

A revision of the Asian tree toad complex *Rentapia hosii* (Anura: Bufonidae) with the description of a new species from Peninsular Malaysia

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Abstract. We present a systematic revision of the *Rentapia hosii* complex based on morphological and bioacoustic data. In conjunction with genetic data from a previous study, our results show that populations from Peninsular Malaysia are distinct from the name-bearing population of *R. hosii* from Sarawak in terms of morphometrics, colour-pattern, and to a lesser degree, male advertisement call. Therefore, we describe the Peninsular Malaysian populations as a new species (*Rentapia flavomaculata*, new species) and provide a discussion on morphological variation among Bornean populations.

Key words. bioacoustics, integrative taxonomy, morphology, systematics

INTRODUCTION

Southeast Asian tree toads of the genus *Rentapia* Chan, Grismer, Zachariah, Brown & Abraham, 2016, were previously subsumed under the genus *Pedostibes* Günther, 1876, but were subsequently split from it based on morphology, life-history traits, genetic divergence, and evolutionary relationships (Chan et al., 2016). Consequently, *Pedostibes* is restricted to the Western Ghats of south-western India (Chandramouli & Amarasinghe, 2016), while *Rentapia* consists of two nominal species that are distributed across the Sundaic region. *Rentapia hosii* (Boulenger, 1892) is the most widespread species, occurring in southern Thailand, Peninsular Malaysia (PM), Sumatra, and Borneo, while *R. everetti* (Boulenger, 1896) is endemic to Borneo (Chandramouli & Amarasinghe, 2016; Inger et al., 2017; Frost, 2020). Chan et al. (2016) highlighted the strongly supported genetic split between populations of *Rentapia hosii* from PM and Borneo and further discussed colour-pattern differences between these two populations (Fig. 1). Additionally, their study also indicated that two distinct morphological variants occurred in Borneo. In particular, a population from Danum Valley, Sabah was found to be morphologically distinct from other populations in Sarawak,

indicating that *R. hosii* could comprise multiple distinct lineages with more restrictive distribution ranges. In this study, we expanded the geographic sampling of Chan et al. (2016) and performed morphological and preliminary bioacoustic analyses to determine whether (1) *Rentapia* from PM is distinct from the true *R. hosii* from Borneo and (2) Bornean *R. hosii* comprises more than one species.

MATERIAL AND METHODS

Sampling. We examined a total of 56 adult specimens (28 females, 28 males) of *Rentapia hosii* representing 19 localities from PM and Borneo. Based on their geographic localities, specimens were grouped into four groups: PM, Kalimantan, Sarawak, and Sabah (Fig. 1). Specimens were obtained from the museum holdings of Lee Kong Chian Natural History Museum, Singapore (LKCNHM); Universiti Malaysia Terengganu Zoological Collection (UMTZC); Field Museum of Natural History, Chicago, USA (FMNH); American Museum of Natural History, New York City, USA (AMNH); Smithsonian Institute, National Museum of Natural History, Washington D. C., USA (USNM); and the Bishop Museum, Hawai‘i, USA (BBM). Type material has been deposited at LKCNHM, UMTZC, and BBM. The list of examined specimens and their associated metadata are presented in Table 1.

Morphometric analysis. The following measurements were measured with a Mitutoyo digital calliper (to the nearest 0.01 mm: snout-vent-length (SVL), cloaca to tip of snout; snout length (SNL), anterior corner of orbit to tip of snout; head length (HL), posterior margin of jaw angle to tip of snout; head width (HW), widest distance of head measured posterior to jaw; tympanum diameter (TYD), measured vertically, including the rim; forearm length (FAL), outer margin of

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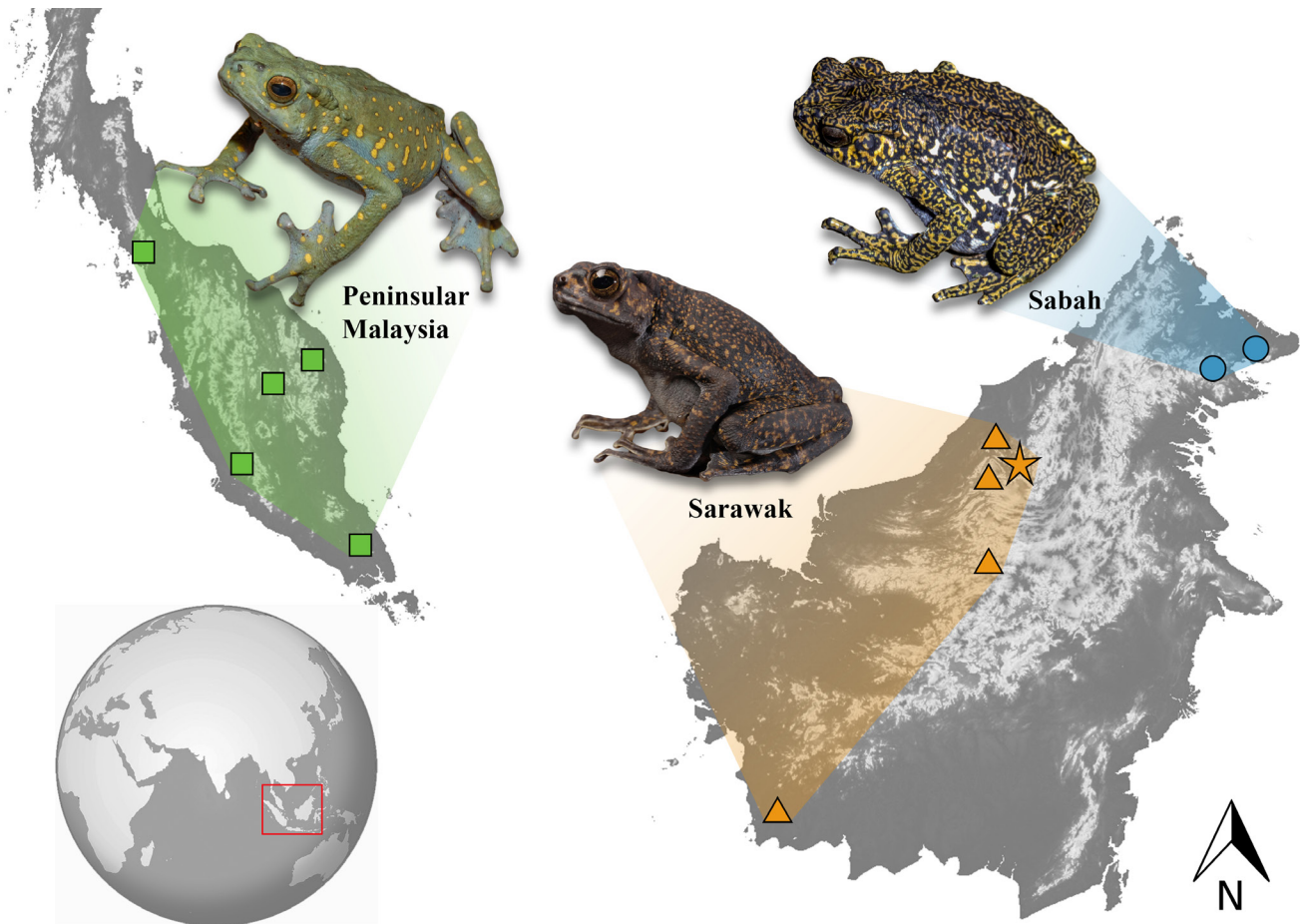


Fig. 1. Distribution of samples used in this study. Inset photographs depict the distinct phenotypes present within the *Rentapia hosii* complex [Photo credit: Alexander Haas (Sarawak); Robert F. Inger (Sabah) ©Field Museum of Natural History]. FMNH 248199. Created by Field Museum of Natural History, Amphibian and Reptile Collection and licensed under CC-BY-SA 4.0.

inflected elbow to posterior margin of outer metacarpal tubercle; femur length (FL), cloaca to outer margin of inflected knee; tibia length (TBL), outer margin of inflected knee to outer margin of inflected ankle; and third finger disc width (3FinDW), horizontal width of third finger disc. To eliminate bias caused by ontogenetic variation, each character (except SVL) was scaled to the same size by adjusting their shape according to allometry (Thorpe, 1983; Leonart et al., 2000). We used the following allometric equation: $X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$, where X_{adj} = adjusted value; X = measured value; β = unstandardised regression coefficient for each population; SVL = measured snout-vent length; SVL_{mean} = overall average SVL of all samples. All downstream analyses were performed on the adjusted values. Male and female measurements were analysed separately to further eliminate bias caused by sexual dimorphism. List of all materials examined and their associated raw data is presented in Table 2.

We used principal components analysis (PCA) to find the best low-dimensional representation of variation in the data to determine whether morphological variation could form the basis of detectable group structure. Eigenvalues >1 were retained according to Kaiser's criterion (Kaiser, 1960). To further characterise group structure, we performed a discriminant analysis on principal components (DAPC) that minimises within-group and maximises between-

group variation (Jombart et al., 2010). Subsequently, an ANOVA was performed to determine whether the means of morphological characters differed significantly among populations, followed by a Tukey HSD test to determine specifically, which population pair of character means differed after adjusting for multiple testing. A Levene's test was performed prior to the ANOVA to check for homogeneity of variance. All morphological analyses were performed and visualised in R (R Core Team, 2014).

Bioacoustic analysis. We obtained call recordings from Mohd Abdul Muin, Lars Fehlandt, and the Frog Voices of Borneo Soundcloud Database (<https://soundcloud.com/frogvoicesofborneo>), where calls were recorded at a sampling rate of 44.1 kHz. Unfortunately, the ambient temperatures at the time of recording were not available. The recordings were cleaned of background noise using Audacity version 2.3.3 (Audacity, GNU General Public License). We generated oscillograms and spectrograms using the R package of SEEWAVE (Sueur et al., 2008). Parameters were only estimated for calls without any disturbance or overlap with other individuals, and thus we considered three single-note and one multi-note call from two individuals from PM, four single-note calls from an individual from Brunei, and three single-note calls from an individual from Sarawak. Call parameters including mean dominant frequency, mean call duration, and call rise and fall times were measured using

Table 1. List of specimens examined in this study and their associated metadata. Museum abbreviations are defined in Material and Methods.

Taxa	Catalogue number	Locality
<i>Rentapia hosii</i>	FMNH 145636	Mengiong River, Nanga Tekalit camp, Kapit, Sarawak
<i>Rentapia hosii</i>	FMNH 194638	Mengiong River, Nanga Tekalit camp, Kapit, Sarawak
<i>Rentapia hosii</i>	FMNH 196595	Mengiong River, Nanga Tekalit camp, Kapit, Sarawak
<i>Rentapia hosii</i>	FMNH 136099	Mengiong River, Nanga Tekalit camp, Kapit, Sarawak
<i>Rentapia hosii</i>	FMNH 194646	Mengiong River, Nanga Tekalit camp, Kapit, Sarawak
<i>Rentapia hosii</i>	FMNH 194660	Mengiong River, Nanga Tekalit camp, Kapit, Sarawak
<i>Rentapia hosii</i>	FMNH 146314	Mengiong River, Nanga Tekalit camp, Kapit, Sarawak
<i>Rentapia hosii</i>	FMNH 148058	Bintulu, Sarawak
<i>Rentapia hosii</i>	FMNH 148055	Bintulu, Sarawak
<i>Rentapia hosii</i>	USNM 257262	Tubau camp on Sungai Pesu, Bintulu, Sarawak
<i>Rentapia hosii</i>	AMNH 90476	Sarawak
<i>Rentapia hosii</i>	USNM 36314	Sungai Landak, Kalimantan Barat, Borneo, Indonesia
<i>Rentapia hosii</i>	USNM 38543	Kendawangan River, Kalimantan Barat, Indonesia
<i>Rentapia hosii</i>	FMNH 156344	Tubau camp on Sungai Pesu, Bintulu, Sarawak
<i>Rentapia hosii</i>	FMNH 156345	Tubau camp on Sungai Pesu, Bintulu, Sarawak
<i>Rentapia hosii</i>	FMNH 156354	Tubau camp on Sungai Pesu, Bintulu, Sarawak
<i>Rentapia hosii</i>	FMNH 156394	Tubau camp on Sungai Pesu, Bintulu, Sarawak
<i>Rentapia hosii</i>	FMNH 119897	Sungai Sekaloh, Niah, Sarawak
<i>Rentapia hosii</i>	FMNH 134217	Sungai Sekaloh, Niah, Sarawak
<i>Rentapia hosii</i>	FMNH 134219	Pengkalan Lobang, Niah, Sarawak
<i>Rentapia hosii</i>	FMNH 219747	Mengiong River, Nanga Tekalit camp, Kapit, Sarawak
<i>Rentapia hosii</i>	FMNH 219743	Mengiong River, Nanga Tekalit camp, Kapit, Sarawak
<i>Rentapia hosii</i>	FMNH 194651	Mengiong River, Nanga Tekalit camp, Kapit, Sarawak
<i>Rentapia hosii</i>	FMNH 194639	Mengiong River, Nanga Tekalit camp, Kapit, Sarawak
<i>Rentapia hosii</i>	AMNH 90474	Tubau camp on Sungai Metallum, Bintulu, Sarawak
<i>Rentapia hosii</i>	AMNH 90475	Tubau camp on Sungai Pesu, Bintulu, Sarawak
<i>Rentapia hosii</i>	FMNH 81245	Lupar River Valley, Sarawak
<i>Rentapia hosii</i>	FMNH 156328	Sungai Pudong, Tubau camp, Bintulu, Sarawak
<i>Rentapia hosii</i>	FMNH 273689	Penyarai, Bintulu, Sarawak
<i>Rentapia hosii</i>	FMNH 156329	Sungai Kanyit, Tubau camp, Bintulu, Sarawak
<i>Rentapia hosii</i>	FMNH 156330	Bintulu, Sarawak
<i>Rentapia hosii</i>	FMNH 156353	Bintulu, Sarawak
<i>Rentapia cf. hosii</i>	FMNH 248199	Sungai Tawau, Tawau Hills Park, Sabah
<i>Rentapia cf. hosii</i>	FMNH 231193	Sungai Palum Tambun, Danum Valley Field Center, Sabah
<i>Rentapia cf. hosii</i>	FMNH 231194	Sungai Palum Tambun, Danum Valley Field Center, Sabah
<i>Rentapia cf. hosii</i>	FMNH 244872	Sungai Palum Tambun, Danum Valley Field Center, Sabah
<i>Rentapia cf. hosii</i>	FMNH 244905	Sungai Palum Tambun, Danum Valley Field Center, Sabah
<i>Rentapia cf. hosii</i>	FNHM 77355	Sungai Tibas camp, Kalabakan, Tawau, Sabah
<i>Rentapia cf. hosii</i>	FMNH 244904	Sungai Palum Tambun, Danum Valley Field Center, Sabah
<i>Rentapia cf. hosii</i>	FMNH 244907	Sungai Palum Tambun, Danum Valley Field Center, Sabah
<i>Rentapia cf. hosii</i>	FMNH 248198	Sungai Tawau, Tawau Hills Park, Sabah
<i>Rentapia cf. hosii</i>	FMNH 244897	Lahad Datu, Sabah
<i>Rentapia cf. hosii</i>	FMNH 244911	Lahad Datu, Sabah
<i>Rentapia cf. hosii</i>	FMNH 244903	Lahad Datu, Sabah
<i>Rentapia cf. hosii</i>	FMNH 244906	Lahad Datu, Sabah
<i>Rentapia flavomaculata</i>	FMNH 172001	Pahang
<i>Rentapia flavomaculata</i>	FMNH 186064	Pahang
<i>Rentapia flavomaculata</i>	FMNH 186063	Selangor
<i>Rentapia flavomaculata</i>	FMNH 186061	Selangor
<i>Rentapia flavomaculata</i>	BBM 8223	Ulu Tahan, Pahang
<i>Rentapia flavomaculata</i>	BBM 8208	Ulu Tahan, Pahang
<i>Rentapia flavomaculata</i>	FMNH 186062	Kampung Eleng (near Semenyih), Selangor
<i>Rentapia flavomaculata</i>	AMNH 35905	Near Satun, Thailand
<i>Rentapia flavomaculata</i>	ZRC 1.13264	Sugai Peres, Sekayu Recreational Park, Terengganu
<i>Rentapia flavomaculata</i>	UMTZC 1404	Sungai Bubu, adjacent to Sekayu Recreational Park, Terengganu
<i>Rentapia flavomaculata</i>	BBM 7252	Kota Tinggi, Johor

Table 2. Raw measurements (mm) of examined specimens. Abbreviations are defined in Material and Methods.

Taxa	Catalogue number	Sex	SVL	SNL	HL	HW	TYD	FAL	FL	TBL	3FinDW
<i>Rentapia hosii</i>	FNMH 145636	F	98.7	12.5	30.6	35.3	4.4	29.8	45.3	44.6	4.8
<i>Rentapia hosii</i>	FMNH 194638	F	91.0	12.4	28.0	32.8	4.3	27.9	43.5	42.5	4.5
<i>Rentapia hosii</i>	FMNH 196595	F	89.5	11.8	27.2	30.8	3.7	24.6	41.3	39.6	4.2
<i>Rentapia hosii</i>	FMNH 136099	F	98.1	13.0	30.8	36.1	4.1	28.0	45.7	42.0	4.8
<i>Rentapia hosii</i>	FMNH 194646	F	90.6	11.9	28.5	31.2	4.1	29.4	44.9	42.9	4.3
<i>Rentapia hosii</i>	FMNH 194660	F	93.9	12.4	30.0	35.2	4.6	28.4	45.3	45.8	4.6
<i>Rentapia hosii</i>	FMNH 146314	F	88.6	10.2	27.4	30.9	4.0	26.9	40.9	40.2	4.3
<i>Rentapia hosii</i>	FMNH 148058	F	100.5	14.2	30.9	36.7	3.1	26.9	46.6	45.6	4.5
<i>Rentapia hosii</i>	FMNH 148055	F	97.0	12.2	30.1	34.8	3.1	27.1	44.7	42.6	3.8
<i>Rentapia hosii</i>	USNM 257262	F	97.5	12.5	30.3	34.1	4.9	28.3	44.6	44.4	4.7
<i>Rentapia hosii</i>	AMNH 90476	F	100.2	12.7	30.7	37.1	5.3	27.6	44.5	44.2	4.6
<i>Rentapia hosii</i>	USNM 36314	F	99.9	12.9	30.6	33.0	4.7	27.6	38.5	42.4	4.4
<i>Rentapia hosii</i>	USNM 38543	F	95.5	12.3	29.6	32.7	4.4	28.7	40.3	43.9	4.5
<i>Rentapia hosii</i>	FMNH 156344	F	98.6	12.2	30.0	33.3	4.2	28.7	44.9	45.8	4.3
<i>Rentapia hosii</i>	FMNH 156345	F	94.9	12.5	29.9	33.3	3.9	25.2	42.5	41.1	4.9
<i>Rentapia hosii</i>	FMNH 156354	F	102.2	13.4	31.2	34.6	3.2	27.1	44.9	43.8	4.6
<i>Rentapia hosii</i>	FMNH 156394	F	90.9	12.7	30.1	33.4	3.4	24.8	44.0	41.2	4.4
<i>Rentapia hosii</i>	FMNH 119897	F	96.1	11.7	28.1	31.7	4.2	28.9	41.0	40.6	4.1
<i>Rentapia hosii</i>	FMNH 134217	F	92.0	12.0	29.1	32.8	4.3	28.0	41.6	42.0	4.0
<i>Rentapia hosii</i>	FMNH 134219	F	95.8	10.9	28.9	33.2	4.3	28.5	43.5	45.1	4.5
<i>Rentapia hosii</i>	FMNH 219747	M	63.5	8.1	20.7	22.7	3.1	20.0	32.2	31.3	3.1
<i>Rentapia hosii</i>	FMNH 219743	M	63.4	7.8	19.7	21.7	3.0	18.2	30.1	29.8	2.7
<i>Rentapia hosii</i>	FMNH 194651	M	61.2	7.4	19.4	22.2	2.7	19.8	29.5	29.3	3.0
<i>Rentapia hosii</i>	FMNH 194639	M	68.1	8.9	20.0	23.7	2.3	19.1	31.0	30.6	3.0
<i>Rentapia hosii</i>	AMNH 90474	M	64.2	8.7	20.7	23.3	3.9	19.5	30.3	29.8	3.0
<i>Rentapia hosii</i>	AMNH 90475	M	67.5	9.7	21.8	24.0	3.7	21.2	32.4	31.9	3.1
<i>Rentapia hosii</i>	FMNH 81245	M	73.1	9.6	20.8	25.2	4.0	18.6	31.4	32.9	3.0
<i>Rentapia hosii</i>	FMNH 156328	M	69.6	8.9	21.2	23.5	3.4	20.6	30.7	30.9	3.2
<i>Rentapia hosii</i>	FMNH 273689	M	66.7	7.8	20.6	23.0	3.7	21.1	32.9	31.2	3.1
<i>Rentapia hosii</i>	FMNH 156329	M	73.2	10.0	23.5	25.9	3.8	21.9	33.4	34.0	3.4
<i>Rentapia hosii</i>	FMNH 156330	M	75.0	10.0	22.8	25.9	2.5	20.4	33.6	32.9	3.3
<i>Rentapia hosii</i>	FMNH 156353	M	73.7	9.3	22.5	24.5	2.3	20.0	33.3	32.8	2.8
<i>Rentapia cf. hosii</i>	FMNH 248199	F	89.0	11.0	26.5	31.3	5.2	23.9	37.1	38.2	4.2
<i>Rentapia cf. hosii</i>	FMNH 231193	F	89.7	11.0	27.5	31.2	5.5	27.3	42.9	41.6	4.0
<i>Rentapia cf. hosii</i>	FMNH 231194	F	91.6	11.3	27.9	32.0	5.1	26.1	37.9	40.1	4.2
<i>Rentapia cf. hosii</i>	FMNH 244872	F	88.1	11.4	27.9	31.1	4.5	25.0	40.2	39.4	4.2
<i>Rentapia cf. hosii</i>	FMNH 244905	F	85.8	11.4	26.5	29.9	4.5	25.0	39.4	38.3	4.0
<i>Rentapia cf. hosii</i>	FNHM 77355	M	71.0	9.1	21.8	24.0	3.9	19.0	30.5	30.6	3.2
<i>Rentapia cf. hosii</i>	FMNH 244904	M	65.8	8.1	21.1	23.9	4.3	20.0	30.9	30.7	2.7
<i>Rentapia cf. hosii</i>	FMNH 244907	M	69.8	8.6	21.4	24.6	4.0	20.0	31.1	30.7	3.1
<i>Rentapia cf. hosii</i>	FMNH 248198	M	66.4	8.6	21.0	24.1	3.8	19.5	30.2	30.4	3.1
<i>Rentapia cf. hosii</i>	FMNH 244897	M	69.8	9.0	20.9	24.2	2.6	18.2	31.6	30.2	2.9
<i>Rentapia cf. hosii</i>	FMNH 244911	M	66.4	8.5	20.1	23.3	2.3	17.7	30.1	29.1	2.8
<i>Rentapia cf. hosii</i>	FMNH 244903	M	64.2	8.4	19.4	21.7	2.3	17.3	29.3	27.8	2.5
<i>Rentapia cf. hosii</i>	FMNH 244906	M	65.0	8.9	20.0	22.8	2.7	18.3	30.0	29.1	2.9
<i>Rentapia flavomaculata</i>	FMNH 172001	M	71.2	9.7	23.5	25.8	2.4	21.8	32.3	33.9	3.9
<i>Rentapia flavomaculata</i>	FMNH 186064	M	69.8	8.8	21.8	25.1	2.6	20.5	33.2	33.9	3.6
<i>Rentapia flavomaculata</i>	FMNH 186063	M	74.1	10.1	23.9	26.5	2.6	20.6	32.3	32.9	3.7
<i>Rentapia flavomaculata</i>	FMNH 186061	M	70.1	9.8	22.3	24.8	3.0	20.5	33.8	32.5	3.4
<i>Rentapia flavomaculata</i>	BBM 8223	M	74.9	9.7	22.7	25.8	3.9	22.4	27.9	33.6	3.3
<i>Rentapia flavomaculata</i>	BBM 8208	M	71.4	9.5	22.4	25.0	4.1	20.8	30.0	30.0	3.5
<i>Rentapia flavomaculata</i>	FMNH 186062	M	74.7	9.6	23.4	26.2	4.0	22.0	33.5	34.4	3.5
<i>Rentapia flavomaculata</i>	AMNH 35905	M	79.2	9.3	24.3	27.6	3.9	21.8	28.6	32.6	3.8
<i>Rentapia flavomaculata</i>	ZRC 1.13264	F	101.0	12.8	31.2	34.2	5.2	27.1	42.6	41.9	4.2
<i>Rentapia flavomaculata</i>	UMTZC 1404	F	99.4	12.9	31.9	34.6	5.9	26.1	43.7	43.1	5.0
<i>Rentapia flavomaculata</i>	BBM 7252	F	102.3	13.7	32.0	37.3	5.0	30.3	42.7	49.4	5.2

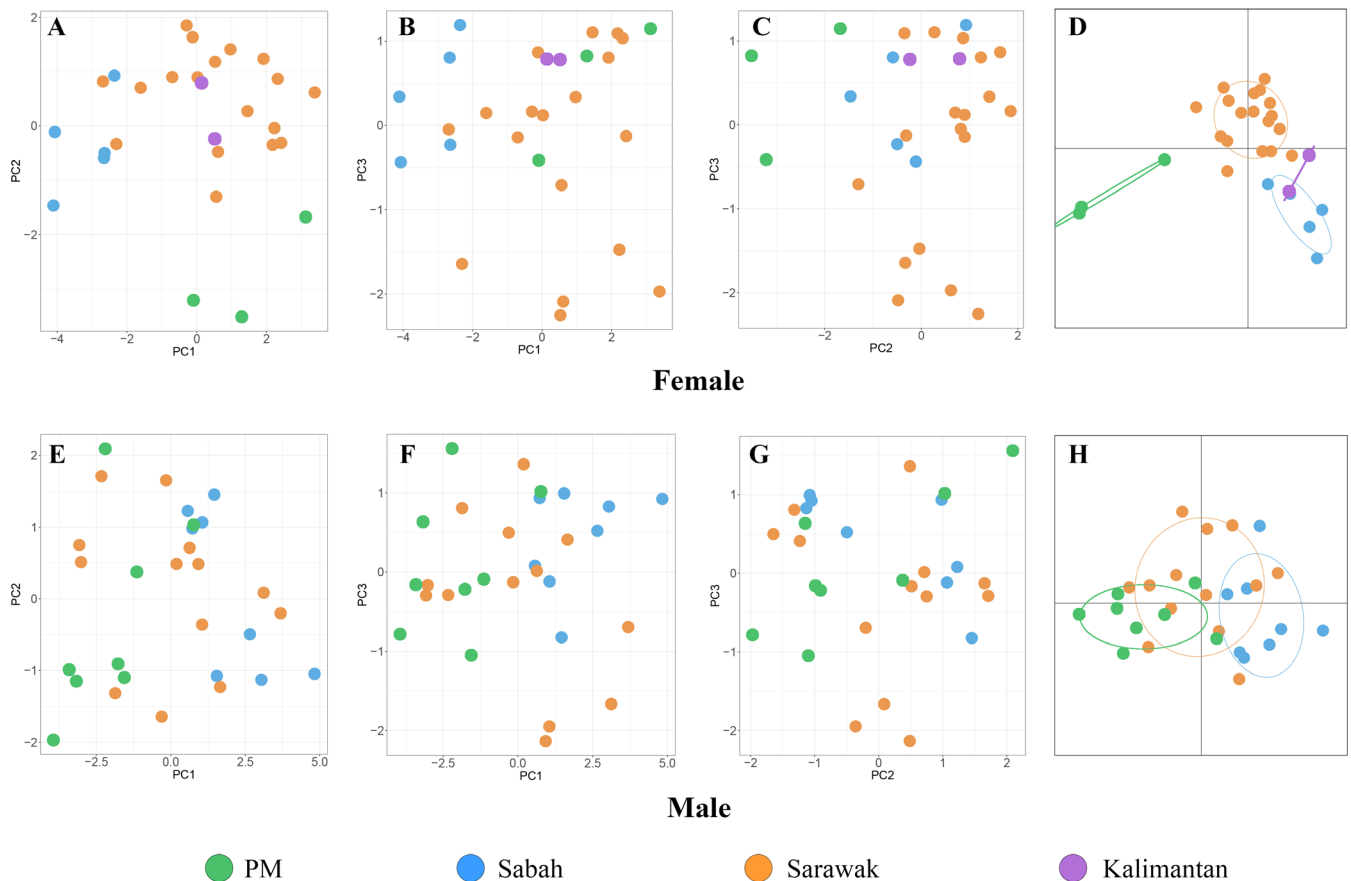


Fig. 2. Clustering of populations in morphospace as inferred from the first three principal components of the PCA analysis (A–C; E–G) and the discriminant analysis of principal components (D, H).

Raven© Pro 1.5 with the Hanning window type and a DFT (discrete Fourier transform) window size of 256 points and 50% overlap with 44.1 Hz sampling rate (Center for Conservation Bioacoustics, 2014).

RESULTS

The first two and three principal components (PCs) had eigenvalues >1 for the male and female datasets respectively. For females, Sabah and PM populations (Sabah-PM) were distinctly separated along the first principal component axis (PC1), while Sabah-Sarawak populations overlapped slightly. Along the second axis (PC2), PM was distinctly separated from Sarawak-Kalimantan populations, whereas PM-Sabah populations showed minimal overlap. No distinct separations were detected along PC3 (Fig. 2). The DAPC analysis showed clear separation between PM-Sabah, PM-Sarawak, and Sabah-Sarawak, while Sabah-Kalimantan overlapped slightly (Fig. 2). For males, PM-Sabah populations showed slight overlap along PC1, but no distinct separations were detected along PC2 and PC3 (Fig. 2). The DAPC analysis showed distinct separation between PM-Sabah, while Sarawak overlapped substantially with both PM and Sabah (Fig. 2).

For females, the ANOVA showed that there were significant differences ($p < 0.05$) among populations for every character

except 3FinDW. The Tukey test further revealed that comparisons between Sabah-Sarawak populations were different in the greatest number of characters (all characters except FAL and 3FinDW), while comparisons between Sarawak-Kalimantan yielded the least significant differences (only FL significant; Table 3). For males, populations from Sabah and PM were significantly different in the greatest number of characters (Table 3), while populations from Sarawak and PM were only different in SVL (Table 3).

The acoustic properties of male advertisement calls from PM and Bornean populations revealed subtle differences in dominant frequency. Call characteristics are as follows: Sarawak [dominant frequency = 1.50 kHz, call duration = 1.3 s (mean = 1.30, range = 1.20–1.41, SD = 0.11, $n = 3$), inter-call interval = 2.84 s (mean = 2.84, range = 2.67–3.0, SD = 0.23, $n = 2$)] (Fig. 3A); Brunei [dominant frequency = 1.55 kHz, call duration 1.09 s (mean = 1.09, range = 0.95–1.22, SD = 0.13, $n = 3$), inter-call interval = 2.90 s (mean = 2.90, range = 2.04–4.46, SD = 1.08, $n = 3$)] (Fig. 3B); PM [dominant frequency = 1.31 kHz, call duration = 1.26 s (mean = 1.26, range = 1.12–1.39, SD = 0.13, $n = 2$), inter-call interval 10.16 s (mean = 10.16, range = 8.63–11.69, SD = 2.17, $n = 2$)] (Fig. 3C). A second recording of a different individual from PM was a multi-note call (dominant frequency = 1.31 kHz) with twelve notes and call duration of 6.04 s.

Table 3. *P*-values of the ANOVA and Tukey HSD tests on female and male morphometric datasets. Asterisks(*) denote characters that were found to be significantly different based on $\alpha=0.05$.

	SVL	SNL	HL	HW	TYD	FAL	FL	TBL	3FinDW
Female:									
ANOVA	0.003*	0.009*	0.000*	0.026*	0.003*	0.007*	0.000*	0.000*	0.109
Tukey HSD									
PM-Kalimantan	0.918	0.999	0.363	1.000	0.391	0.029*	0.048*	0.002*	0.953
Sabah-Kalimantan	0.042*	0.084	0.030*	0.793	0.797	0.146	0.942	0.091	0.541
Sarawak-Kalimantan	0.830	0.964	0.990	0.708	0.729	0.764	0.008*	0.859	1.000
Sabah-PM	0.007*	0.059	0.000*	0.846	0.746	0.536	0.003*	0.098	0.224
Sarawak-PM	0.337	0.909	0.076	0.635	0.017*	0.024*	0.996	0.000*	0.927
Sarawak-Sabah	0.009*	0.009*	0.001*	0.020*	0.023*	0.131	0.000*	0.031*	0.101
Male:									
ANOVA	0.014*	0.018*	0.019*	0.056	0.816	0.001*	0.038*	0.000*	0.002*
Tukey HSD									
Sabah-PM	0.016*	0.019*	0.014*	0.046*	0.923	0.001*	0.030*	0.000*	0.001*
Sarawak-PM	0.045*	0.059	0.153	0.233	0.799	0.405	0.425	0.063	0.096
Sarawak-Sabah	0.713	0.680	0.323	0.506	0.975	0.010*	0.205	0.007*	0.078

SYSTEMATICS AND TAXONOMY

The type material for *Rentapia hosii* consists of a single male holotype (BMNH 92.6.3.19; BMNH = British Museum of Natural History, London, UK, currently, The Natural History Museum, London) from Mount Dulit, Sarawak (Boulenger, 1892). This study showed that males of the *R. hosii* species complex are phenotypically similar, while females are easily diagnosable. Hence, we provide a formal description of female *R. hosii* that can be used for diagnostic purposes in lieu of the holotype. Although there are no female specimens from the type locality in existing collections, we were able to examine specimens and vouchered photographs from populations throughout Sarawak and the adjacent country of Brunei Darussalam. Based on obvious and consistent diagnostic colour-pattern characteristics, females from these populations (some merely ca. 60 km from the type locality) were determined to be conspecific with each other; and we are confident that these populations are also conspecific with the type material (see below for discussion on colour-pattern variation). As such, we consider all populations from Sarawak and Brunei to belong to the species *R. hosii* sensu stricto (s.s.).

Morphometric analyses of female specimens showed that populations from PM and Sabah were significantly different from *Rentapia hosii* s.s. from Sarawak in a number of characters (Table 3); populations from PM and Sabah were also shown to be significantly distinct from each other. However, although morphometric differences were detected, they are non-discrete and do not adequately represent the full range of intrapopulation variation due to limited sampling size. Similarly, our bioacoustic analysis revealed subtle differences between male advertisement calls from PM and

Sarawak + Brunei, while no significant differences were detected between calls from Sarawak and Brunei (Fig. 3). Therefore, we do not consider morphometric characters and bioacoustic attributes to be objective diagnostic characters. Instead, we utilise qualitative characters pertaining to dermal tuberculation and colour-pattern (presented and compared in the species accounts below), genetic differentiation, and geographic distribution as primary criteria to assess lineage independence. Following the unified concept of species (de Queiroz, 2005), we determined PM populations to be a distinct evolutionary lineage that can be differentiated from the name-bearing population of *R. hosii* from Sarawak based on allopatry (separate landmasses), morphological, and genetic divergence. Although the Sabah population can be morphologically distinguished from *R. hosii* s.s., data from additional sources such as bioacoustics and vouchered genetic material are still lacking. As such, we tentatively consider the Sabah population as *R. cf. hosii*, pending the acquisition of more data.

Rentapia hosii (Boulenger, 1892)

Brown Tree Toad
(Figs. 4, 7C)

Nectophryne hosii Boulenger, 1892: 508.

Pedostibes hosii Barbour, 1938: 192.

Material examined. FMNH 156344–45, 156354, 156394, adult females, collected by W. Hosmer at Tubau camp on Sungai Pesu (3°06'N 113°38'E), Bintulu, Sarawak, Malaysia on 27 May 1964, 15 April 1964, 7 June 1964, and 7 August 1964 respectively; FMNH 119897, 134217, adult females, collected by Lord Medway and Tom Harrison respectively, at Sungai Sekaloh, Niah, Sarawak, Malaysia on 31 August

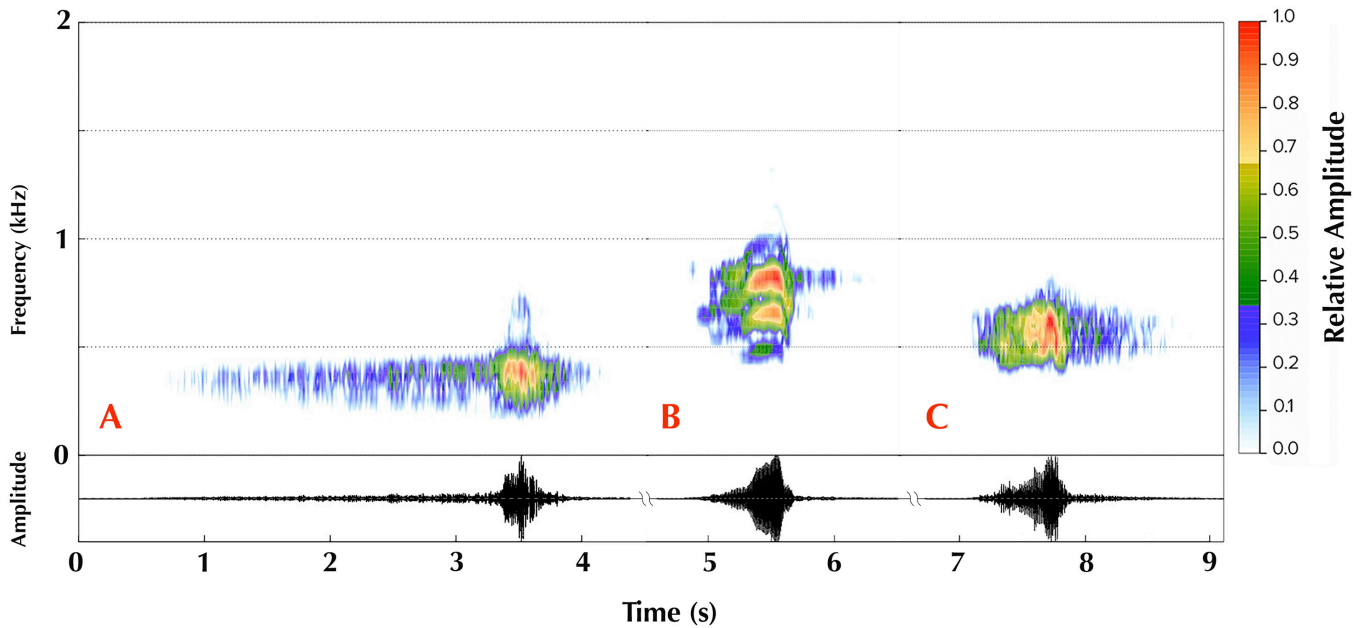


Fig. 3. Comparative spectrograms and corresponding oscillograms of a single call of the advertisement vocalisation of individuals of the *Rentapia hosii* complex from (A) Sarawak; (B) Brunei; and (C) Peninsular Malaysia.

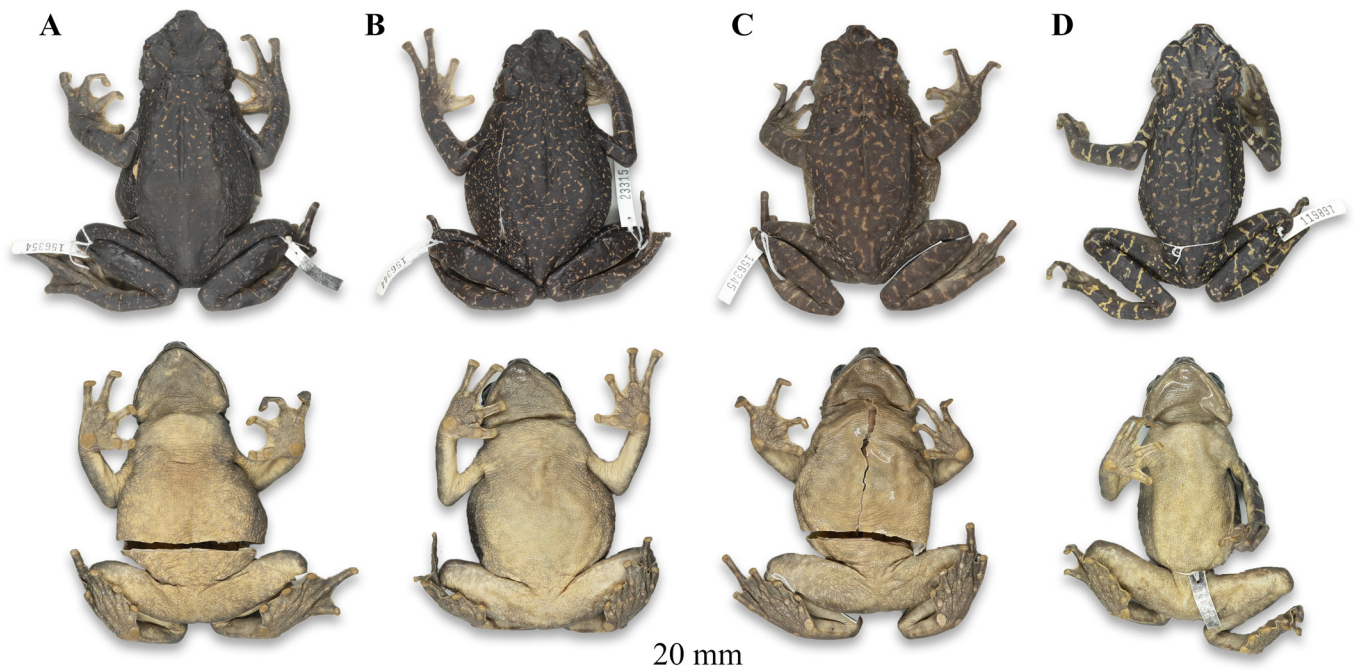


Fig. 4. Dorsal and ventral representations of preserved adult female *Rentapia hosii* from Sarawak. A–C, FMNH 156354, 156344–45 respectively, from Bintulu; D, FMNH 119897 from Niah.

1959 and 6 September 1960, respectively; FMNH 134219, adult female, collected by Tom Harrison at Pengkalan Lobang, Niah, Sarawak, Malaysia in 1960.

Description of female. Body large, habitus robust; head wider than long; top of head flat; interorbital space concave; snout angular, truncate in dorsal profile, slightly projecting beyond lower jaw in lateral profile; nostrils elongated, diagonally oriented, located laterally at tip of snout; canthus rostralis distinct, rounded; lores slightly concave; eyes large; tympanum distinct, oval, higher than wide, tympanic rim slightly elevated; vomerine teeth absent.

Forelimbs relatively long, robust; relative length of fingers, I < II < IV < III; all fingers webbed at base; finger tips expanded into large discs not bearing circummarginal grooves; basal subarticular tubercles distinct, others indistinct, numbering one on fingers I and II, two on fingers III and IV; large palmar tubercle at base of manus; supernumerary tubercles absent.

Hind limbs robust; toe tips expanded into small discs not bearing circummarginal grooves; toe webbing formula I 0 1 II 0 2 III 0 2.5–3 IV 2.5–3 1 V; subarticular tubercles distinct, round; inner metatarsal tubercle large, oval; outer metatarsal tubercle distinct, half the size of inner.

Skin on back, flanks and upper surfaces of limbs covered with indistinct, low tubercles; tubercles on upper eyelids, and lateral and dorsal aspects of nuchal and scapular region more pronounced; parotoid gland D-shaped in dorsal profile, continuous with upper eyelid; scapular swelling indistinct; venter finely granulate; tarsal ridge present.

In preservative, dorsal base colour dark grey, venter brownish-grey; entire dorsal surface covered with yellowish reticulations that are relatively evenly distributed; entire ventral surface lacks distinct markings. Measurements of specimens are provided in Table 2.

Diagnosis. *Rentapia hosii* can be differentiated from other congeners by the following combination of characters: adult females large (up to 105 mm SVL); skin on back, flanks and upper surfaces of limbs covered with indistinct, low tubercles; tubercles on upper eyelids, and lateral and dorsal aspects of nuchal and scapular region more pronounced; in life and preservative, dorsal base colour dark grey, venter brownish-grey; entire dorsal surface covered with yellowish reticulations that are relatively evenly distributed; entire ventral surface lacks distinct markings. In males, dorsal colouration uniform brown to reddish-brown with no distinct markings; venter light grey with no distinct markings; gular sac blackish; nuptial pad present on dorsal surface of thumb; single, internal subgular vocal sac.

Variation. The amount and density of dorsal reticulations vary among individuals (Fig. 4). Base dorsal colouration also varies from brownish to dark grey. However, females of this species group are known to exhibit drastic changes in dorsal colouration in response to stress, such as during handling and euthanasia (pers. obs.). A series of female specimens from Kapit district in Sarawak had light brown dorsal colouration with no distinct markings, which are similar to males. However, these individuals were confirmed to be females by their large size (90–100 mm SVL; Table 2) and examination of internal reproductive organs. At present, we are unable to determine if the preserved colour-pattern of these individuals is reflective of that in life, or whether it is a result of the preservation process. Because the Kapit population cannot be morphometrically differentiated from other populations in Sarawak, we provisionally consider it as *Rentapia hosii* s.s., pending the acquisition of fresh material.

Distribution. *Rentapia hosii* occurs in the state of Sarawak, Malaysia, the country of Brunei Darussalam, as well as in Kalimantan, and provisionally also in Sumatra, Indonesia (see Discussion).

***Rentapia flavomaculata*, new species**

Yellow-spotted Tree Toad
(Figs. 5, 6, 7A, B)

Nectophryne hosii Boulenger, 1892: 508.

Pedostibes hosii Barbour, 1938: 192.

Rentapia hosii Chan et al., 2016: 9.

Holotype (Fig. 5). ZRC 1.13264, adult female, collected by Baizul Hafsyam at Sungai Peres (4°57'44.45"N 102°57'13.77"E; 64 m a.s.l.), Sekayu Recreational Park, Terengganu, Malaysia on 7 April 2016 (1000 hours).

Paratypes (Fig. 6). UMTZC 1404, adult female, collected by Baizul Hafsyam at Sungai Bubu (4°58'1.41"N 102°57'20.71"E, 47 m a.s.l.), adjacent to Sekayu Recreational Park, Terengganu, Malaysia on 14 February 2015 (2300 hours); BBM 7252, adult female, collected by J. A. LeDoux and J. R. Hendrickson at Kota Tinggi, Johor, Malaysia on 20 October 1956.

Description of holotype. Adult female; large, habitus robust; head wider than long; top of head flat; interorbital space concave; snout angular, truncate in dorsal profile, slightly projecting beyond lower jaw in lateral profile; nostrils elongated, diagonally oriented, located laterally at tip of snout; canthus rostralis distinct, rounded; lores distinctly concave; eyes large; tympanum distinct, oval, higher than wide, tympanic rim slightly elevated; vomerine teeth absent.

Forelimbs relatively long, robust; relative length of fingers, I < II < IV < III; all fingers webbed at base; finger tips expanded into large discs not bearing circummarginal grooves; subarticular tubercles indistinct, numbering one on fingers I and II, two on fingers III and IV; large palmar tubercle at base of manus; supernumerary tubercles absent.

Hind limbs robust; toe tips expanded into small discs not bearing circummarginal grooves; toe webbing formula I 0–1 II 0–2 III 0–3 IV 3–1 V; subarticular tubercles indistinct; inner metatarsal tubercle large, oval; outer metatarsal tubercle indistinct.

Skin on dorsal surfaces smooth except for a small tubercle slightly above the jaw articulation and a series of indistinct tubercles on the posterolateral aspect of head level with the scapula; no tubercles on dorsal aspect of nuchal region; cranial ridge absent; parotoid gland D-shaped, continuous with upper eyelid; scapular swelling present; venter finely granulate; tarsal ridge present (Fig. 5).

In preservative, dorsal base colour dark grey, venter brownish-grey; irregularly-sized cream spots on back, side of head and snout, flanks, dorsal surface of limbs (including the manus, pes, and digits), gular, ventrolateral region, and chest; spots absent on top of head; spots fuse together to form stripes on front limbs; belly with indistinct creamy, irregular patches (Fig. 5). Measurements of type material are provided in Table 2.

Diagnosis. *Rentapia flavomaculata*, new species, can be differentiated from other congeners by the following combination of characters: adult females large (up to 105 mm SVL); dorsum relatively smooth; no distinct tubercles on dorsal aspect of nuchal region; in life, dorsal colour light green, ventral colour greyish-green; bright yellow spots on back, side of head, flanks, dorsal surface of limbs, gular, ventrolateral region, and chest; spots absent on top of head

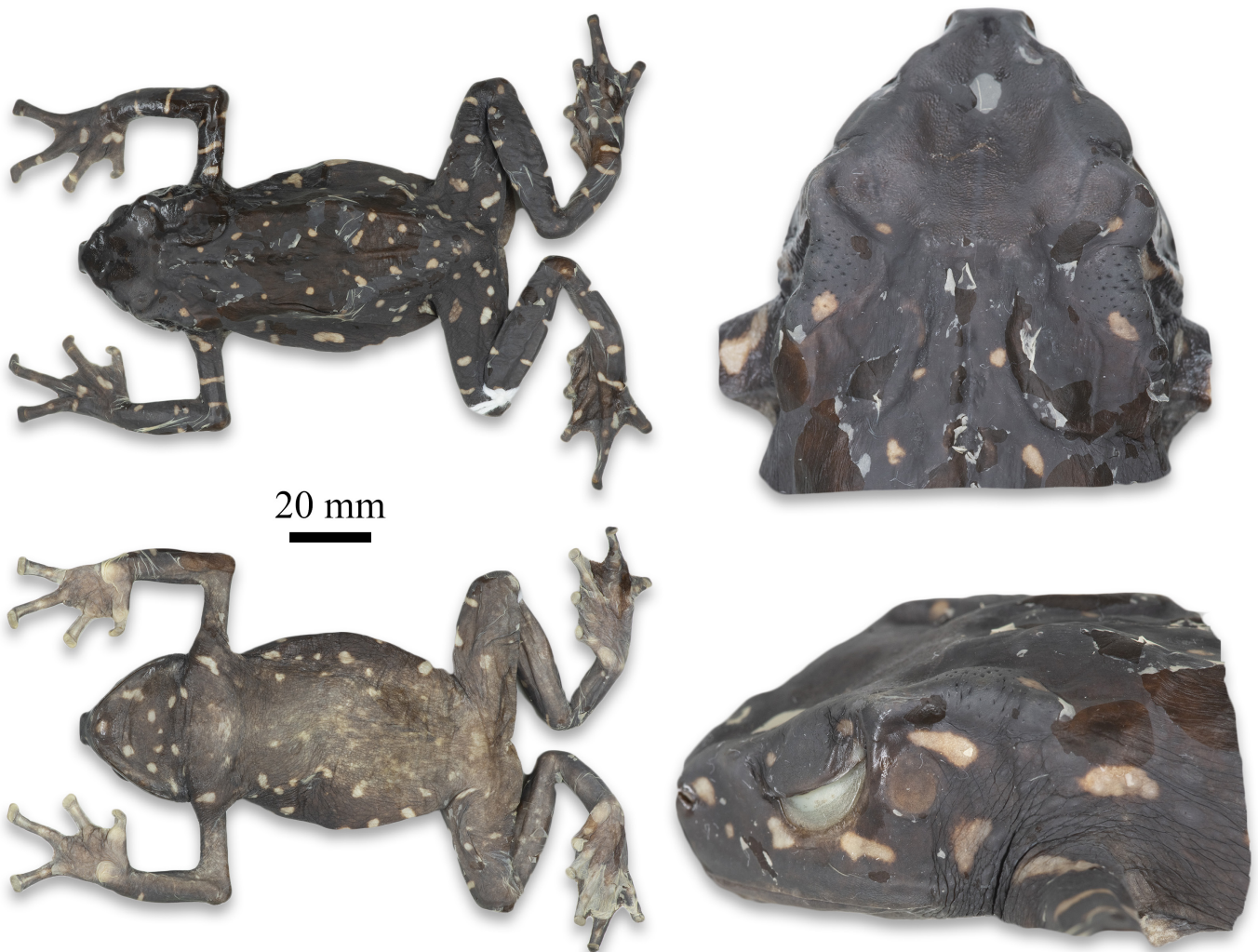


Fig. 5. Dorsal (A) and ventral (B) images of the adult female holotype (ZRC 1.13264) of *Rentapia flavomaculata*, new species, including close-ups of the head (C, D).

and sparser (sometimes absent) on back. In males, dorsal colouration uniform brown to reddish-brown with no distinct markings; venter light grey with no distinct markings; gular sac blackish; nuptial pad present on dorsal surface of thumb; single, internal subgular vocal sac.

Variation. In females, the amount and density of spots vary among individuals. Some lack spots on the back, while others have spots on the belly. Some specimens have slightly more tuberculation on the lateral aspect of the scapular/nuchal region (Fig. 6). Males are uniform brown to orangish with no distinct pattern, but have a higher degree of tuberculation, especially at the flanks, supraocular, sacral, and femoral region.

Comparison. Because males are morphologically similar, all comparisons are based on females. *Rentapia flavomaculata*, new species, can be differentiated from *R. hosii* s.s. by having a smoother dorsum and lacking prominent tubercles on the upper eyelids and dorsal part of the nuchal and scapular region; dorsal colouration light green (vs. dark brown to grey); dorsum and parts of venter (gular and sometimes chest and belly region) covered with bright yellow spots (vs. dorsum covered with yellowish to light brown reticulations and venter lacking distinct markings). Although our morphometric

analyses revealed significant differences in a number of mensural characters (Fig. 2; Table 3), those characters are non-discrete and do not adequately represent the full range of intrapopulational variation due to limited sampling size. Therefore, dorsal tuberculation and discrete differences in female colour-pattern should be used as primary diagnostic characters.

Phylogenetic definition. *Rentapia flavomaculata*, new species, is a crown clade name that is reciprocally monophyletic with *R. hosii* (Chan et al., 2016). Due to the unavailability of molecular data from the type material, we provisionally designate a 12S + 16S rRNA mitochondrial gene sequence from an individual from Krau Wildlife Reserve, Pahang (GenBank accession number AY325993) that was used in Chan et al. (2016) to serve as a representative genetic barcode.

Distribution. *Rentapia flavomaculata*, new species, is confirmed to occur throughout Peninsular Malaysia and southern Thailand (south of the Isthmus of Kra).

Natural history. All species in the *Rentapia hosii* group are typically arboreal and occur in lowland forests from 20–525 m a.s.l. (Inger, 1966). Females are encountered

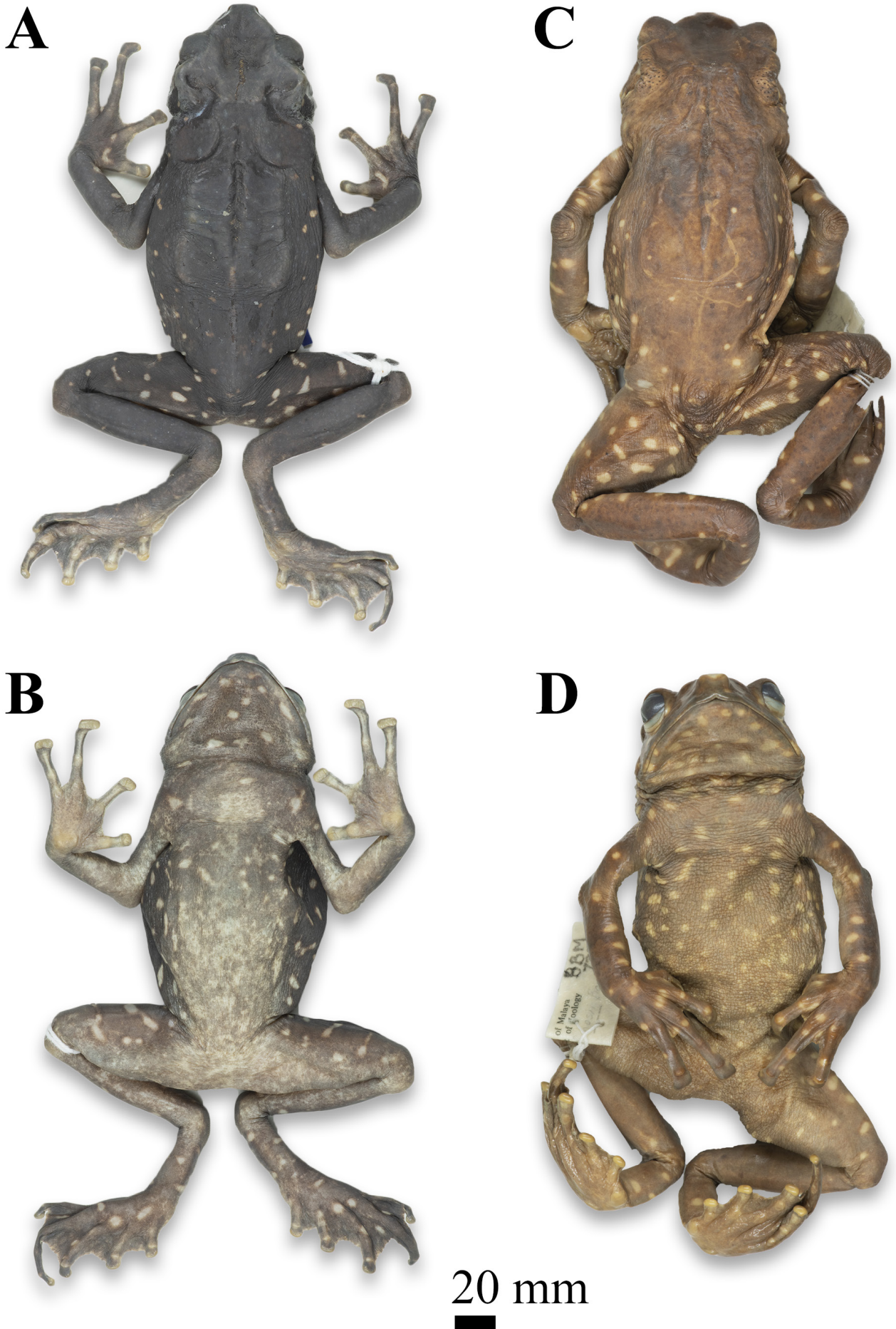


Fig. 6. Dorsal and ventral images of *Rentapia flavomaculata*, new species, paratype UMTZC 1404 (A, B) from Sungai Bubu, Terengganu, Malaysia and BBM 7252 (C, D) from Kota Tinggi, Johor, Malaysia.



Fig. 7. Live photographs of: amplexing *Rentapia flavomaculata*, new species, displaying (A) normal and (B) stressed colouration; (C) female *R. hosii* s.s. from Sarawak (Photo by Alexander Haas); (D) female *R. cf. hosii* from Tawau, Sabah (Photo by Robert F. Inger; ©Field Museum of Natural History. FMNH 248199. Created by Field Museum of Natural History, Amphibian and Reptile Collection and licensed under CC-BY-SA 4.0); and (E) uncollected female from Tawau, Sabah (Photo by A. Haas).

much less frequently than males and are usually observed during breeding, where they descend from treetops to breed in pools of water along small to moderately sized forest streams. Females have been observed perched on branches up to 25 m above ground in the forest canopy near fast-flowing rivers. Males call from elevated perches and multiple individuals can usually be heard along a single stretch of stream. In females, base colour changes relatively rapidly from light green to dark grey when handled, stressed, and preserved (Fig. 7A, B). Males can change from light to a darker shade of brown.

Etymology. The specific epithet is constructed from the Latin adjectives *flavo* (= yellow) and *maculata* (= spotted) in reference to the species' diagnostic yellow spots.

DISCUSSION

Results from our bioacoustic analysis was based on a small sample size and hence, should be considered as preliminary. Although the lack of significant differentiation in our call data could be an artefact of sampling size, it is also possible that advertisement calls in this species complex are under less selection pressure due to female-biased sexual dimorphism and the lack of sympatric congeners (Bell & Zamudio, 2012; Portik et al., 2019). The exceptional phenotypic differences in females in contrast with high similarities in males, suggest that selection pressure is heavier on females. We further expect calls to be less divergent in the absence of competition from other congeners (the only other congener is *Rentapia everetti*, which is restricted to upland regions) because high selection pressure on calls acts to prevent heterospecific mating and is usually associated with assemblages consisting of multiple closely related species (Hebets & Papaj, 2005). This would suggest that the primary function of calls in the *R. hosii* complex is for advertisement, as opposed to species recognition. We hypothesise that calls help females locate males and that male mate-choice increases the selection pressure on female colouration.

An increasing number of Sundaic taxa that were once considered to be widespread across separate landmasses (e.g., mainland Asia, Borneo, Indonesian islands) have been split into distinct species with more restricted distributions (e.g., McLeod, 2008; Wood et al., 2008; Chan & Grismer, 2010; Chan et al., 2014; Grismer et al., 2014; Matsui et al., 2014). This study shows a similar pattern by demonstrating that populations from PM are distinct from the true *Rentapia hosii* from Borneo. Although our data was insufficient to distinguish the Sabah population as a distinct species, it is evident that there is some level of divergence between populations in eastern Sabah and Sarawak. The distinction between populations from eastern and western Borneo is an emerging and relatively unstudied pattern (Lim et al., 2017; Mason et al., 2019) that potentially alludes to a yet uncharacterised biogeographic transition zone within Borneo. Sampling at a broader geographic scale and deeper genetic resolution is urgently needed, especially from Kalimantan, which represents a crucial missing piece that has severely

hampered efforts to provide a more comprehensive understanding of the region's biodiversity and evolutionary history.

Rentapia hosii has been reported from Sumatra, Indonesia, but the identity of that population remains to be verified. The presence of *Rentapia* in Sumatra is not unexpected as numerous species of amphibians are co-distributed between Peninsular Malaysia, Sumatra, and Borneo (AmphibiaWeb, 2019). However, the absence of vouchered material prevents us from ascertaining whether *Rentapia* from Sumatra is conspecific with *R. flavomaculata*, new species, or *R. hosii*. As such, we do not propose to make any taxonomic amendments and tentatively consider the Sumatran population as *R. hosii*.

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