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Re-examination of Larval Assignment of *Meristogenys poecilus* in Sarawak, Borneo, with a Diagnostic Table of *Meristogenys* Larvae

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Abstract: Larval morphology offers some of the more important characters for the taxonomy of *Meristogenys*, and larval information of almost all species has been reported for this genus. However, some larval assignments in previous studies were not based on reliable methods and should be re-examined using modern techniques. In this study, we used molecular methods to re-examine the larval assignments for *M. poecilus*, whose larvae had been assigned previously based on conventional morphological methods. The analysis revealed that the larvae of this species had been misidentified as *M. phaeomerus*, a sympatric species. Here we correct the erroneous assignment and briefly comment about the taxonomic status of *M. phaeomerus* and *M. orphnocnemis*, based on our results.

Key words: Larval assignment; *Meristogenys phaeomerus*; *Meristogenys poecilus*; Mitochondrial DNA; Sarawak

Introduction

Meristogenys is a ranid genus endemic to Borneo and containing 13 species at present. It has been emphasized in previous accounts that larval morphology was an important source of features that contribute to the taxonomy of this genus, particularly because interspecific differences in some species of this genus were apparent in larvae but adult disparity between species was less distinct (e.g., Shimada et al., 2007, 2011b, 2015).

Some observations of *Meristogenys* larvae were reported in early studies (Boulenger, 1893; Mocquard, 1890), but it was Inger and Gritis (1983) who began to demonstrate verifiable evidence in the larval assignment of *Meristogenys*. They assigned two larval forms ("larva A" and "larva B"), that had already been reported by Inger (1966), to two species newly described by themselves, i.e., *M. phaeomerus* and *M. poecilus*. Their assignment was mainly based on the comparison of thigh patterns in metamorphosing specimens. However, it was not demonstrated conclusively if such metamorphic stages truly exhibit the character status of adults in an identical

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fashion. After their study, further accounts on frogs of this genus often were accompanied by data about larval morphology (Inger, 1985; Matsui, 1986; Yang, 1991; Malkmus et al., 2002; Matsui et al., 2010; Shimada et al., 2007, 2011a, 2011b, 2015; Gan et al., 2015). At present, descriptions of almost all species are available with data about their respective larval form. Recently, species assignments of larvae (after Shimada et al., 2007) have been accomplished by matching sequences of mitochondrial DNA from adults with that of larvae. These techniques were not available in the earlier studies and, therefore, larval assignment in such studies should be tested and verified by the modern genetic approach whenever possible.

We examined mitochondrial DNA samples of *Meristogenys* adults and larvae from Lanjak Entimau, central Sarawak, East Malaysia (Borneo) and compared the results to the previous account by Inger and Gritis (1983). From the new evidence, we conclude that the larvae of *M. poecilus* were misidentified by Inger and Gritis (1983).

Materials and Methods

Sample collection

Sampling took place at Sungei (=river) Jelak, a branch of Sungei Engkari, Bukit Lanjak, Division Sri Aman, Sarawak, Malaysia (1°20'N, 112°00'E), alt. 250 m (Fig. 1), on 24 August 1993. After collecting frogs, we took muscle tissues for later biochemical analysis and preserved the frogs as vouchers. Adult specimens were anesthetized with acetone chloroform (chloretone), fixed in 10% formalin, and later preserved in 70% ethanol. Larvae were directly fixed and preserved in 5% formalin solution except for two samples for DNA analyses, which were crudely homogenized with 99% ethanol using a pair of scissors. The assignment of larvae to species was based on matching of mtDNA sequences to that of adult forms. Specimens examined are stored at the Graduate School of Human and Environmental Studies, Kyoto University (KUHE) (see Appendix 1).

Fig. 1 Research sites of previous studies and this study. Star: Nanga Tekalit (the type locality of both *M. phaeomerus* and *M. poecilus*), Closed circle: Lanjak Entimau (our study site).

Molecular analysis

We obtained sequence data for DNA from the muscle samples preserved in 99% ethanol (adults) or whole body homogenized with 99% ethanol (larvae). DNA was extracted using a standard phenol-chloroform extraction procedure (Stenesh, 1989). For adult specimens, we used the primers L1091 and Hnew shown in Shimada et al. (2011a) to amplify approximately 410 bp of 12S rRNA (12S) in mitochondrial DNA, but we could not amplify that length for larvae. Thus, to amplify larval sequences, we used primers designed to amplify each quarter of this region (L1091, L1173, L1264, L1371, H1243, H1352, H1472, and Hnew; Shimada et al., 2011b) which resulted in good amplification.

For the genetic comparison with our samples and known sequences (DNA barcoding), we also obtained the sequences of 12S, 16S rRNA (16S), NADH dehydrogenase subunit 1 and 2 (ND1 and ND2), and tRNAs locating between them, using the primers

12Sh (Cannatella et al., 1998) and 46RishiAla (Shimada et al., 2011a). We calculated genetic distances (p-distance) from these sequences and published data of congeneric species, *M. amoropalamus*, *M. dyscritus*, *M. jerboa*, *M. kinabaluensis*, *M. maryatiae*, *M. orphnocnemis*, *M. penrissenensis*, *M. stenocephalus*, *M. stigmachilus*, and *M. whiteheadi* (see Appendix 2 for detail) using 16S and ND1 regions which have been examined to measure genetic diversity among *Meristogenys* species (Shimada et al., 2015). The polymerase chain reaction (PCR) cycling, precipitation, and sequencing procedures were identical to those described by Shimada et al. (2009). Newly obtained sequences were deposited in GenBank (LC438789–LC438793).

Morphological analysis

For preserved adult specimens, we took the following four body measurements to the nearest 0.1 mm with dial calipers: (i) snout–vent length (SVL); (ii) head width (HW); (iii) eye length (EL); (iv) tibia length (TL), from knee joint to heel joint, measured with hindlimb completely folded. We observed the status of the characters reported in Shimada et al.'s (2015) diagnostic table (1—body size, 2—pattern of rear of thigh, 3—amount of ventral pigmentation on ventral surface of tibia, 4—extent of excision of toe web between fourth and fifth toes, 5—extent of broad webbing on the tip of fourth toe ["broad webbing" indicates the relatively broad webs connecting each toe, excluding fringe-like webs observed on the tip of toes], 6—black marking on flank region, 7—head width, 8—eye length, 9—large black spots on upper lip) except for two characters which could not be checked in preserved specimens (10—pattern of upper iris, 11—reddish brown color of iris). Patterns of rear of thigh (2) were recorded following Inger and Gritis (1983): D—Dusted with small irregular light dots, B—blotched with large clear light spots. Amount of pigmentation on ventral surface of tibia (3) were recorded following Inger and Gritis (1983): A—heavy pigmentation over entire ventral surface; B—patches in which melanophores form continuous bands or spots across the surface; C—isolated, scattered melanophores; D—wide, longitudinal strip clear of melanophores. It should be noted that Inger and Gritis (1983) established the category "B/C" indicating intermediate between "B" and "C", and summarized their result in three category groups, "A-B", "B/C", and "C-D". Excision of toe web between fourth and fifth toes (4) were also recorded following Inger and Gritis's (1983) categories, relative to subarticular tubercles of fourth toe: A—excision to proximal edge of distal subarticular tubercle; B—between distal and middle subarticular tubercle; C—distal edge of middle tubercle; D—center of middle tubercle; E—proximal edge of middle tubercle.

For larval specimens, we observed the formulae of rows of keratodont, presence or absence of glands on the body and the tail, projections on body surface, and color pattern of body surface.

Results

In the field, we found two distinct morphospecies both in adults and larvae. The two forms of adults were clearly distinguishable by body size; thus, we shall refer to them herein as "small form" and "large form", respectively. Because of their distinct body color pattern, we shall refer to the two larval morphs as "yellow larvae" and "gray larvae", respectively. The yellow form was quite abundant, whereas we collected only one specimen of the gray form. Only a photo of the dorsal aspect of this specimen is available for documentation (Fig. 2), because we chose to homogenize the whole body of this specimen for molecular analysis. We will show the result of observation below:

Adult of the small form

A total of 31 specimens (26 males and five females) was recognized as the small form. The character states according to Shimada et al.'s (2015) diagnostic table were as follows:

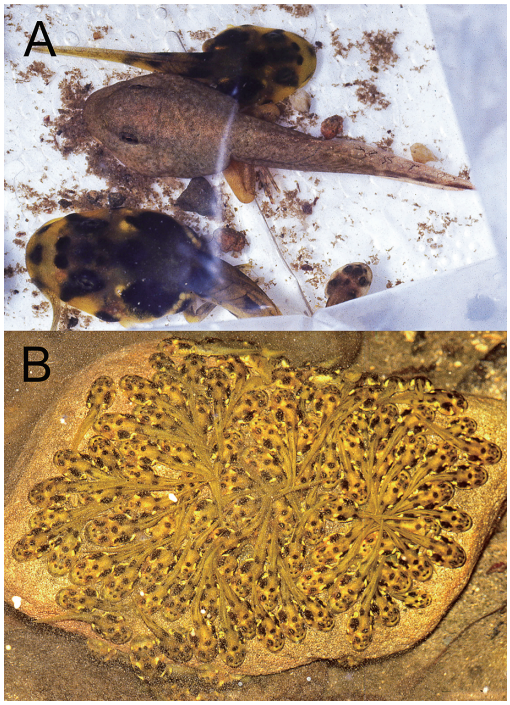

FIG. 2 Specimens taken at Lanjak Entimau: A. Yellow form larvae (top and bottom individuals) and gray form larva (middle); B. Yellow form larvae gathering in large numbers on the surface of a rock. Photographs by T. Hikida.

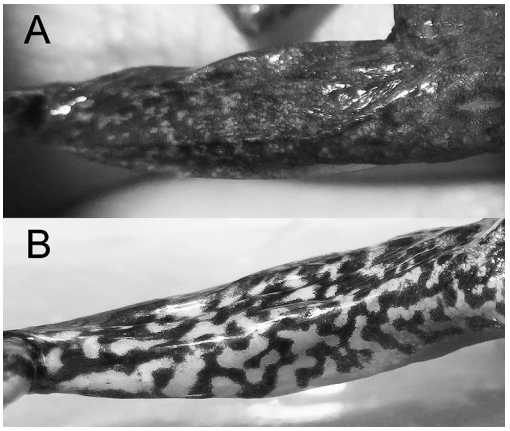

FIG. 3 Patterns of posterior surface of the thigh of the small form (A: *M. phaeomerus*) and large form (B: *M. poecilus*) collected from Lanjak Entimau.

(1) body relatively small (SVL 32.4–37.4 mm in males, SVL 58.7–63.2 mm in females), (2) posterior part of thigh dusted with small irregular light dots (Fig. 3A), (3) ventral surface of tibia scattered with melanophores ("B/C" or "C" in Inger and Gritis's [1983] categories; Table 1), (4) excision of webbing between fourth and fifth toes reached at least to the level of the distal edge of the middle subarticular tubercle of the fourth toe ("B" or "C" in Inger and Gritis's [1983] categories; Table 1), (5) broad webbing reaches the tip of toes, (6) black marking of flanks absent, (7) HW/SVL less than 0.36 (median [range]: 0.332 [0.310–0.346] in males; 0.341 [0.327–0.353] in females), (8) EL<snout length, and (9) large black spots on upper lip absent. According to these characters, this form fits the original description of *M. phaeomerus* (Inger and Gritis, 1983), and differ from other congeneric species described subsequently (Matsui, 1986, Shimada et al., 2015).

For this form, we obtained DNA samples from 10 individuals. The sequence of mtDNA (12S rRNA) exhibited two haplotypes (haplotypes 1–2) with a genetic distance p=0.2%. The comparison to previously reported sequences (Appendix 2) suggested high sequence similarity to samples of *M. orphnocnemis* (1.5% in 16S and 3.0% in ND1; Table 2).

Adult of the large form

A total of 21 specimens (19 males and two females) was recognized as belonging to the large form. The morphological characters were as follows: (1) body relatively large (male SVL 37.6–44.6 mm, female SVL 68.4–69.7 mm), (2) posterior part of thigh blotched with large clear light spots (Fig. 3B), (3) ventral surface of tibia scattered with melanophores ("B/C" and "C" in Inger and Gritis's [1983] categories; Table 1), (4) excision of webbing between fourth and fifth toes reach the level between distal and middle subarticular tubercle ("B" in Inger and Gritis's [1986] categories; Table 1), (5) broad webbing

TABLE 1. Thigh pattern, body size, relative leg length, tibia pattern, and extent of web of examined specimens and the topotypic specimens of *M. phaeomerus* and *M. poecilus*. Character states are as follows: Thigh pattern: D—Dusted with small irregular light dots, B: blotched with large clear light spots. Tibia pattern: A—heavy pigmentation over entire ventral surface; B—patches in which melanophores form continuous bands or spots across the surface; C—isolated, scattered melanophores; D—wide, longitudinal strip clear of melanophores. Extent of web: A—excision to proximal edge of distal subarticular tubercle; B—between distal and middle subarticular tubercle; C—distal edge of middle tubercle; D—center of middle tubercle; E—proximal edge of middle tubercle.

	Inger and Gritis (1983) Nanga Tekalit		Present study Lanjak Entimau	
	M. phaeomerus	*M. poecilus*	Small form	Large form
Thigh pattern	D	B	D	B
Male SVL				
N	160	233	26	19
Range	33.0–43.0	34.5–51.0	32.4–37.4	37.6–44.6
mean	38.25	44.08	35.08	40.78
Female SVL				
N	62	107	5	2
Range	57.2–71.5	60.1–77.0	58.7–63.2	68.4–69.7
mean	64.58	70.28	60.76	69.05
Male TL/SVL				
N	160	160	26	19
Range	.630–.765	.666–.849	.674–.744	.702–.777
mean	.707	.747	.706	.737
Female TL/SVL				
N	62	107	5	2
Range	.635–.771	.682–.807	.691–.734	.728–.748
mean	.708	.744	.722	.738
Tibia pattern				
A–B	—	—	1	—
B/C	5	1	10	13
C–D	20	24	20	8
Extent of web				
A–B	17	22	14	14
C	8	1	11	4
D–E	—	1	1	1

reaches the tip of toes, (6) black marking of flanks absent, (7) HW/SVL less than 0.35 (median [range]: 0.330 [0.296–0.344] in males; 0.331 [0.330–0.331] in females), (8) EL<snout length, and (9) large black spots on upper lip absent. The character states of the large form fit the original description of *M. poecilus* (Inger and Gritis, 1983), and differ from other congeneric species described subsequently (Shimada et al., 2015).

We obtained DNA samples from seven individuals of this form and the sequencing

Table 2. Mean uncorrected p-distances (%) among major lineages of *Meristogenys* for 16S rRNA (above diagonal) and ND1 (bellow diagonal). Shaded columns indicate distances between an unidentified sample from Lanjak Entimau and other congeneric species.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. *M.* sp. small form	—	5.6	6.4	5.0	6.0	7.2	6.7	11.7	7.7	1.5	6.8	7.7	6.0	6.2	6.4
2. *M.* sp. large form	14.5	—	5.4	6.4	6.4	6.5	6.3	10.9	6.5	5.7	5.8	7.0	4.5	4.4	4.3
3. *M. amoropalamus*	15.3	14.9	—	5.9	6.4	6.6	6.7	10.8	7.2	6.5	5.5	6.5	5.5	5.8	5.6
4. *M. dyscritus* Lineage 3	10.9	12.3	13.1	—	3.1	7.8	7.6	10.6	7.6	5.2	6.6	7.7	6.3	6.2	6.3
5. *M. dyscritus* Lineage 4	11.5	10.8	12.6	6.0	—	8.0	8.0	10.9	7.8	6.0	7.5	8.0	6.6	6.6	6.5
6. *M. jerboa* Lineage A	17.6	14.4	16.0	14.0	15.4	—	3.0	11.8	8.9	7.1	4.4	7.4	6.0	6.4	6.9
7. *M. jerboa* Lineage B	17.0	14.7	16.7	14.8	16.0	7.7	—	11.4	8.4	6.7	4.8	7.4	6.1	6.7	6.9
8. *M. kinabaluensis*	26.1	21.7	24.5	23.3	23.3	21.9	22.2	—	13.2	11.6	11.3	11.6	11.5	10.6	11.0
9. *M. maryatiae*	16.3	15.1	16.2	14.0	14.0	16.5	18.1	22.8	—	7.6	8.3	7.8	7.2	7.1	7.2
10. *M. orphnocnemis*	3.0	14.4	15.6	10.3	11.4	16.9	16.3	25.8	15.9	—	6.7	7.5	5.9	5.9	6.3
11. *M. penrissenensis*	16.8	15.6	15.5	14.7	15.4	12.4	12.7	23.3	18.1	16.3	—	7.2	5.0	6.2	6.4
12. *M. stenocephalus*	17.0	14.2	16.1	15.4	16.0	13.9	14.8	22.6	17.3	16.5	15.9	—	6.3	7.1	7.5
13. *M. stigmachilus*	12.7	12.6	13.7	11.4	12.3	15.7	15.8	23.2	15.0	13.0	16.2	15.1	—	5.0	5.0
14. *M. whiteheadi* (Sarawak)	13.7	11.5	12.9	11.2	11.4	15.0	15.2	25.0	14.5	13.1	15.1	14.4	11.3	—	2.3
15. *M. whiteheadi* (Sabah)	14.5	12.7	13.5	11.9	11.9	15.2	15.6	25.6	15.0	13.8	15.6	14.3	11.2	5.2	—

revealed three haplotypes (haplotypes 3–5) with a maximum genetic distance p=0.5%. These sequences were divergent from haplotypes 1–2 by genetic distances p=4.8–5.0% (12S). A part of sequences of this form had already been reported as "*M. poecilus*" in Shimada et al. (2011a, 2011b, and 2015), without detailed morphological remarks. No other sequences reported so far were genetically highly similar to this form (Table 2).

Yellow larvae

Twenty specimens in stage 28–40 in Gosner's (1960) table exhibited the following character states: large black blotches on body surface, both jaw sheaths divided, rows of keratodonts 6(4–6)/5(1), no surface projections, no ventral glands, no tail glands. Color in life was yellowish on body and tail (Fig. 2), but this color faded rapidly in preservation. These characters were consistent with the description of "Larva A" in Inger (1966). We obtained haplotype 3 from a specimen of this form, that matches the haplotype collected from large form of adults (=*M. poecilus*). However, the yellow larvae match the morphological larval description of "*Amolops* (=*M.*) *phaeomerus*" in Inger and Gritis (1983) and Inger (1985).

Gray larva

A specimen at Stage 41 according to Gosner's (1960) table was collected. Although the preserved specimen is not available any more, the photo taken in the field (Fig. 2A) reveals surface projections. Body and tail were grayish brown in color with small dark spots in a marbled pattern. From this specimen, we obtained haplotype 1, that completely matched the haplotype from the small adult form.

Discussion

In adult morphology, the small and large forms of *Meristogenys* collected in our study site were consistent with Inger and Gritis's (1983) descriptions of *M. phaeomerus* and *M. poecilus*, respectively. This result was highly plausible because our study site, Lanjak Entimau, was not very far (approx. 60 km) from the type locality of these species, Nanga

TABLE 3. Diagnostic characters separating the larvae of the *Meristogenys*. Character status are as follows: 1—numbers of divided rows of upper keratodont, 2—numbers of undivided rows of lower keratodont of old larvae, 3—status of the lower jaw sheath (D: divided, U: Undivided), 4: surface projections on head and body (P: present, A: absent), 5: ventral glands, 6: glands on upper fin, 7: glands on lower fin, 8: large blotches on body.

	1	2	3	4	5	6	7	8	Citation
M. amoropalamus	4	7–8	D–U*1	A	A	P	P	A	Shimada et al. (2011b)
M. dyscritus	3	6–7	D	P*2	A	A	P	A	Shimada et al. (2011b)
M. kinabaluensis (Kinabalu)	3	5	U	A	A*3	A*3	A*3	A	Inger (1985), Yang (1991), Malkmus et al. (2002), Shimada's unpublished data
M. kinabaluensis (Crocker Range)	3	5	U	A	P	P	P	A	Shimada et al. (2007)
M. jerboa	3	5–7	D	P	A	A	P	A	Shimada et al. (2015)
M. cf. *macrophthalmus**4	3	5	D	P	A	A	P	A	Matsui (1986)
M. maryatiae	4	5	D*5	P	A	A	P	A	Matsui et al. (2010)
M. orphnocnemis	3	5–6	D	P	A	A	P	A	Shimada et al. (2007)
M. penrissenensis	4	7	D	P	A	A	P	A	Shimada et al. (2015)
M. phaeomerus	3	4–5	D	P	A	A	P	A	Inger and Gritis (1983) as "*Amolops poecilus*"
M. poecilus	3	5	D	A	A	A	A	P	Inger and Gritis (1983) as "*Amolops phaeomerus*"
M. stenocephalus	4	6–7	U	P	A	A	P	A	Shimada et al. (2011a)
M. stigmachilus	4	?*6	U	P	A	A	P	A	Shimada et al. (2011a)
M. whiteheadi	4	5–6	U	P	A	A	P	A	Shimada et al. (2011a)

*1: Lower jaw sheaths divided in young larvae, but connected in old larvae, *2: Surface projections limitted only on head, *3: Ventral glands and upper and lower fin glands usually absent, but present in some individuals *4: Matsui (1986) reported the morphological status of the larvae collected at the type locality of *M. macrophthalmus*. Although Matsui (1986) did not clearly conclude that this form was the larvae of *M. macrophthalmus*, here we preliminary show it as "*M.* cf. *macrophalmus*". *5: Lower jaw sheaths divided, but touched with each other. *6: Old larvae has not been collected yet.

Tekalit, Sarawak, Malaysia (Fig. 1).

However, our molecular sequence comparisons indicated that the larval form originally introduced as *Meristogenys phaeomerus* by Inger and Gritis's (1983) (at that time as "*Amolops phaeomerus*") was actually the larval stage of *M. poecilus*. Unfortunately, we are uncertain about the true larvae of *M. phaeomerus*, because our specimen had already been homogenized before detailed morphological observations. However, if there was no third species in Nanga Tekalit, it is likely that the larval description of "*Amolops poecilus*" (today *M. poecilus*) in Inger and Gritis (1983) should have been assigned to *M. phaeomerus*. The dorsal view in our photo of the gray larval form shows grayish brown dorsal color without any large blotches; surface projections were absent. These features are at least not contradictory to Inger and Gritis's (1983) description of larval "*A. poecilus*".

Some further comments about the status of *Meristogenys phaeomerus* are warranted. In adult morphology, *M. phaeomerus* shares many character states with the Sabahan species *M. orphnocnemis*. Although these two species were supposed to be distinguished by different thigh pattern, tibia pattern, and the extent of webbing excision (Matsui, 1986), these characters actually exhibit a wide range of variation in *M. orphnocnemis* in Sabah, and it is not easy to distinguish the two species by adult morphology alone (Shimada

and Matsui, unpublished data). Provided that Inger and Gritis's (1983) larval assignment was correct, larval morphology could be an effective diagnostic character to distinguish these species because the description of larval "*A. phaeomerus*" in Inger and Gritis (1983) clearly differs from larval *M. orphnocnemis* (Shimada et al., 2007) in several character states such as presence/absence of surface projections, tail glands, and blotches on dorsum (Table 3). However, our study rejects this conclusion. According to our genetic evidence and matching of morphological features, the larval description of "*A. phaeomerus*" in Inger and Gritis (1983) should actually have been assigned to *M. poecilus*. The true larvae of *M. phaeomerus* is probably quite similar to larval *M. orphnocnemis*, exhibiting the similar tendencies as in adult morphology.

The 16S and ND1 sequence of *M. phaeomerus* obtained in our study was very similar to *M. orphnocnemis* from Sabah (1.5% in 16S and 3.0% in ND1; Table 2). A genetic distance of this degree is lower than any known interspecific distances in species of *Meristogenys* and even lower than intraspecific genetic distances between Sabahan and Sarawakian populations of *M. whiteheadi* (2.3% in 16S and 5.2% in ND1: Shimada et al., 2011a) or intrapopulational variation in *M. dyscritus* (3.1% in 16S and 6.1% in ND1: Shimada et al., 2011b) as well as in *M. jerboa* (3.0% in 16S and 7.7% in ND1: Shimada et al., 2015). Considering these genetic similarities in adults and larvae, careful re-examination of the specific validity of *M. orphnocnemis* and *M. phaeomerus* are recommended.

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Appendix 1

Specimens of adults examined morphologically in this study. KUHE: Graduate School of Human and Environmental Studies, Kyoto University. Vouchers with an underline were also examined in genetic analyses.

M. poecilus: KUHE 17346, 17379, 17416, 17423, 17432, 17435, 17447, 17448, 17449, 17450, 17466, 17467, 17468, 17469, 17487, 17497, 17498, 17519, 17520

M. phaeomerus: KUHE 17303, 17347, 17349, 17352, 17353, 17371, 17378, 17387, 17393, 17402, 17403, 17404, 17405, 17406, 17407, 17408, 17410, 17411, 17412, 17413, 17414, 17415, 17422, 17425, 17431, 17438, 17446, 17451, 17458, 17470, 17471

Appendix 2

Specimens vouchers, localities, and GenBank accession numbers cited from previous studies for the comparison. All from Malaysian territory. SP: Sabah Parks, BORNEENSIS: University Malaysia Sabah, KUHE: Graduate School of Human and Environmental Studies, Kyoto University.

M. amoropalamus: SP 3808 from Sg. Liwagu (larva), Kinabalu, Sabah; AB526619.

M. dyscritus (lineage 3): BORNEENSIS 12621 from Mahua, Sabah; AB526615.

M. dyscritus (lineage 4): BORNEENSIS 12623 from Mahua, Sabah; AB526616.

M. jerboa (Lineage A): KUHE 12055 from Matang, Sarawak; LC055962.

M. jerboa (Lineage B): KUHE 53207 from Ranchan, Sarawak; LC055963.

M. kinabaluensis: SP21546 from Mahua, Sabah; AB526618.

M. maryatiae: BORNEENSIS 8132 from Kimanis, Sabah; AB526611.

M. orphnocnemis: BORNEENSIS 12443 from Mahua, Sabah; AB526613.

M. poecilus: KUHE 17346 from Lanjak Entimau, Sarawak; AB526610.

M. penrissenensis: KUHE 54464 from Mt. Penrissen, Sarawak; LC055964.

M. stenocephalus: BORNEENSIS 8684 from Kimanis, Sabah; AB526612.

M. stigmachilus: BORNEENSIS 12561 from Mahua, Sabah; AB526614.

M. whiteheadi (Sarawak): KUHE 12369 from Bario, Sarawak; AB526609.

M. whiteheadi (Sabah): BORNEENSIS 23010 from Kinabalu, Sabah; AB526617.