< 0.001
<i>megalonesa</i> vs. <i>raniceps</i>	< 0.001	0.07	0.20	0.08	0.20	–
<i>megalonesa</i> vs. <i>rufipes</i>	< 0.001	0.84	0.07	0.05	0.08	0.11
<i>megalonesa</i> vs. <i>chalconota</i>	0.21	< 0.001	0.34	0.67	0.003	< 0.001
<i>raniceps</i> vs. <i>rufipes</i>	< 0.001	0.05	0.30	0.001	0.26	–
<i>raniceps</i> vs. <i>chalconota</i>	< 0.001	0.10	0.20	0.02	0.20	–
<i>rufipes</i> vs. <i>chalconota</i>	< 0.001	0.038	0.11	0.11	0.04	< 0.001
Females						
<i>labialis</i> vs. <i>eschatia</i>	< 0.001	0.20	0.002	0.07	0.002	0.002
<i>labialis</i> vs. <i>parvaccola</i>	0.04	0.22	0.30	0.25	0.002	–
<i>labialis</i> vs. <i>raniceps</i>	< 0.001	0.01	0.20	0.02	< 0.001	0.002
<i>labialis</i> vs. <i>megalonesa</i>	< 0.001	0.16	0.08	0.55	< 0.001	0.002
<i>labialis</i> vs. <i>rufipes</i>	< 0.001	0.05	0.40	0.88	0.008	0.003
<i>labialis</i> vs. <i>chalconota</i>	< 0.001	0.07	< 0.001	0.18	0.09	–
<i>parvaccola</i> vs. <i>eschatia</i>	< 0.001	0.13	0.006	0.13	0.60	0.055
<i>parvaccola</i> vs. <i>megalonesa</i>	< 0.001	0.78	0.003	0.14	0.41	< 0.001
<i>parvaccola</i> vs. <i>raniceps</i>	< 0.001	0.49	0.14	0.29	0.17	< 0.034
<i>parvaccola</i> vs. <i>rufipes</i>	< 0.001	0.50	0.41	0.10	< 0.001	0.035
<i>parvaccola</i> vs. <i>chalconota</i>	< 0.001	0.10	0.002	–	0.02	–
<i>eschatia</i> vs. <i>megalonesa</i>	0.014	0.15	0.68	0.90	0.45	0.006
<i>eschatia</i> vs. <i>raniceps</i>	< 0.001	0.01	0.07	0.89	0.36	0.20
<i>eschatia</i> vs. <i>rufipes</i>	< 0.001	0.03	0.46	0.15	0.001	0.07
<i>eschatia</i> vs. <i>chalconota</i>	< 0.001	0.049	0.28	–	0.001	–
<i>megalonesa</i> vs. <i>raniceps</i>	< 0.001	0.18	0.07	0.79	0.49	0.06
<i>megalonesa</i> vs. <i>rufipes</i>	< 0.001	0.24	0.43	0.11	< 0.001	0.12
<i>megalonesa</i> vs. <i>chalconota</i>	< 0.001	0.16	0.033	–	< 0.001	–
<i>raniceps</i> vs. <i>rufipes</i>	< 0.001	0.11	0.11	0.10	< 0.001	0.12
<i>raniceps</i> vs. <i>chalconota</i>	< 0.001	0.96	0.024	–	< 0.001	–
<i>rufipes</i> vs. <i>chalconota</i>	0.21	0.10	0.04	–	0.04	–

Student's *t*-test used for SVL, Mann–Whitney test used for body proportions. Abbreviations are as defined in the Material and Methods.

Rana chalconota (part) Boulenger, 1920: 201; Smith, 1930: 109.

Rana chalconota raniceps (part) Inger, 1966: 177.

The type locality of this taxon is Malacca, Peninsular Malaysia. Boulenger (1887) stated that the

types of *labialis* had dark spots dorsally, illustrated in his plate X, fig. 1, and that males had no humeral glands. Boulenger (1920) gave the SVL range of three male syntypes as 34–36 mm and that of three female syntypes as 42–49 mm. We have examined the type series and have detected weak humeral glands in the

Table 7. Comparison of syntypes of *Rana labialis* Boulenger with two Peninsular Malaysian clades and with a sample from Selangor, Peninsular Malaysia

	<i>Rana labialis</i>	Clade*	Clade†	Selangor	Sg. Tupah‡
	types	<i>Rana cf. labialis</i>	<i>Rana sp.</i>	<i>Rana labialis</i>	<i>Rana cf. labialis</i>
Females					
<i>N</i>	1	1	1	19	2
SVL (mm)	48.8	47.7	43.5	38.2–48.3	38.3–47.7
T/SVL	0.582	0.595	0.566	0.543–0.604	0.577–0.595
HW/SVL	0.305	0.310	0.306	0.275–0.304	0.287–0.310
HL/SVL	0.377	0.356	0.391	0.356–0.391	0.356–0.379
TYM/SVL	0.074	0.092	0.092	0.068–0.083	0.086–0.092
DF3/SVL	0.045	0.058	0.065	0.045–0.060	0.046–0.058
Back§	+	0	0	+ = 11, 0 = 7	0
Males					
<i>N</i>	2	1	1	14	2
SVL (mm)	33.6–35.8	37.2	30.4	28.6–34.9	30.8–34.0
T/SVL	0.562–0.581	0.581	0.589	0.508–0.603	0.578–0.600
HW/SVL	0.293–0.303	0.323	0.309	0.273–0.318	0.288–0.302
HL/SVL	0.397–0.414	0.390	0.421	0.369–0.418	0.393–0.406
TYM/SVL	0.101–0.119	0.105	0.122	0.089–0.119	0.106–0.117
DF3/SVL		0.060	0.047	0.043–0.061	0.047–0.049
Back§	+	+	0	+ = 11 0 = 3	+ = 1, 0 = 1

*Female FRIM 1539, male FRIM 829.

†Female FRIM 1418, male FRIM 826; = unnamed lineage of Figure 2.

‡Females FRIM 1539, 1048, males FRIM 1047, 1415; tissues not available.

§+ = back spotted, 0 = back not spotted.

males, which have constricted nuptial pads. Our measurements are 33.6–35.8 mm for two syntypic males and 48.8 mm for a single female. We here designate that female, BMNH 1947.2.3.40, as the lectotype of *Rana labialis* Boulenger. A description of the lectotype is given below.

The relationships and specific assignments of frogs from Peninsular Malaysia are not clear. The continental populations (Thailand and Peninsular Malaysia) of the *chalconota*-like frogs clearly exhibit a great deal of genetic structure. The molecular phylogenetic analysis (Fig. 2) shows three distinct, genetically divergent clades (maximum uncorrected pairwise sequence divergence of 11.90%; Table 5) from Peninsular Malaysia, one of which is phylogenetically unrelated to the other two (Fig. 2). We attempted to amplify historical mtDNA from the lectotype of *labialis* following the extraction protocol of Stuart *et al.* (2006), but did not succeed. Consequently, assigning any of these clades to *labialis* must at this point depend on morphological data alone.

The Peninsular Malaysian specimens (and tissues) are from three localities: Gunung Jerai (about 450 km from the type locality of *labialis*), Penang Island (about 410 km) and Selangor (about 125 km). Five specimens from Penang Island and three from

Gunung Jerai, in northern Peninsular Malaysia, constitute a clade ('*cf. labialis*'; Fig. 2), ten from Selangor ('*labialis*'; Fig. 2) constitute another and four more from Gn. Jerai form the third, distantly related clade ('unnamed lineage'; Fig. 2). We have examined an additional 22 long-preserved specimens from Selangor without associated tissues. All Selangor specimens resemble the lectotype and the other type specimens of *labialis* in the prevalence of dorsal spotting; all of the types have the dorsal spots and 25 of the 32 from Selangor are also spotted. The Selangor frogs also agree with types in size and body proportions (Table 7), but differ from frogs from nearby southern Thailand (Table 8). We assign these Selangor frogs to the species *labialis*.

Taxonomic assignment of the '*cf. labialis*' Malaysian frogs is not certain. They differ from the types of *labialis* and the Selangor frogs we assign to that species in dorsal spotting; only one of seven '*cf. labialis*' frogs is spotted. Males of this clade have slightly wider heads (median 0.323 of SVL) than males from Selangor (median 0.296); the two arrays differ significantly (Mann–Whitney test; $P < 0.02$). Yet the morphological differences between these two Malaysian clades are not as great as the differences between sympatric pairs of species, e.g. *raniceps* and *megalonesa* in Borneo (see

Table 8. Comparison of southern Thailand frogs with *Rana labialis* from Selangor, Peninsular Malaysia

	Males		Females	
	Selangor	Thailand	Selangor	Thailand
SVL (mm)				
<i>N</i>	16	22	20	17
Range	28.6–34.9	30.6–39.6	38.2–48.3	41.7–56.6
Mean ± SE	32.46 ± 0.55	34.14 ± 0.39	44.10 ± 0.12	47.57 ± 0.96
	$T = 2.50, P = 0.018$		$T = 3.12, P = 0.004$	
<i>T</i> /SVL				
<i>N</i>	15	20	20	16
Range	0.532–0.603	0.538–0.622	0.543–0.641	0.557–0.609
Median	0.559	0.590	0.580	0.582
	$U = 239, P = 0.012$		$U = 191, P = 0.52$	
HW/SVL				
<i>N</i>	16	20	20	17
Range	0.273–0.318	0.275–0.326	0.248–0.307	0.288–0.325
Median	0.296	0.310	0.290	0.307
	$U = 242, P = 0.009$		$U = 270, P = 0.002$	
HL/SVL				
<i>N</i>	16	20	20	17
Range	0.369–0.418	0.379–0.424	0.356–0.391	0.356–0.412
Median	0.398	0.401	0.382	0.389
	$U = 225, P = 0.038$		$U = 240.5, P = 0.032$	
TYM/SVL				
<i>N</i>	17	20	20	17
Range	0.089–0.119	0.096–0.127	0.068–0.083	0.077–0.095
Median	0.105	0.109	0.078	0.087
	$U = 215, P = 0.09$		$U = 273.5, P = 0.002$	
DF3/SVL				
<i>N</i>	10	13	17	14
Range	0.046–0.061	0.053–0.065	0.045–0.060	0.052–0.063
Median	0.052	0.057	0.052	0.060
	$U = 101, P = 0.025$		$U = 208, P < 0.001$	

Student's *t*-test (*T*) used for SVL, Mann–Whitney test (*U*) used for body proportions.

below) and *parvacola* and *rufipes* in Sumatra (see below). We believe that further sampling in Peninsular Malaysia is needed before the status of the northern Malaysian frogs can be resolved. Treating them now as conspecific with *labialis* would render that species paraphyletic (Fig. 2).

We have had only two vouchers of the clade 'unnamed lineage', and these are phylogenetically unrelated to other frogs from Peninsular Malaysia (Fig. 2). The small sample size precludes identification of morphological distinctions. Consequently, despite the phylogenetic divergence of these two frogs, we believe it is premature to designate them formally as a species at this time. More specimens (with associated tissues) are needed from the northern portions of Peninsular Malaysia in order to evaluate the status of this clade. What is clear at this point

is that there are three divergent mitochondrial lineages of this complex in Peninsular Malaysia.

Description of lectotype

BMNH 1947.2.3.40: Adult female. Habitus slender, head as wide as trunk; legs long and slender. Head narrow, triangular; snout pointed, longer than eye diameter, slightly depressed dorsally near tip, projecting beyond lower jaw; nostril on side of snout, much closer to tip of snout than to eye; canthus sharply angular, not constricted; lores slightly sloping, concave; interorbital wider than upper eyelid and wider than internarial; tympanum distinct, diameter 2/5 diameter of eye; vomerine teeth in short, oblique groups between choanae, distance between groups subequal to distance from choanae but less than length of one group.

Fingers long, slender, third finger slightly longer than snout; fingers without webbing, but a narrow dermal fringe along medial edge of three outer fingers; tips of fingers expanded into distinct discs, that of first finger much narrower than that of second, disc of third finger slightly greater than half diameter of tympanum, discs of all with horizontal, circum-marginal grooves; relative finger lengths $3 > 4 > 2 > 1$; subarticular tubercles elevated; a supernumerary tubercle at base of three outer fingers. Tips of toes expanded into discs with circummarginal grooves, discs not as wide as those of two outer fingers; webbing extensive, reaching base of discs on outer margins of first three toes and on inner margin of fifth toe; fourth toe fully webbed to distal subarticular tubercle, with narrow fringe extending to base of disc; a narrow dermal ridge along outer margin of fifth toe; inner metatarsal tubercle oval, length about half its distance to subarticular tubercle of first toe; a distinct, round outer metatarsal tubercle.

Skin of back granular, densely covered with low, round tubercles; an indistinct dorsolateral fold continued forward to eye as supratympanic fold; sides tubercular, rugose; throat, chest and anterior half of abdomen smooth, rear of abdomen rugose; a low rictal gland below tympanum, separated from a second smaller post-rictal gland.

Colour in preservative of back brown, darker on sides; back with many small, round black spots; upper lip and rictal glands chalky white; venter cream-coloured, chin, chest and anterior portion of abdomen marked with brown spots; dorsal surfaces of limbs brown, with dark crossbars; posterior surface of thigh brown with indistinct light areas; ventral surfaces of thigh and calf cream-coloured, heavily spotted with dark brown.

Measurements (mm) of lectotype: SVL 48.8, T 28.4, HW 14.9, HL 18.4, snout 8.8, eye diameter 6.1, tympanum 3.6, width of disc third finger 2.2.

In specimens from Selangor the pineal body is faintly visible roughly in line with the anterior corners of the upper eyelid; we failed to note this character in the lectotype. In males from Selangor the granules of the skin on the back bear fine spinules. The hind limb of most frogs from Selangor have distinct dark crossbars.

Material examined

Peninsular Malaysia: Melaka (= Malacca) (2°14'N/102°14'E) BM 1947.2.3.40, 1947.2.3.44–45 syntypes; Johore, near Tangkak (2°14'N/102°33'E) FMNH 100963; Selangor, Kepong, Bukit Lagong Forest Reserve (3°12'N/101°38'E) FMNH 143789, 143798-99, 143801, 143806, 143813, 143819, 143825, 143827, 143832, 143834, 143838, 143851, 143863, 143867, 143869, 143875, 143879, 143883-4, 186317; Selangor,

Forest Research Institute compound FRIM 1118-27; Pahang, Janda Baik (3°21'N/101°53'E) FMNH 186304; Penang, Air Hitam Dam (5°30'N/100°28'E) FRIM 1225-28; Penang, Teluk Bahang Recreational Forest FRIM 1231; Pahang, Pekan (3°30'N/103°25'E) FRIM 663-66; Kedah, Gunung Jerai (5°47'N/100°26'E) FRIM 828-9, 1047-8, 1415, 1539.

Comparisons

Rana labialis as defined here is smaller than *R. chalconota* from Java and southern Sumatra, *R. megalonesa* from Borneo and *R. rufipes* from Sumatra (Table 2). It also differs from *R. chalconota* and *rufipes* in the constriction of the nuptial pad (not constricted in *chalconota* or *rufipes*). Comparison with the species from Thailand is made below.

***RANA ESCHATIA* SP. NOV.**

(Previously referred to as Thailand morphotype)

Rana labialis Smith, 1916: 168.

Rana chalconota Smith, 1930: 109.

Holotype

THNHM 05677 (field number 66721), an adult female from Ngao Falls National Park (9°56'N/98°43'E), Ranong Province, Thailand. Collected on a gravel bank 0.1 m from the edge of a stream in secondary forest, 26.xi.2004, by Jennifer Sheridan and Tanya Chan-ard.

Paratypes

From the type locality FMNH 268523, 268526-28, 268530 (adult males with nuptial pads) FMNH 268524, 268529 (adult females with convoluted oviducts), FMNH 268521, 268525 (juveniles).

Etymology

Specific name from *eschatia*, Gr., outskirts, referring to distribution at the edge of the geographical range of the group.

Referred material

Thailand: FMNH 268852-54, 268856-57 Khao Luang National Park (8°30'N/99°45'E), Nakhon Si Thammarat Prov.; FMNH 268858, 268860, 268869 Khao Phanom Bencha National Park (8°14'N/99°E), Krabi Prov.; FMNH 268872, 268874-84 Khao Sok National Park (8°56'N/98°34'E), Surat Thani Prov.; FMNH 268531-4, 268536-9, THNHM 05690, 05695 Kaeng Krung National Park (9°34'N/98°49'E), Surat Thani Prov..

Diagnosis

A moderate-sized species of the *chalconota* group with males up to 40 mm SVL, females up to 57 mm, no

dorsal spotting, relatively wide head (HW/SVL usually > 0.305), relatively long leg (T/SVL usually > 0.575) and males with constricted or divided nuptial pads.

Description

Habitus slender, head slightly wider than trunk, legs long. Head triangular; snout obtusely pointed, rounded in profile, projecting beyond lower jaw, longer than diameter of eye; nostril lateral, very close to tip of snout; canthus angular, not constricted; lores concave, vertical; interorbital wider than upper eyelid and internarial; tympanum distinct, about two-thirds eye diameter in females, slightly larger in males, inside its rim the tympanum is slightly depressed relative to the surface of the temporal region; vomerine teeth in oblique groups, gap between groups less than length of one group and equal to distance from choana.

Fingers long, third finger longer than snout; fingers without webbing; second and third fingers with narrow, movable fold of skin along medial margins; tips of three outer fingers with wide discs, that of third finger almost equal diameter of tympanum in female; disc of first finger much narrower than that of second; all discs with circummarginal grooves; subarticular tubercles conspicuous; third finger with two small supernumerary tubercles, bases of second and fourth fingers with a single supernumerary tubercle. Tips of toes expanded into discs smaller than those of outer fingers, but with circummarginal grooves; webbing extensive, reaching discs of first three toes on lateral margins and disc of fifth toe medially; fourth toe webbed to distal subarticular tubercle medially and slightly beyond that laterally; no dermal ridge along outer margins of first and fifth toes; a low oval inner metatarsal tubercle and a round outer one.

Skin of back granular, in males granules weakly spinose; dorsolateral fold distinct, low; ventral surfaces smooth, except weakly rugose at rear of abdomen; rectal glands present.

Colour in preservative dark brown dorsally and laterally; no black spots on dorsal surfaces; ventral surfaces cream-coloured or white; in some individuals throat with round dark spots; limbs without dark crossbars; rear of thigh dark brown with indistinct lighter round areas.

Measurements (mm) of holotype: SVL 55.6, T 31.0, HW 16.0, HL 19.8, TYM 4.6, DF3 3.2.

Variation

Adult females 42.8–56.6 mm, mean 47.57 ± 0.96 mm ($N = 17$), males 30.6–39.6 mm, mean 34.14 ± 0.39 mm ($N = 22$). Variation in body proportions given in Table 8. Relative tympanum diameter in females 0.077–0.095, in males 0.096–0.127. The sexes do not differ in relative head width; HW/SVL in females

0.288–0.325 (median 0.308), in males 0.275–0.326 (median 0.310). All males have constricted or divided nuptial pads and vocal sac openings at the corners of the mouth.

Comparisons

Males of *Rana eschatia* are most similar in size to those of *R. labialis* (Selangor) and *R. parvaccola* (Table 2), but females of *eschatia* are larger than females of those two (Tables 2 and 6). *Rana eschatia* also differs from those two species in the absence of black spots on the back and in having a wider head in both sexes (Tables 2 and 6). *Rana eschatia* is larger than *R. raniceps* (both sexes) and has a longer leg (T/SVL) and a smaller tympanum in males (Tables 2 and 6). *Rana eschatia* is smaller than *R. megalonesa*, *R. rufipes* and *R. chalconota* and differs from the latter two in the length of the tibia (T/SVL) and in the form of the nuptial pad, which is constricted or divided only in *eschatia*.

RANA RANICEPS (PETERS, 1871)

(Previously referred to as Borneo Small morphotype)

Polypedates raniceps Peters, 1871: 580 – Sarawak.

Rana raniceps Iskandar & Colijn, 2000: 91; Stuart *et al.*, 2006: 473.

Rana (Chalcorana) raniceps Dubois, 1992: 328.

Rana chalconota raniceps Inger, 1966: 177.

Material examined

MSNG 29376 lectotype (see Capocaccia, 1957) from 'Sarawak,' Bintulu Division: Labang Forest Reserve (3°21'N/113°27'E) FMNH 148083-219; Samarakan (2°56'N/113°07'E) FMNH 267965-66; Bukit Sarang (2°39'N/113°03'E) FMNH 267958-64. The paralectotype designated by Capocaccia (MSNG 50536) is a rhacophorid, with intercalary cartilages, a distinct projection at the heel and the entire abdomen coarsely granular, but no outer metatarsal tubercle.

Diagnosis

SVL of lectotype female 40.4 mm, other females 33.1–42.3 mm, mean 38.20 ± 0.48 mm ($N = 30$); males 27.6–34.1 mm, mean 30.35 ± 0.93 mm ($N = 8$). DF3/SVL 0.055–0.068, median 0.060. Back usually without dark spots. Males with nuptial pad constricted; male TYM/SVL 0.089–0.127 ($N = 6$).

Descriptive notes

The head is triangular and the snout slightly projecting. Inside its rim, the tympanum is slightly depressed relative to the surface of the temporal

region. The pineal body is faintly visible and is in line with the anterior borders of the upper eyelids. The skin of the back is granular and in males is set with many fine spinules. The hind limb is without cross-bars in most preserved specimens.

Comparisons

This is the smallest member of the *chalconota* group, differing significantly ($P \leq 0.001$, both sexes) from all other species except males of *parvaccola* (see below) (Tables 2 and 6). It differs from the two species from Padang, West Sumatra (*parvaccola* and *rufipes* see below), *labialis* and co-occurring *R. megalonesa* (see below) samples in the low frequency of dark dorsal spots. The uncorrected pairwise sequence divergence between *R. raniceps* and the co-occurring *R. megalonesa* (see below) is 13.11–13.97% (Table 4).

This species is known only from low-lying areas of west-central Sarawak.

***RANA MEGALONESA* SP. NOV.**

(Previously referred to as Borneo Large morphotype)

Rana chalconota (part) Boulenger, 1920: 201; van Kampen, 1923: 217.

Rana chalconota raniceps Inger, 1966: 177.

Rana cf. chalconota Stuart *et al.*, 2006: 473.

Holotype

FMNH 267821, an adult female from Bukit Sarang (2°39'N/113°03'E), Bintulu Division, Sarawak (Borneo), Malaysia. Collected in a freshwater swamp forest (20 m a.s.l.) 1 m above ground on a shrub, 11.xi.2004, by Freddy Paulus and Patrick Francis.

Paratypes

From type locality FMNH 267814-15, 267818, 267825 adult males with nuptial pads, FMNH 267816, 267819, 267824 adult females with convoluted, enlarged oviducts; FMNH 267817, 267820, 267822-23 subadult females.

Etymology

Specific name from *megalo-*, Gr., large, and *nesos*, Gr., island, referring to its distribution on the large island of Borneo.

Referred material

Sarawak: Belaga District, Sg. Segaham (2°44'N/113°55'E) FMNH 220474, 220477-78, 220484, 220492, 220512-13, 220526, 220541-43, 220547, 220549, 220551-52, 220554; Kapit District, Nanga Tekalit (1°37'N/113°35'E) FMNH 220264, 220267-68, 220286, 220297, 220379, 220381, 220383, 220396, 220399,

220404, 220417, 220434, 220447, 220559-60, 220563-64, 220568, 220570, 220572-74, 220576-77, 220579, 220581, 220586, 222955-56; Bintulu Division, Labang Forest Reserve (3°21'N/113°27'E) FMNH 148203-07; Bintulu Division, Sg. Pesu camp (3°07'N/113°48'E) FMNH 156607, 156610-11, 156622, 156627, 156631, 156634-35, 156638, 156640, 156643, 156653-56, 156658, 156660, 156666, 156668, 156674-77, 156680-84, 156687, 156709-13, 156716, 156718, 156720, 156729-31, 156735, 156741, 156747, 156749, 156756-59, 156762, 156765-68. Sabah: Kota Marudu District, Marak Parak (6°18'N/116°42'E) FMNH 235639-45; Lahad Datu District, Danum Valley Research Centre (5°12'N/117°50'E) FMNH 203953-62, 203965, 203969-71, 203974-78, 203980, 203983, 203985, 203987-88, 203991-92; Sipitang District, Mendolong (4°54'N/115°42'E) FMNH 128334, 238336, 238348, 238362, 242797-98, 242801, 242804, 242806-07, 242811; Tawau District, Bukit Tawau Park (4°37'N/117°54'E) FMNH 248339-42, 248345-46, 248348-49; Tawau District, Kalabakan (4°25'N/117°30'E) FMNH 76694, 76696, 76702, 76705, 76715-16, 76718, 76722, 76733, 76738, 76742-43, 76753, 76762-64, 76770, 76779, 76781-82, 76784-86, 76789.

Diagnosis

A large-sized member of the *R. chalconota* group; distinguished from other forms by combination of females usually > 50 mm, males > 35 mm; T/SVL usually > 0.56, HW/SVL usually > 0.30, DF3/SVL > 0.06; males with nuptial pad constricted or divided and with weak humeral gland discernible only upon dissection.

Description

Habitus moderately slender, head slightly wider than trunk, legs long. Head triangular; snout obtusely pointed, projecting beyond lower jaw, longer than diameter of eye; nostril on side of snout, closer to tip of snout than to eye; canthus angular, not constricted; lores concave, weakly sloping; interorbital wider than upper eyelid and wider than internarial; pineal body faintly visible, between anterior corners of upper eyelids; tympanum distinct, about two-thirds eye diameter in female, slightly larger in males, slightly depressed relative to surface of temporal region; vomerine teeth in short, oblique groups between choanae, distance between groups shorter than distance from choanae.

Fingers long, length of third finger equal to distance from rear of eye to nostril; fingers without webbing; second and third fingers with narrow, movable fold of skin on medial margins; tips of three outer fingers with wide discs, that of third finger about two-thirds diameter of tympanum in female, disc of first finger about half width of disc of second

finger, all discs with circummarginal grooves; subarticular tubercles conspicuous, rounded; base of third finger with one or two supernumerary tubercles, bases of second and fourth fingers with one supernumerary tubercle. Tips of toes expanded into discs smaller than those of fingers, but with circummarginal grooves; webbing extensive, to base of discs on lateral margins of three inner toes and on medial margin of fifth, to base of disc on medial margin of fourth toe or between disc and distal subarticular tubercle; a narrow ridge of skin medially along first toe and a similar one along outer edge of last joint of fifth toe; a low, oval inner metatarsal tubercle and a distinct, round outer one.

Skin of back weakly granular with scattered colourless spinules in females; males with densely crowded, taller spinules on all dorsal surfaces including head and eyelid, similar spinules on lores; a distinct, but low dorsolateral fold; ventral surface of body smooth, weakly rugose at rear of abdomen; a ridge-like rictal glandular swelling followed after a narrow gap by a glandular swelling above the axilla.

Colour in preservative brown above and on sides, darker on side of head, upper lip white; many scattered dark spots on back and usually on head; ventral surfaces white, throat and chest with or without small dark spots; hind limb without dark crossbars in most preserved individuals; rear of thigh brown with faint, round lighter markings.

Measurements (mm) of holotype: SVL 53.8, T 28.4, HW 16.6, HL 21.1, TYM 4.4, DF3 3.4.

Variation

Females 45.4–65.6 mm, mean 53.66 ± 0.45 mm ($N = 115$); males 33.3–48.2 mm, mean 39.21 ± 0.34 mm ($N = 113$). DF3/SVL 0.054–0.076, median 0.064 ($N = 104$). TYM/SVL of males 0.089–0.135, median 0.112 ($N = 76$). Humeral gland in males usually detectable only by dissection. Frequency of dark spotting on back varies among samples. In two samples from eastern Sabah dorsal spots were present in 18 of 28 frogs; in two samples from western Sabah dorsal spots were present in only seven of 29. The spots were present in two-thirds of frogs from the Bintulu Division of west-central Sarawak but in only four of 90 from south-eastern Sarawak. Frequency of constriction of the nuptial pad of males also varies. In frogs from eastern Sabah (three localities) the nuptial pad was constricted or divided in 22 of 28 males. The frequency of constriction in males from western Sabah (two localities) was five of 13. In males from south-eastern Sarawak (three localities) the frequency of constricted or divided nuptial pads was 24 of 51 individuals. The nuptial pad was constricted or divided in four of eight males from the Bintulu Division, west-central Sarawak.

Comparisons

The difference between this species and the co-occurring *R. raniceps* in size is striking. The mean SVL of males of *R. megalonesa* is roughly 10 mm larger than that of *R. raniceps* and the difference between means of females is almost 15 mm (Table 2). Individuals of *Rana megalonesa* that co-occur with *R. raniceps* differ from the latter in higher frequency of dark spots on the back.

Although it is a large form of the *chalconota* group, females of *R. megalonesa* are smaller than those of both *R. rufipes* (see below) and Javan *R. chalconota* and its males smaller than those of *R. rufipes* (Tables 2 and 6). In addition to the size difference, the new species also differs from *R. rufipes* in having a relatively larger tympanum (Tables 2 and 6) and in the form of the nuptial pad (not constricted or divided in *R. rufipes*). Both males and females of *R. megalonesa* are larger than those of *R. labialis*, *R. eschatia* and *R. parvaccola* (see below). Relative head width (HW/SVL) of *R. megalonesa* is larger than that of *R. labialis* and *R. parvaccola*. Relative width of the tympanum (TYM/SVL) of *R. megalonesa* is larger than that of *R. labialis* in both sexes (Tables 2 and 6).

The uncorrected pairwise sequence divergence between *R. megalonesa* and the co-occurring *R. raniceps* is 13.11–13.97% (Table 4).

RANA RUFIPES SP. NOV.

(Previously referred to as Padang Large morphotype)

Rana cf. *chalconota* Inger & Iskandar, 2005: 138; Stuart *et al.*, 2006: 473.

Holotype

FMNH 268580 (field no. 15864), an adult female from Limau Manis, 373 m (0°54'S/100°28'E), Padang, West Sumatra, Indonesia. Collected in a disturbed forest 7.vii.2001, by Djong Hon-Tjong and David Gusman.

Paratypes

FMNH 268572, 268578–79, two adult females and one juvenile collected at same site and elevation as holotype on 3.vii. and 7.vii.2001; FMNH 268573–77, 268581–83, four adult males, four adult females from same locality as holotype, but at 405 m on 4.vii. and 10–11.vii.2001; FMNH 268584, 268587–88 two adult males, one adult female from Padang Jernih (0°52'S/100°28'E) 255–340 m, Padang, West Sumatra, 26.vii.2001; FMNH 268585–86, one adult male, one juvenile from Sikayan Ubi (0°53'S/100°27'E) 292 m, Padang, West Sumatra, 23.vii.2001. All with same collectors as holotype.

Etymology

Specific name from *rufus*, L., meaning reddish, and *pes*, L., meaning foot, referring to the reddish tinge on the underside of the webbing in life.

Diagnosis

A large form of the *Rana chalconota* group, adult females 46–64 mm SVL, males with nuptial pads 44–48 mm. Dark spots present on back. Nuptial pad of males not constricted. Humeral gland of males visible only by dissection. Tympanum relatively small, TYM/SVL of females usually < 0.068, of males usually < 0.106.

Description

Habitus moderately slender, head slightly wider than trunk, legs long. Head triangular, slightly longer than broad; snout obtusely pointed, projecting slightly beyond lower jaw, longer than diameter of eye; nostril on side of snout, closer to tip of snout than to eye; canthus angular, not constricted; lores vertical, concave; interorbital wider than upper eyelid and wider than internarial; pineal body faintly visible between anterior corners of upper eyelids; tympanum distinct, about diameter of eye in females, slightly larger in males, inner portion slightly depressed; vomerine teeth in short, oblique groups, distance between groups equal to distance from choanae.

Fingers long, length of third finger equal to distance from rear of eye to nostril; without webbing; second and third fingers with narrow, movable fold of skin on medial margins; tips of three outer fingers with wide discs, that of third finger three-quarters or more the diameter of the tympanum in females, disc of first finger about half width of disc of second finger, all discs with circummarginal grooves; subarticular tubercles conspicuous; bases of third and fourth fingers with one or two supernumerary tubercles, base of second finger with one; finger lengths $3 > 4 > 2 > 1$. Tips of toes expanded into discs smaller than those of fingers, but with circummarginal grooves; webbing extensive, to base of discs on lateral margins of first three toes and on medial margin of fifth, medial edge of fourth toe fully webbed to just beyond the distal subarticular tubercle; narrow dermal ridge along medial edge of distal joint of first toe and along lateral edge of distal joint of fifth toe; a low, oval inner metatarsal tubercle, shorter than distance to subarticular tubercle of first toe; a distinct, round outer metatarsal tubercle.

Skin of back granular in females, in males granules tipped with colourless asperities or spinules; similar spinules present on lores in some males, the variation probably an artefact of preservation; a distinct, low dorsolateral fold; rear of abdomen rugose, rest of venter smooth.

Males with paired vocal sac openings on floor of mouth. Whitish, velvety nuptial pad on dorsal and medial surfaces of first finger, not constricted. The humeral gland is detectable only by cutting and folding back the skin of the upper arm.

Colour in preservative medium brown dorsally and on sides; side of head dark brown, upper lip white; dorsal surfaces with small dark spots; ventral surfaces of body whitish, unmarked; dark crossbars visible on hind limb only in a few individuals; ventral surface of webbing reddish, the colour fading in preservative.

Measurements (mm) of holotype: SVL 62.0, tibia 34.3, head width 18.9, head length 23.2, tympanum diameter 4.8, width of disc of third finger 4.1.

Variation

Females 53.8–64.4 mm, mean 60.58 ± 1.55 mm ($N = 6$); males 43.7–48.4 mm, mean 45.36 ± 0.51 mm ($N = 8$). In the following data on body proportions, $N = 7$ for both sexes. T/SVL 0.537–0.591, median 0.560 ($N = 12$), HW/SVL of females 0.267–0.312, of males 0.287–0.309, HL/SVL of females 0.360–0.397, of males 0.370–0.389, TYM/SVL of females 0.065–0.077, of males 0.097–0.108; DF3/SVL 0.053–0.072, median 0.062 ($N = 11$).

Comparisons

Rana rufipes differs conspicuously from the form with which it co-occurs in West Sumatra, *R. parvaccola* (see below), in size, coloration of the webbing (Inger & Iskandar, 2005), relative size of the tympanum (TYM/SVL) and width of the disc of the third finger (DF3/SVL) (see Tables 2 and 6). The uncorrected pairwise sequence divergence between *R. rufipes* and the co-occurring *R. parvaccola* (see below) is 14.75–14.93% (Table 4).

Rana rufipes is one of the largest members of this species group, with males larger than those of any other form and females larger than those of any other except the Javan species (Tables 2 and 6). This new species has the relatively smallest tympanum in the group, differing from all except males of *R. labialis* in TYM/SVL (Tables 2 and 6). It is also the only member of the group in which the ventral surface of the webbing is reddish.

***RANA PARVACCOLA* SP. NOV.**

(Previously referred to Padang Small morphotype)

Rana chalconota Inger & Iskandar, 2005: 138.

Rana cf. chalconota Stuart *et al.*, 2006: 473.

Holotype

FMNH 268605 (field tag 16279) adult female from Sarasah Buntah 528 m (0°06'S/100°40'E), Paya-

kumba, West Sumatra. Collected in disturbed forest on 8.viii.2001, by Djong Hon-Tjong and David Gusman.

Paratypes

FMNH 268604, 268606-47, 27 adult males, ten adult females, six juveniles from same locality and elevation as holotype, 9–17.viii.2001; FMNH 268589-92, four adult males from Limau Manis 373 m (0°54'S/100°28'E), Padang, West Sumatra, 2–9.vii.2001; FMNH 268593, one juvenile from Padang Jernih 340 m (0°52'S/100°28'E), Padang, West Sumatra, 27.vii.2001; FMNH 268594-603, ten adult males from Batang Harau 566 m (0°04'S/100°39'E), Payakumbuh, West Sumatra, 5–7.viii.2001; FMNH 268648-50, one adult male, two adult females from Akar Berayun 546 m (0°06'S/100°39'E), Payakumbuh, West Sumatra, 20–21.viii.2001. All with same collectors as the holotype.

Etymology

Specific name from *parvus* L., meaning small, and *accola* L., meaning neighbour, referring to its size relative to the co-occurring species *rufipes*.

Diagnosis

A small form of the *Rana chalconota* group, SVL of females < 45 mm, of males < 40 mm. Dark spots present on back. Nuptial pad of males not constricted.

Description

Habitus slender, head very slightly wider than trunk, legs long. Head triangular, longer than broad; snout narrowly rounded, projecting slightly beyond lower jaw, longer than diameter of eye; nostril on side of snout, much closer to tip of snout than to eye; canthus angular, not constricted; lores concave, weakly oblique; interorbital wider than upper eyelid, wider than internarial; pineal body visible, in line with front borders of upper eyelids; tympanum distinct, about two-thirds diameter of eye in females, larger in males; vomerine teeth in short, oblique groups, distance between groups equal to or slightly greater than distance between groups and choanae.

Fingers long, length of third finger less than distance from rear of eye to nostril; without webbing; second and third fingers with narrow, movable dermal fold on medial margins; tips of three outer fingers with wide discs, that of third finger about two-thirds diameter of tympanum in females, disc of first finger about half width that of second finger, all discs with circummarginal grooves; subarticular tubercles conspicuous; three outer fingers with a supernumerary tubercle; finger lengths $3 > 4 > 2 > 1$. Tips of toes expanded into discs smaller than those of fingers, but with circummarginal grooves; webbing extensive, to

base of discs on lateral margins of first three toes and medial margin of fifth, medial edge of fourth toe fully webbed to distal subarticular tubercle; narrow dermal ridge along outer edge of last joint of fifth toe and medial edge of last joint of first toe; a low, oval inner metatarsal tubercle and a distinct, round outer one.

Skin of back granular, those on back of males tipped with small, colourless spinules; similar spinules present on eyelid and lower portion of lores in males; a distinct, low dorsolateral fold; rear of abdomen rugose, rest of venter smooth.

Males with paired vocal sac openings on floor of mouth. Whitish, velvety nuptial pad on dorsal and medial surfaces of first finger, nuptial pad not constricted. A weak humeral gland detectable by folding back skin of upper arm.

Colour in preservative brown dorsally and on sides; side of head darker; upper lip lighter, but dusted with melanophores; dorsal surfaces with small black spots; ventral surfaces of body whitish, lightly dusted with melanophores; hind limb without dark crossbars in most individuals; ventral surface of webbing black.

Measurements (mm) of holotype: SVL 41.8, tibia 23.7, head width 12.2, head length 15.4, diameter of tympanum 3.8, width of disc of third finger 2.3.

Variation

Mature females 37.8–43.0 mm, mean 41.54 ± 0.68 mm ($N = 15$), males 29.0–38.1 mm, mean 32.39 ± 0.76 mm ($N = 13$); T/SVL 0.523–0.608, median 0.574; HW/SVL of females 0.268–0.309, of males 0.273–0.330; HL/SVL of females 0.344–0.403, of males 0.376–0.418; TYM/SVL of females 0.081–0.101, of males 0.103–0.130; DF3/SVL 0.046–0.064, median 0.056.

Comparisons

Comparisons with the co-occurring species, *R. rufipes*, have been made under the heading of that species. *Rana parvaccola* is one of the smallest members of the *chalconota* group. The females are larger than those of *R. raniceps*, and *R. parvaccola* differs from the latter species in higher frequency of dark spotting on the back and in absence of constriction of the nuptial pads. Females of *R. parvaccola* are smaller than those of *R. labialis* and *R. eschatia* (Tables 2 and 6). Relative tympanum diameter is larger in *R. parvaccola* than in Selangor *labialis*. Both sexes of this species are smaller than those of the larger members of the group – *R. chalconota*, *R. megalonesa* and *R. rufipes*. The uncorrected pairwise sequence divergence between *R. parvaccola* and the co-occurring *R. rufipes* is 14.75–14.93% (Table 4).

DISCUSSION

The morphological and molecular data sets and the co-occurrence of distinct forms provide evidence that the concept of *Rana chalconota* as a single, widespread species (as in Boulenger, 1920; Frost, 2006) must be rejected. Similarly, for the same reasons, the concept of this group as a set of two or three forms consisting of *chalconota*, *raniceps* and *labialis* (whether as species or subspecies) (van Kampen, 1923; Inger, 1966; Iskandar & Colijn, 2000) does not fully reflect the diversity seen in this group. Instead the present data suggest that this is a complex of at least seven species in Sundaland – one in Java and southern Sumatra [*R. chalconota* (Schlegel)], two partially co-occurring in Sarawak, Borneo [*R. raniceps* (Peters) and *R. megalonesa* described herein], two partially co-occurring in West Sumatra (*R. rufipes* and *R. parvaccola*, described herein), at least one and possibly three partially co-occurring in Peninsular Malaysia (*R. labialis* Boulenger and one or two unnamed species) and a species in southern Thailand (*R. eschatia*, described herein). Additionally, at least one species in this complex occurs in Sulawesi (*R. mocquardii*). The unnamed lineages in Peninsular Malaysia remain so because, in one case, the morphological evidence is weaker and less convincing than the molecular evidence, while in the second case, we have had available only two specimen vouchers, thus making it difficult to provide a satisfactory, convincing morphological diagnosis. We assume that other workers will collect specimens of these mitochondrial lineages from the northern portion of Peninsular Malaysia and will then be able to assess their taxonomic status more adequately.

A series of hypotheses concerning the distribution of the frogs of Sundaland (Inger & Voris, 2001) suggested that, for species occurring in Peninsular Malaysia, Sumatra and Borneo, intraspecific variation would be less for Malay Peninsula/Sumatra and Malay Peninsula/Borneo pairs of populations than for Borneo/Sumatra pairs. However, the *Rana chalconota* group, with pairs of sympatric species on each of these land masses, indicates the geographical relationships, at least for this complex, are much more complicated. Describing the historical, geographical relations of the species within this complex is also hampered partly because significant portions of the likely range of this species group are not represented in the samples available to us. In particular, the absence of samples from the eastern, low-lying parts of Sumatra, the lowlands and hilly areas of south-eastern Borneo and the southern lowlands of Peninsular Malaysia have prevented the present investigation from providing an entire view of the species. At the very least, material from those

areas will round out the pattern of variation in the species group and provide insight into geographical relationships.

The northward extent of the known distribution of the *R. chalconota* group is approximately 10°N (Ngao Falls National Park 9°56'N) where *R. eschatia* occurs. We have searched for it but have failed to find it at 11°43'N (Huai Yang National Park) and 12°42'N (Kaeng Krachan National Park) in suitable habitats. Woodruff (2003) noted a change from wet seasonal rain forest to mixed deciduous forest just north of the Isthmus of Kra at 11–13°N and he also pointed out that at 10°31'N there were no 'dependably dry months' whereas a dry period of 3–4 months occurred at 11°50'N. It appears that the *R. chalconota* group is limited by the northern extent of perhumid forest.

The occurrence of *R. raniceps* in swamp forests in Sarawak suggests that dispersal of some lineage(s) among present land masses may have been possible during Pleistocene recessions of the sea (Voris, 2000). Peat swamp forests were relatively common on exposed portions of the South China Sea (Hanebuth, Statterger & Grootes, 2000) as they developed behind mangrove forests (Anderson, 1964) that advanced and retreated with changes in sea level. If this were, in fact, the pattern during the Pleistocene, undiscovered representatives of this species group in eastern Sumatra and the lowlands of southern Peninsular Malaysia may be closely related to *R. raniceps*. Another relatively recent event is the barrier to gene exchange between the Sumatran and Javan populations of *R. chalconota*, which, based on changes in sea level (Voris, 2000), could have occurred as recently as 8000 years ago.

The fact that none of the pairs of species from a single land mass consists of species that are each others' sister species provides reason for assuming multiple dispersals or multiple vicariant events among land masses. *Rana parvaccola* from West Sumatra, for example, is the sister species of the Thailand form, *R. eschatia*, but is distantly related to the partially sympatric *R. rufipes* (Fig. 2). *Rana raniceps* in Sarawak is distantly related to the partially sympatric *R. megalonesa*, which is the sister lineage to one consisting of *R. labialis* (Peninsular Malaysia) and *R. parvaccola* (West Sumatra). The two unnamed lineages in northern Peninsular Malaysia are also very distantly related. The timing of these implied dispersals is far from clear. The molecular phylogenetic analysis suggests two biogeographical sets of species that diverged early in the history of the *chalconota*-group: a Borneo–Java–Sumatra sub-group (*raniceps–chalconota–rufipes*) and a Borneo–Sumatra–Malay Peninsula sub-group (*megalonesa–labialis–eschatia–parvaccola*–unnamed peninsular lineage). The most recent land connections available

among sub-group members for each of these were during the Pleistocene sea recessions. However, as the phylogenetic separation of these two sub-groups appears to be quite deep (Fig. 2), their divergence probably pre-dates the Pleistocene. Borneo and the Malay Peninsula had broad land connections through most of the Cenozoic (Hall, 1998) and remained approximately at their present latitude throughout that interval (Hall, 2002). The land mass they formed is the most likely place of origin of the *chalconota* group as both Sumatra and Java experienced subsidence and reduction to small islets during the Miocene and had only tenuous connections with the Borneo–Malay block between the end of the Oligocene (25 Ma) and the Pleistocene sea regressions (Hall, 1998; Voris, 2000). Morley (2000) indicates the existence of rain forest, the vegetation type in which the *R. chalconota* group is prevalent, from the latest Early Miocene into the Pliocene in the areas of present-day Borneo and Malaya.

Had the *raniceps–chalconota–rufipes* subgroup been in existence and widespread during the Miocene, the reduction of Sumatra and Java to fragmented parcels of land would have isolated these populations and provided opportunity for local genetic differentiation.

We postulate the widespread distribution of the ancestor of the clade encompassing *eschatia*, *labialis*, *parvaccola*, *megalonesa* and unnamed northern Peninsular Malaysia in rain forests of the southern part of the mainland peninsula, Borneo and the western range of Sumatra in pre-Quaternary times. The savannas caused by the deterioration of climate accompanying the northern glacial episodes in the Pleistocene (Morley, 2000) fragmented this distribution, forcing populations into the remaining rain forest areas postulated by Morley (2000) in northern Borneo and western Sumatra. Isolated minor refugia in sheltered valleys may have persisted elsewhere (Gathorne-Hardy *et al.*, 2002) on the continental peninsula. The restriction of the *chalconota* group now to areas south of present-day seasonal climates suggests that Pleistocene populations may have been similarly restricted so that, despite the broad land connections available during the periodic sea regressions of the Pleistocene, the geographical fragmentation we see today in this clade was maintained.

The results of this review, like those of several other ranids of Southeast Asia, e.g. the *Odorrana livida* group (Bain *et al.*, 2003; Stuart *et al.*, 2006), suggest that current views of species diversity of the forest frogs of this floristically and geologically complex region are serious under-estimates. Application of molecular techniques to other widespread ‘species’ is likely to expose co-occurring taxa that, once separated by molecular genetics, will also be

seen to differ morphologically. Changes of this nature in our views of species diversity and distribution are likely to affect our views of historical geographical relationships, to stimulate ecological investigations and to have implications for conservation.

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APPENDIX

Tissue samples sequenced in this study. ID refers to the individuals in Figure 2. Institutional abbreviations: FMNH = Field Museum of Natural History, Chicago; FRIM = Forest Research Institute Malaysia, Kuala Lumpur; MZB = Museum Zoologicum Bogoriense, Bogor; UTA = University of Texas, Arlington. Geographical coordinates are provided only if they are not reported in Species Accounts in the text.

ID	Voucher	Field no.	Locality	GenBank accession no.	
				16S	ND3
<i>Rana erythraea</i>					
1	FMNH 257282	63681	Cambodia, Siem Reap Prov., Siem Reap Dist., 13°22'29"N, 103°50'44"E	DQ650393	DQ650353
<i>Rana nigrovittata</i>					
2	FMNH 255434	63396	Laos, Bolikhamxay Prov., Thaphabat Dist., 18°27'N 103°10'E	EF487446	EF487354
<i>Rana chalconota</i>					
3	UTA 53665	MBH 5308	Indonesia, Java, Barat, Desa Sukamahi, near Bogor	DQ650428	DQ650388
4	UTA 53666	MBH 5309	Indonesia, Java, Barat, Desa Sukamahi, near Bogor	Missing	EF487444
5	UTA 53685	ENS 7634	Indonesia, Sumatra, Selatan, outside of Pagaram on road to Lahat	DQ650429	DQ650389
6	UTA 53686	ENS 7769	Indonesia, Sumatra, Lampung, Kalianda, S. side of Gunung Rajabasa	EF487531	EF487445
<i>Rana eschatia</i>					
7	FMNH 268851	50803	Thailand, Nakhon Si Thammarat Prov., Khao Luang National Park	EF487470	EF487379
8	FMNH 268859	50891	Thailand, Krabi Prov., Khao Phanom Bencha National Park	EF487479	EF487388
9	FMNH 268861	50816	Thailand, Nakhon Si Thammarat Prov., Khao Luang National Park	EF487472	EF487381
10	FMNH 268853	50827	Thailand, Nakhon Si Thammarat Prov., Khao Luang National Park	EF487473	EF487382
11	FMNH 268854	50828	Thailand, Nakhon Si Thammarat Prov., Khao Luang National Park	EF487474	EF487383
12	FMNH 268855	50833	Thailand, Nakhon Si Thammarat Prov., Khao Luang National Park	EF487475	EF487384
13	FMNH 268856	50837	Thailand, Nakhon Si Thammarat Prov., Khao Luang National Park	EF487476	EF487385
14	FMNH 268857	50882	Thailand, Nakhon Si Thammarat Prov., Khao Luang National Park	EF487477	EF487386
15	FMNH 268869	50936	Thailand, Krabi Prov., Khao Phanom Bencha National Park	EF487483	EF487392
16	FMNH 268524	66724	Thailand, Ranong Prov., Ngao Falls National Park	EF487501	EF487410
17	FMNH 268860	50894	Thailand, Krabi Prov., Khao Phanom Bencha National Park	EF487480	EF487389
18	FMNH 268862	50900	Thailand, Krabi Prov., Khao Phanom Bencha National Park	EF487481	EF487390

APPENDIX *Continued*

ID	Voucher	Field no.	Locality	GenBank accession no.	
				16S	ND3
19	FMNH 268863	50901	Thailand, Krabi Prov., Khao Phanom Bencha N	EF487482	EF487391
20	FMNH 268858	50888	Thailand, Krabi Prov., Khao Phanom Bencha National Park	EF487478	EF487387
21	FMNH 268870	50976	Thailand, Surat Thani Prov., Khao Sok National Park	EF487484	EF487393
22	FMNH 268872	50980	Thailand, Surat Thani Prov., Khao Sok National Park	EF487485	EF487394
23	FMNH 268873	50981	Thailand, Surat Thani Prov., Khao Sok National Park	EF487486	EF487395
24	FMNH 268531	66803	Thailand, Surat Thani Prov., Kaeng Krung National Park	EF487507	EF487417
25	FMNH 268875	50984	Thailand, Surat Thani Prov., Khao Sok National Park	EF487488	EF487397
26	FMNH 268876	50985	Thailand, Surat Thani Prov., Khao Sok National Park	EF487489	EF487398
27	FMNH 268877	50986	Thailand, Surat Thani Prov., Khao Sok National Park	EF487490	EF487399
28	FMNH 268878	50989	Thailand, Surat Thani Prov., Khao Sok National Park	EF487491	EF487400
29	FMNH 268879	50998	Thailand, Surat Thani Prov., Khao Sok National Park	EF487492	EF487401
30	FMNH 268528	66752	Thailand, Ranong Prov., Ngao Falls National Park	EF487505	EF487414
31	FMNH 268538	66818	Thailand, Surat Thani Prov., Kaeng Krung National Park	EF487513	EF487424
32	FMNH 268521	66717	Thailand, Ranong Prov., Ngao Falls National Park	Missing	EF487407
33	FMNH 268529	66755	Thailand, Ranong Prov., Ngao Falls National Park	EF487506	EF487415
34	FMNH 268530	66756	Thailand, Ranong Prov., Ngao Falls National Park	Missing	EF487416
35	FMNH 268522	66721	Thailand, Ranong Prov., Ngao Falls National Park	EF487499	EF487408
36	FMNH 268523	66723	Thailand, Ranong Prov., Ngao Falls National Park	EF487500	EF487409
37	FMNH 268527	66742	Thailand, Ranong Prov., Ngao Falls National Park	EF487504	EF487413
38	FMNH 268525	66729	Thailand, Ranong Prov., Ngao Falls National Park	EF487502	EF487411
39	FMNH 268852	50815	Thailand, Nakhon Si Thammarat Prov., Khao Luang National Park	EF487471	EF487380
40	FMNH 268874	50982	Thailand, Surat Thani Prov., Khao Sok National Park	EF487487	EF487396
41	FMNH 268532	66808	Thailand, Surat Thani Prov., Kaeng Krung National Park	EF487508	EF487418
42	FMNH 268533	66809	Thailand, Surat Thani Prov., Kaeng Krung National Park	EF487509	EF487419
43	FMNH 268534	66810	Thailand, Surat Thani Prov., Kaeng Krung National Park	EF487510	EF487420
44	FMNH 268537	66817	Thailand, Surat Thani Prov., Kaeng Krung National Park	EF487512	EF487423

APPENDIX *Continued*

ID	Voucher	Field no.	Locality	GenBank accession no.	
				16S	ND3
45	FMNH 268536	66816	Thailand, Surat Thani Prov., Kaeng Krung National Park	EF487511	EF487422
46	FMNH 268535	66811	Thailand, Surat Thani Prov., Kaeng Krung National Park	Missing	EF487421
47	FMNH 268526	66741	Thailand, Ranong Prov., Ngao Falls National Park	EF487503	EF487412
48	FMNH 268539	66819	Thailand, Surat Thani Prov., Kaeng Krung National Park	EF487514	EF487425
49	FMNH 268540	66820	Thailand, Surat Thani Prov., Kaeng Krung National Park	Missing	EF487426
<i>Rana labialis</i>					
50	FRIM 1123	–	Malaysia, Selangor, FRIM campus	EF487520	EF487433
51	FRIM 1119	–	Malaysia, Selangor, FRIM campus	Missing	EF487429
52	FRIM 1120	–	Malaysia, Selangor, FRIM campus	EF487517	EF487430
53	FRIM 1121	–	Malaysia, Selangor, FRIM campus	EF487518	EF487431
54	FRIM 1122	–	Malaysia, Selangor, FRIM campus	EF487519	EF487432
55	FRIM 1118	–	Malaysia, Selangor, FRIM campus	EF487516	EF487428
56	FRIM 1127	–	Malaysia, Selangor, FRIM campus	EF487524	EF487437
57	FRIM 1125	–	Malaysia, Selangor, FRIM campus	EF487522	EF487435
58	FRIM 1126	–	Malaysia, Selangor, FRIM campus	EF487523	EF487436
59	FRIM 1124	–	Malaysia, Selangor, FRIM campus	EF487521	EF487434
<i>Rana cf. labialis</i> 'Peninsular Malaysia'					
60	FRIM 1539	JS 00327	Malaysia, Kedah, Gunung Jerai, Lower Tupah River	DQ650421	DQ650381
61	FRIM 1735	JS 00330	Malaysia, Kedah, Gunung Jerai, Lower Tupah River	DQ650422	DQ650382
62	FRIM 829	JS 00497	Malaysia, Kedah, Gunung Jerai, Perigi Cascade	DQ650427	DQ650387
63	FRIM 1225	–	Malaysia, Pinang, Air Itam Dam	EF487525	EF487438
64	FRIM 1226	–	Malaysia, Pinang, Air Itam Dam	EF487526	EF487439
65	FRIM 1227	–	Malaysia, Pinang, Air Itam Dam	EF487527	EF487440
66	FRIM 1228	–	Malaysia, Pinang, Air Itam Dam	EF487528	EF487441
67	FRIM 1231	–	Malaysia, Pinang, Teluk Bahang Recreational Forest	EF487529	EF487442
<i>Rana sp.</i> 'Peninsular Malaysia'					
68	FRIM 1736	JS 00381	Malaysia, Kedah, Gunung Jerai, Batu Hampar River	DQ650423	DQ650383
69	FRIM 1418	JS 00390	Malaysia, Kedah, Gunung Jerai, Batu Hampar River	DQ650424	DQ650384
70	FRIM 826	JS 00408	Malaysia, Kedah, Gunung Jerai, Batu Hampar River	DQ650426	DQ650386
71	FRIM 1401	JS 00393	Malaysia, Kedah, Gunung Jerai, Batu Hampar River	DQ650425	DQ650385
<i>Rana megalonesa</i>					
72	FMNH 230956	35452	Malaysia, Sabah, Danum Valley Research Centre	EF487456	EF487365
73	FMNH 230957	35456	Malaysia, Sabah, Danum Valley Research Centre	EF487457	EF487366
74	FMNH 230971	35945	Malaysia, Sabah, Danum Valley Research Centre	EF487458	EF487367
75	FMNH 235641	41446	Malaysia, Sabah, Marak Parak	EF487459	EF487368
76	FMNH 235643	41582	Malaysia, Sabah, Marak Parak	EF487461	EF487370

APPENDIX *Continued*

ID	Voucher	Field no.	Locality	GenBank accession no.	
				16S	ND3
77	FMNH 235642	41580	Malaysia, Sabah, Marak Parak	EF487460	EF487369
78	FMNH 238397	44301	Malaysia, Sabah, Purulon	EF487462	EF487371
79	FMNH 238361	44302	Malaysia, Sabah, Purulon	EF487463	EF487372
80	FMNH 238376	44757	Malaysia, Sabah, Mendolong	EF487464	EF487373
81	FMNH 238374	44927	Malaysia, Sabah, Mendolong	EF487465	EF487374
82	FMNH 238333	45116	Malaysia, Sabah, Mendolong	EF487466	EF487375
83	FMNH 242824	46509	Malaysia, Sabah, Mendolong	EF487467	EF487376
84	FMNH 242827	46548	Malaysia, Sabah, Mendolong	EF487468	EF487377
85	FMNH 268985	51685	Malaysia, Sarawak, Bukit Sarang	DQ650431	DQ650391
86	FMNH 267814	51068	Malaysia, Sarawak, Bukit Sarang	DQ650403	DQ650363
87	FMNH 267819	51160	Malaysia, Sarawak, Bukit Sarang	DQ650409	DQ650369
88	FMNH 267815	51076	Malaysia, Sarawak, Bukit Sarang	DQ650404	DQ650364
89	FMNH 267817	51080	Malaysia, Sarawak, Bukit Sarang	DQ650406	DQ650366
90	FMNH 267823	51219	Malaysia, Sarawak, Bukit Sarang	DQ650414	DQ650374
91	FMNH 267818	51157	Malaysia, Sarawak, Bukit Sarang	DQ650407	DQ650367
92	FMNH 268820	51173	Malaysia, Sarawak, Bukit Sarang	DQ650410	DQ650370
93	FMNH 268981	51624	Malaysia, Sarawak, Tubau	EF487497	EF487405
94	FMNH 267816	51078	Malaysia, Sarawak, Bukit Sarang	DQ650405	DQ650365
95	FMNH 267822	51216	Malaysia, Sarawak, Bukit Sarang	DQ650413	DQ650373
96	FMNH 267824	51234	Malaysia, Sarawak, Bukit Sarang	DQ650415	DQ650375
97	FMNH 267825	51242	Malaysia, Sarawak, Bukit Sarang	DQ650416	DQ650376
98	FMNH 268980	51615	Malaysia, Sarawak, Tubau	EF487496	EF487404
99	FMNH 268984	51676	Malaysia, Sarawak, Bukit Sarang	Missing	EF487406
100	FMNH 268983	51640	Malaysia, Sarawak, Bukit Sarang	DQ650430	DQ650390
101	FMNH 267821	51182	Malaysia, Sarawak, Bukit Sarang	DQ650411	DQ650371
102	FMNH 248327	47780	Brunei, Belait, Labi, Sungai Mendaram	EF487469	EF487378
<i>Rana mocquardii</i>					
103	MZB (uncataloged)	BSI 1218	Indonesia, Sulawesi, Desa Kalibulu, 00.45126°S, 119.76804°E	EF487515	EF487427
104	MZB (uncataloged)	JAM 5019	Indonesia, Sulawesi, Desa Dampala, 02.76261°S, 122.03676°E	EF487530	EF487443
<i>Rana parvaccola</i>					
105	FMNH 268572	15527	Indonesia, Sumatra Barat, Padang, Limau Manis	DQ650394	DQ650354
106	FMNH 268579	15657	Indonesia, Sumatra Barat, Padang, Limau Manis	DQ650399	DQ650359
107	FMNH 268591	15534	Indonesia, Sumatra Barat, Padang, Limau Manis	DQ650395	DQ650355
108	FMNH 268630	16375	Indonesia, Sumatra Barat, Payakumbu, Sarasa Bunta	EF487453	EF487361
109	FMNH 268600	16268	Indonesia, Sumatra Barat, Payakumbu, Batang Harau	EF487451	EF487359
110	FMNH 268613	16303	Indonesia, Sumatra Barat, Payakumbu, Sarasa Bunta	EF487452	EF487360
111	FMNH 268599	16245	Indonesia, Sumatra Barat, Payakumbu, Batang Harau	EF487450	EF487358
112	FMNH 268646	16529	Indonesia, Sumatra Barat, Payakumbu, Sarasa Bunta	EF487454	EF487362
113	FMNH 268648	16618	Indonesia, Sumatra Barat, Payakumbu, Akar Berayun	Missing	EF487363
114	FMNH 268649	16638	Indonesia, Sumatra Barat, Payakumbu, Akar Berayun	EF487455	EF487364

APPENDIX *Continued*

ID	Voucher	Field no.	Locality	GenBank accession no.	
				16S	ND3
<i>Rana raniceps</i>					
115	FMNH 267958	51158	Malaysia, Sarawak, Bukit Sarang	DQ650408	DQ650368
116	FMNH 267959	51193	Malaysia, Sarawak, Bukit Sarang	EF487493	Missing
117	FMNH 267960	51198	Malaysia, Sarawak, Bukit Sarang	DQ650412	DQ650372
118	FMNH 267961	51244	Malaysia, Sarawak, Bukit Sarang	DQ650417	DQ650377
119	FMNH 267962	51259	Malaysia, Sarawak, Bukit Sarang	DQ650418	DQ650378
120	FMNH 267963	51261	Malaysia, Sarawak, Bukit Sarang	DQ650419	DQ650379
121	FMNH 268982	51639	Malaysia, Sarawak, Bukit Sarang	EF487498	Missing
122	FMNH 267965	51434	Malaysia, Sarawak, Samarakan	EF487494	EF487402
123	FMNH 267966	51520	Malaysia, Sarawak, Samarakan	EF487495	EF487403
124	FMNH 267964	51310	Malaysia, Sarawak, Bukit Sarang	DQ650420	DQ650380
<i>Rana rufipes</i>					
125	FMNH 268573	15560	Indonesia, Sumatra Barat, Padang, Limau Manis	DQ650396	DQ650356
126	FMNH 268574	15568	Indonesia, Sumatra Barat, Padang, Limau Manis	DQ650397	DQ650357
127	FMNH 268575	15575	Indonesia, Sumatra Barat, Padang, Limau Manis	DQ650398	DQ650358
128	FMNH 268580	15664	Indonesia, Sumatra Barat, Padang, Limau Manis	DQ650400	DQ650360
129	FMNH 268584	15864	Indonesia, Sumatra Barat, Padang Jernih	EF487447	EF487355
130	FMNH 268585	15987	Indonesia, Sumatra Barat, Padang, Sikayan Ubi	DQ650401	DQ650361
131	FMNH 268586	15994	Indonesia, Sumatra Barat, Padang, Sikayan Ubi	DQ650402	DQ650362
132	FMNH 268587	16030	Indonesia, Sumatra Barat, Padang Jernih	EF487448	EF487356
133	FMNH 268588	16151	Indonesia, Sumatra Barat, Padang Jernih	EF487449	EF487357