The slugs and semislugs of Sabah, Malaysian Borneo (Gastropoda, Pulmonata: Veronicellidae, Rathouisiidae, Ariophantidae, Limacidae, Philomycidae)

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As a part of an inventory of the terrestrial malacofauna of the Malaysian state of Sabah (northern Borneo), the slugs and semislugs were given particular attention. Except for several exotic and presumed exotic species, slugs and semislugs are generally rare and infrequently encountered, mostly at high altitudes, where several short-range endemics appear to exist. We describe one new species, viz: Ibycus rachelae nov. spec. (Ariophantidae). We furthermore present new records and characters for identification of other species, namely: the veronicellids Laevicaulis alte (Férussac, 1821), Valiguna flava (Heynemann, 1885), and Semperula wallacei (Issel, 1874), the rathouisiid Atopos punctata Collinge, 1902, the ariophantids Microparmarion pollonerai Collinge & Godwin Austen, 1895, M. simrothi Collinge & Godwin Austen, 1895, Parmarion martensi Simroth, 1893, and Philippinella möllendorffi (Collinge, 1899), the limacid Deroceras reticulatum (Müller, 1774), and the philomycids Meghimatium striatum (Van Hasselt, 1824), M. uniforme Laidlaw, 1937, and M. pictum (Stoliczka, 1872). For the genus Meghimatium, our taxonomy is based on a molecular phylogenetic reconstruction, which we present. Finally, we provide reports and illustrations on several species for which the available material is currently insufficient for formal identification, namely, an unidentified Atopos (Rathouisiidae), for which only juveniles (preying on Opisthostoma) were found, a second unidentified Atopos (Rathouisiidae) and an unidentified Microparmarion (Ariophantidae) for each of which only a single adult was available, as well as an unidentified Parmarion (Ariophantidae) known only from a photo-

Key words: Gastropoda, Pulmonata, Veronicellidae, Rathouisidae, Ariophantidae, Limacidae, Philomycidae, taxonomy, alien species, Sabah, Borneo.

INTRODUCTION

The terrestrial molluscs of Sabah, Malaysian Borneo, have been studied intermittently by various malacologists since the mid-1800s. In the second half of the 19th century and the early 20th century, several authors published more or less comprehensive reports of the malacological results from expeditions, e.g., by Wallace (Wallace & Adams, 1865), Doria & Beccari (Issel, 1874), Everett (Godwin Austen, 1891; Smith, 1895), the Dutch Scientific Expedition to Central Borneo (Schepman, 1896), Schmidt (Martens, 1908), and Pendlebury & Chasen (Laidlaw, 1937). This profusion of early work has ensured that for many species, names are available. However, in many groups, the diversity, the number of available names, and the brevity of the published descriptions have necessitated taxonomic revisions. Some such revisions have appeared more recently on the entire Borneo fauna of several selected taxa such as Pupillidae, Hydrocenidae, and Helicinidae (Thompson & Dance, 1983), Streptaxidae (Dance, 1970; Vermeulen, 1990, 1991, 2007), Diplommatinidae (Vermeulen, 1991a,b, 1993, 1996a,b), and certain cyclophorid and dyakid genera (Vermeulen, 1999; Liew, Schilthuizen & Vermeulen, in press). Still, the majority of the malacofauna remains unsatisfactorily known.

In 2000, the Institute for Tropical Biology and Conservation at Universiti Malaysia Sabah began an inventory of the land molluscs of the Malaysian State of Sabah (northern Borneo). This project involves an ongoing series of longer and shorter expeditions throughout the state, the building of a reference collection (now comprising around 6,000 lots) within ITBC's BORNEENSIS collection, and a monograph-cum-field guide (Vermeulen, Schilthuizen & Liew, in prep.) describing and illustrating all ca. 330 known species of terrestrial slugs and snails (of which about 25% concern new species). While this latter book is being prepared, we make selected parts of the inventory accessible in other manners. One example is the current checklist, which may be found at the website of Discover Life (www.discoverlife.org, under 'IDNature Guides' and 'Others in Development'). Another example is the present paper, in which we offer an overview of the slugs and semislugs recorded to date from Sabah.

We here define slugs as snails without a visible shell, and semislugs as snails with a partially visible shell that is, however, too small to withdraw the body into. For the Sabah fauna, these categories encompass all Veronicellidae, all Philomycidae, all Rathouisiidae, and all Limacidae, plus several genera (*Ibycus, Parmarion, Philippinella*, and *Microparmarion*) of the Ariophantidae. We have excluded the ariophantid genus *Sabalimax* because its shell has several whorls and would qualify as a snail shell when found in soil samples (Tillier & Bouchet 1988). We have also excluded the Onchidiidae, which we consider as marine/estuarine as they live in mangroves and on periodically flooded seashores.

Slugs and semislugs form a relatively cryptic portion of the malacofauna of Sabah. This is partly due to the fact that snail sampling relies to a certain extent on techniques for finding empty shells (e.g., flotation; see Schilthuizen & Rutjes, 2001). In fact, in soil samples from some areas (e.g. in the foot-hills of the Crocker range) we have found relatively large numbers of *Microparmarion* shells without ever coming across any living individuals, suggesting that this genus of semislugs is commoner than thought. Nevertheless, in general it appears that slugs and semislugs form a relatively minor component of the terrestrial molluscan fauna. Just one percent of our collection samples concern (semi)slugs and living individuals are encountered infrequently and mostly only in high altitudes and under special conditions (during rain at night or early in the morning). Below, we briefly characterise and illustrate all species so far known to us, and give a full description where a new species is concerned. We also include several highly characteristic species for which at present we have insufficient material (only juveniles and/or photographs of living individuals) to allow formal identification or description.

MATERIAL AND METHODS

Specimens were collected in the field, relaxed in deoxygenated water, and then transferred to 70 % ethanol. For molecular phylogenetics (genus *Meghimatium* only), a fragment of foot tissue was kept in 100 % ethanol for DNA extraction. The material mentioned is stored in the *BORNEENSIS*-collection at Universiti Malaysia Sabah (acronym: BORN; collection numbers of the Mollusc collection preceded by "BOR/MOL"), whereas we also refer to some material from the Sabah Parks Museum, Kinabalu Park Headquarters, Malaysia (acronym: SP).

For the molecular taxonomy of *Meghimatium*, genomic DNA from 2 – 3 mm³ of foot tissue of single individuals was extracted using DNeasyTM nucleic acid extraction kits (QIAGEN[®]). We amplified two mitochondrial DNA regions, namely *16S* and *COI*, with primer pairs 16Sbr-L and 16Sbr-H (Palumbi *et al.*, 1991), and LCO1490 and HCO2198 (Folmer *et al.*, 1994). Furthermore, a nuclear rDNA region of *ITS-1* was amplified by using

No.a	Species	Locality	Colour Morph
1 ^C	Meghimatium cf. pictum	Mount Kinabalu, western slope (1450 m alt.)	Fig. 14
2	Meghimatium cf. pictum	Mount Kinabalu, western slope (1450 m alt.)	Fig. 14
3	Meghimatium cf. pictum	Crocker range, western slope (1200 m alt.)	Fig. 14
4	Meghimatium cf. pictum	Crocker range, western slope (500 m alt.)	Fig. 19
5	Meghimatium cf. pictum	Crocker range, eastern slope (1200 m alt.)	Fig. 19
6	Meghimatium cf. pictum	Crocker range, eastern slope (1200 m alt.)	Fig. 19
7	Meghimatium cf. pictum	Crocker range, eastern slope (1200 m alt.)	Fig. 19
8 ^A	Meghimatium cf. pictum	Mt. Kinabalu, eastern slope (1200 m alt.)	Fig. 19
9	Meghimatium cf. pictum	Tawau Hills Park, Mt. Magdalena (1400 m alt.)	Fig. 20
10	Meghimatium cf. pictum	Tawau Hills Park, Mt. Magdalena (1400 m alt.)	Fig. 20
11 ^D	Meghimatium striatum	Mount Kinabalu, southern slope (2400 m alt.)	Fig. 18
12	Meghimatium striatum	Mount Kinabalu, eastern slope (2000 m alt.)	Fig. 18
13	Meghimatium striatum	Mount Kinabalu, eastern slope (2300 m alt.)	Fig. 18
14	Meghimatium striatum	Mount Kinabalu, eastern slope (2400 m alt.)	Fig. 18
15 ^B	Meghimatium uniforme	Mount Kinabalu, eastern slope (3400 m alt.)	Fig. 17
16 ^B	Meghimatium uniforme	Mount Kinabalu, eastern slope (3400 m alt.)	Fig. 17
17	Meghimatium uniforme	Mount Kinabalu, eastern slope (3300 m alt.)	Fig. 17
18 ^B	Meghimatium uniforme	Mount Kinabalu, southern slope (3200 m alt.)	Fig. 15
19 ^B	Meghimatium uniforme	Mount Kinabalu, southern slope (3300 m alt.)	Fig. 16
20	Meghimatium uniforme	Mount Kinabalu, southern slope (3300 m alt.)	Fig. 16

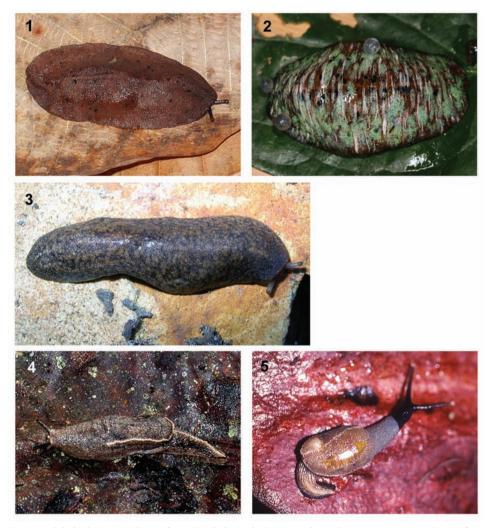
Table 1. Specimens used for the molecular genetic analysis. 'Colour morph' refers to the pigmentation patterns in figures 14 - 20. ^a Specimen numbers and annotations refer to the codes used in figure 21.

the primer pair 5.8c "silkworm" and 18d "fruitfly" (Hillis & Dixon, 1991).

Reactions were performed in 50- μ l volumes, using 5 μ l 10 × reaction buffer, 5 μ l 2mM dNTP, 6 μ l 25mM MgCl₂, 2 μ l for each primer (5 pmol), 26.85 μ l de-ionized autoclaved water and 1 unit of Taq polymerase. The following cycling profile was used: 2 min at 95 °C, followed by 35 cycles of 1 min at 95 °C, 1 min at 55 °C for 16S and COI (60 °C for ITS-1) and 2 min at 72 °C, and a final extension period of 10 min at 72 °C.

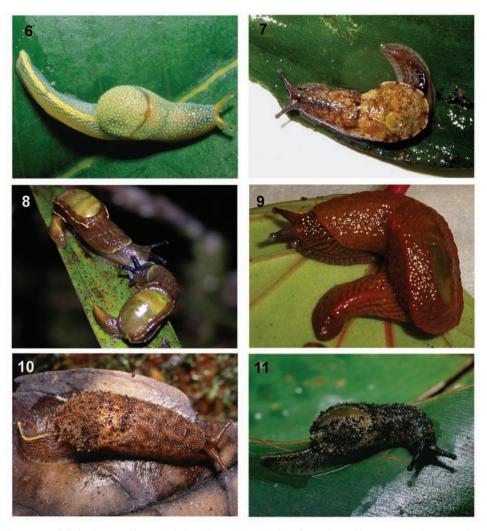
DNA sequencing was performed directly on purified PCR products for both directions by using the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems Ltd) according to the manufacturer's protocol. Genetic data were collected from an ABI 3100 Genetic Analyser (Applied Biosystems Ltd).

The DNA sequences were aligned using the ClustalW Multiple alignment algorithm in the BioEdit Sequence Alignment Editor, version 7.0 (Hall, 1999), then subsequently checked and adjusted manually using the same program. Phylogenetic relationships were analysed using maximum-parsimony (MP) and maximum-likelihood with PAUP*4.0b10 (Swofford, 2002), and Bayesian analysis (BA) with MrBayes 3.1 (Huelsenbeck & Ronquist, 2001). The analyses were run for a combined dataset of *ITS-1*, *COI* and *16S*; and for each gene separately. We also repeated the analyses for the respective gene under exclusion of ambiguously aligned regions (i.e., *16S*) and the third codon position of *COI*. Modeltest 3.7 (Posada & Crandall, 1998) was used to find the best substitution model from 56 models



Figs 1-5. Sabah slugs. 1, Valiguna flava (Kinabalu Park: Poring); photo: Peter Koomen;. 2, Valiguna flava (Kinabalu Park: Poring), diseased individual (with eggs); photo: Eduard Linsenmair;. 3, Semperula wallacei (Kota Kinabalu); photo: Menno Schilthuizen; 4, Parmarion martensi (Lower Kinabatangan: Sukau); photo: Peter Koomen; 5, Parmarion spec. (Kinabalu Park: Marai Parai); photo: Ravi Mandalam.

for all data matrices. For the ML analysis on the combined dataset, we did a heuristic search based on the model selected by Modeltest. For the MP analysis, gaps were included as a fifth character state and each character was given equal weight. One thousand bootstrap replicates were carried out, with ten replicates of a heuristic search with random addition sequence at each bootstrap replicate. Branches were swapped under the tree bisection reconnection (TBR) algorithm. Based on the selected substitution model from Modeltest, the data matrix was analyzed in BI with 1 million generations and sampled every 100th generation. Then, we discarded 25% of the samples obtained during the first



Figs. 6-11. Sabah slugs. 6, *Ibycus rachelae* (Mount Trus Madi); photo: Peter Koomen; 7, *Microparmarion* spec. (Upper Padas: Long Pa Sia); photo: Liew Thor Seng; 8, *Microparmarion pollonerai* (Kinabalu Park: Layang-layang) photo Paul Yambun; 9, *Microparmarion pollonerai* (Kinabalu Park: Mesilau), anatomically aberrant individual; photo: Liew Thor Seng; 10, *Microparmarion simrothi* (Mount Trus Madi), light individual; photo: Peter Koomen; 11, *Microparmarion simrothi* (Mount Trus Madi), dark individual; photo: Peter Koomen.

1 million generations and the remain trees were calculated to produce a consensus tree with a cut-off value of 50 %.

SYSTEMATIC PART

Note: family, genus, and species descriptions are applicable to Sabah material only.

Family Veronicellidae Gray, 1840

Diagnosis. — Slugs with no internal shell. Body long elliptical, dorsolaterally flattened. Dorsal side covered by the thick, leathery notum, separated from the ventral side by a keel, the perinotum. Ventral side with a narrow central sole, separated by a pedal groove from the lateral hyponota. The female genital pore is situated roughly centrally on the right hyponotum (on the left in ventral view). The male genital pore is hidden near the base of the right lower tentacle. Body colour ranges from pale mottled yellowish to almost black, with great intraspecific variability. When active, the head remains hidden under the notum, only the upper tentacles visible. In lowland primary and secondary forest, and gardens. Herbivorous and detritivorous, some invasive species are considered agricultural pests. Nocturnal, by daytime resting under logs and stones. Occasionally, diseased individuals are found of which the skin has become rugulose and covered in a mottled green (fungal or bacterial?) film. Herbert & Kilburn (2004: 283) picture such an individual of Laevicaulis natalensis from South Africa, and we have been shown photos of similarly affected (unidentified) veronicellids from Singapore (Chan Sow Yan, pers. comm.) and Sabah (Jaap Vermeulen, pers. comm. and Eduard Linsenmair, pers. comm.; fig. 2). The affliction appears to be veronicellid-specific and might be of interest for biocontrol of agricultual pest species.

Externally, the genera are so similar that we refrain from giving descriptions for each genus separately.

Laevicaulis Simroth, 1913

Laevicaulis alte (Férussac, 1821)

Vaginulus alte Férussac, 1821: 14 (Pondicherry, India) Material studied. – Kota Kinabalu (BOR/MOL 3437)

Diagnosis. – Body dark grey, almost black, usually with a pale yellow median stripe. Sole pale grey, about as wide as one hyponotum. Dorsal side with densely arranged, relatively coarse granules, giving the surface a velvet-like appearance. Female pore situated at ca. 55% of the body length, measured from the front, and removed from the pedal groove by c. 1/4 the width of the hyponotum. Penial verge 8 mm long and terminally tapered, with a collar-like ring at the base. Body length: 50-80 mm; body width: 20-30 mm.

Biology and distribution. – Introduced; occurring in disturbed vegetation near human habitation. Sabah distribution: known from Kota Kinabalu; probably in other towns and cities as well. Distibution elsewhere: pantropical (Gomes & Thomé, 2001, 2004). Natural range: Africa.

Valiguna Grimpe & Hoffmann, 1925

Valiguna flava (Heynemann, 1885) (figs 1-2)

Vaginula flava Heynemann, 1885: 10-11 (Borneo)

Material studied. - Poring, 500 m alt. (BOR/MOL 3439; BOR/MOL 3411); Danum Valley 300 m

(BOR/MOL 3409; BOR/MOL 3410); Tenom, 327-400 m asl. (BOR/MOL 3438)

Diagnosis. – Body ranging from pale yellowish brown to dark reddish brown, dorsally with scattered blackish spots. Sole about 1/5 of the body width. Dorsal side relatively smooth, only with some widely spaced granules. Female pore situated at c. 45% of the body length, measured from the front, and removed from the pedal groove by c. 2/5 the width of the hyponotum. Penial verge 3 mm long and with a complex shape: a lateral lobe is present and the terminus is studded by numerous teeth. Body length: 45-60 mm; body width: 22-30 mm. A more detailed description and a comparison with the related *V. siamensis* (Martens, 1867) can be found in Gomes et al. (2008).

Biology and distribution. – This appears to be the only native one of the three veronicellid species presently known from Sabah. It only occurs in primary forest below 1000 m alt. Sabah distribution: scattered localities on the East and West Coast. Distribution elsewhere: Sumatra and Borneo.

Semperula Grimpe & Hoffmann, 1924

Semperula wallacei (Issel, 1874) (fig. 3)

Vaginula wallacei Issel, 1874: 385 (Sarawak)

Material studied. – Sepilok (BOR/MOL 3408); Kota Kinabalu (BOR/MOL 3435, BOR/MOL 3436; BOR/MOL 3440)

Diagnosis. – Body relatively pale yellowish brown, dorsally with scattered blackish spots, usually leaving a lighter median stripe. Sole about 1/5 of the body width. Dorsal side relatively smooth, with widely spaced coarse granules, interspersed with smaller ones. Female pore situated at c. 60% of the body length, measured from the front, and removed from the pedal groove by c. 1/2 the width of the hyponotum. Penial verge 2 mm long and terminally rounded. Body length: 30-45 mm; body width: 10-14 mm.

Biology and distribution. – Although the holotype of this species is from Sarawak, and hails from a period that exotic species introductions were relatively rare, this species appears not to be native to Borneo, as it is only found in disturbed vegetation near human habitation. Distribution in Sabah: Present in and around most towns and cities. Distribution elsewhere: Southeast Asia, Pacific islands.

Family: Rathouisiidae Sarasin, 1899

Diagnosis. – Slugs without any internal shell. Body more or less cylindrical. Dorsal side fully enclosed in the notum, foot with a broad central sole that is separated from the notum by a pedal groove. The animals are predators.

Atopos Simroth, 1891

A genus of slender, large-bodied carnivorous slugs. The animals of certain species can reach over 7 cm in length. They are often a mottled grey or brown, with a granulose, thick and dry, not slimy, notum. Upon touching the live animal it tends to become stiff and motionless. The genus ranges throughout Southeast Asia and Australia, and a fair number of species have been reported from Peninsular Malaysia and Sulawesi. Distribution areas may be large, and with a taxonomic revision still lacking, it is very difficult to deter-



Fig. 12-14. Kinabalu slugs. 12, *Deroceras* cf. *laeve* (Kinabalu Park: Laban Rata); photo: Liew Thor Seng; 13, *Atopos* spec. (Lower Kinabatangan: Sukau); photo: Peter Koomen; 14, *Meghimatium pictum* (Kinabalu Park: Park Headquarters, 1400 m alt.); photo: Liew Thor Seng.

mine if the Bornean forms are conspecific with any known taxa. For this reason, we refrain from identifying two out of the three species that we have collected in Sabah.

Atopos spec. 1 (fig. 13)

Unidentified *Atopos* (Philomycidae): Schilthuizen et al. 2003 Unidentified *Atopos* (Rathouisiidae): Schilthuizen et al. 2006 Material studied. – Sukau (BOR/MOL 3418, 3420), many juveniles.

Diagnosis. – (Based on juvenile individuals.) Long and slender (length: 7-22 mm; width 1-3 mm). Notum keeled, covered in circular, brownish-grey granules of varying diameter and darkness. The rostralmost part of the notum is devoid of such granules. The rest of the body is unpigmented. Foot with a narrow sole, which (in preserved specimens) is less than one-quarter of the body width. Mouth on either side, at the basis of the lower tentacles, with a two-lobed lip.

Biology and distribution. – The animals (juveniles only) were observed at night (20.00-23.00 h.) on vertical limestone rock faces on the northern flank of Batu Tomanggong Besar near Sukau (Lower Kinabatangan). During the day, *Atopos* was never seen, which suggests that they hide in crevices in the limestone rocks. (A similar behaviour was recorded for *A. leonina* Heude 1883 on brick walls in China, whereas *A. sarasini* Collinge 1902 was reported from limestone outcrops in Kedah, West-Malaysia; Laidlaw, 1940). The



Fig. 15-20. Meghimatium slugs 15, Meghimatium uniforme (Kinabalu Park: Laban Rata, 3100 m alt.), brownish individuals; photo: Liew Thor Seng; 16, Meghimatium uniforme (Kinabalu Park: Laban Rata, 3200 m alt.), bluish individual; photo: Liew Thor Seng; 17, Meghimatium uniforme (Kinabalu Park: Eastern slope, 3200 m alt.), individuals with spare black spotting; photo: Liew Thor Seng; 18, Meghimatium striatum (Kinabalu Park, 2500 m alt.); photo: Liew Thor Seng; 19, Meghimatium pictum (Crocker Range: Sugud); photo: Menno Schilthuizen; 20, Meghimatium pictum (Tawau Hills Park); photo: Sinail Dunsul.

slugs were seen attacking juvenile and adult individuals of *Opisthostoma fraternum* E. A. Smith, 1905, Caenogastropoda, Diplommatinidae. Juvenile prey were eaten via the aperture, whereas adult prey were reached via holes bored into the shell surface with the radula. Although the slug was so far only encountered in one locality, its traces on empty shells of *Opisthostoma* and other genera on the forest floor were found on limestone outcrops throughout Sabah, suggesting that the species (and/or close relatives) are widespread.

Atopos spec. 2

Material studied. - Kinabalu Park, 2600 m alt. leg. Martinah (SP12661), 1 adult.

Diagnosis. – Body long and slender (length 33 mm; width 4 mm). Notum keeled, pale ochraceous, mottled with dark brown and black. Foot unpigmented, with a narrow sole, c. one-thrid of the body width. Tentacles with dark grey pigmentation. No obvious lip present. Female genital pore situated at about 20% of the body length, when measured from rostral. Penis everted in the specimen studied, c. 4 mm long, studded with numerous short spines and one long terminal spine.

Biology and distribution. – Based on the differences in colouration and mouthparts, A. spec. 1 and A. spec. 2 are not conspecific. Also, A. spec. 1 lives at sea-level, whereas A. spec. 2 was found at 2600 m altitude.

Atopos punctata Collinge 1902

Atopos punctata Collinge 1902: (Kelantan) Material studied. – Pulau Bohey Dulang (BOR/MOL 5357), 1 adult.

Diagnosis. – Animal thin and long. Length 30 mm, width 4 mm. Notum keeled, with irregular yellowish brown and black granulated pigmentation. Female genital pore at 40% of the body length, measured from rostral. Based on the size, habitus, and colouration of *A. punctata* from Peninsular Malaysia (figured and described by Collinge [1902]), which is rather unusual within the genus (Sarasin and Sarasin, 1899; Simroth, 1892), we tentatively assign this individual from Sabah to this species.

Biology and distribution. - Semporna Islands, Pulau Bohey Dulang.

Family Ariophantidae Godwin-Austen, 1888

Diagnosis. – A large family of mostly large-shelled forms, in which several lineages exist with reduced shell. If we exclude the genus *Sabalimax*, at least seven of these semislug species occur in Sabah.

Ibycus Heynemann, 1862

Semislugs. Characterised by the long tail and the right mantle lobe that is developed to a wing-like flap covering most of the shell.

Ibycus rachelae spec. nov. (figs 6, 22)

Material studied. – Holotype: Mount Kinabalu, 1500 m alt. (BOR/MOL 3427); paratypes: Crocker Range (Kimanis), 1400 m alt. (BOR/MOL 3426); Crocker Range (Gunung Mas) (BOR/MOL 3444); Mount Trus Madi, 1400 m (BOR/MOL 3427); Mount Kinabalu, 1500 m alt (BOR/MOL 5463, 5466); 1200 m alt (BOR/MOL 5464); 1800 m alt. (BOR/MOL 5465); 1800 m alt. (BOR/MOL 5466); 1900 m alt. (BOR/MOL 5467); Mount Tambuyukon, 1600 m alt. (BOR/MOL 5468).

Description. – Semislug. Shell: yellowish brown (protoconch whitish), globose, almost hemispherical, 1.5 whorls. Body yellowish green, with dorsal line of the tail yellow. Head (usually hidden under the dorsum) light or dark grey. In preserved specimens, the green and yellow coloration is lost and the animals look almost entirely white. Tail long,

three times as long as the head. Shell lobes and posterior part of the body covered in small, densely arranged tubercles, which are circular and of varying size on the shell lobes. Tail covered by regularly arranged, diamond-shaped rugae. Left shell lobe small, right shell lobe very large and wing-like. Penis straight, regular in girth, terminally bent back upon itself, where the vas deferens joins it laterally. Two dilations are visible in the vas deferens where it attaches to the penis. Dart-sac club-shaped, slightly shorter than the penis but of equal girth. Vagina short, almost immediately giving way to the receptaculum. Body length: up to 40 mm.

Biology and distribution. – In primary montane forest from 1200 to 1900 m alt., on leaves. Apparently distributed throughout the montane areas on the west coast and in the interior (we have seen a photo of an adult individual taken during the Universiti Malaysia Sabah expedition to Maliau Basin). The living animal has the habit of wrapping its long tail around the body when in rest.

Remarks. – We place this species in the genus *lbycus* for its long, laterally compressed tail and the arrangement of the shell lobes. It may be identical to the species described by Laidlaw (1937) as *lbycus* sp. from Kinabalu, although the genitalia as figured by laidlaw do not seem to correspond perfectly with those in our material. In Laidlaw's drawing, the dart sac is longer than the penis, whereas it is shorter in our material, and Laidlaw shows the receptaculum as a separate organ at the basis of the vagina, whereas it appears to be a blind sac of the vagina in our specimens.

Etymology. - The species is named after Rachel Esner for reasons known to her.

Microparmarion Simroth, 1893

Semislugs. Characterised by the relatively stout habitus, short tail, and the large, partly exposed shell, which carries about two whorls.

Microparmarion pollonerai Collinge & Godwin Austen, 1895 (figs 8, 9, 23a,b,d)

Microparmarion pollonerai Collinge & Godwin Austen, 1895: 244 (Borneo, Sabah, Mount Kinabalu). Material studied. – Mount Kinabalu, 1900-2200 m alt. (BOR/MOL 5445 – 5450); Mount Kinabalu, Paka, 3000 m alt. (BOR/MOL 2872); Mount Kinabalu, 2700 m alt. (BOR/MOL 4584); Mount Kinabalu, 2700 m alt. (BOR/MOL 5451); Mount Kinabalu, Mesilau, 2000 m alt. (BOR/MOL 3430)

Diagnosis. – Semislug. Body more or less uniform pale to dark bluish grey, crest of the tail and rugae yellow (pink in preserved specimens). Mantle yellowish grey (pink in preserved specimens). Juveniles may have a more mottled colour pattern. The border of the mantle that encircles the shell carries two keels on the right and one on the left. Posterior portion of the mantle border is more angular in specimens from Mesilau (fig. 9), more rounded in those from Paka. Shell with almost two whorls. Body length up to 40 mm. Width up to 15 mm. Genitalia: see figs 23a.

Biology and distribution. — Primary montane forest, from 1900 to 3000 m alt. Endemic to Mount Kinabalu. Less common than *M. simrothi*.

Remarks. – The individuals from Mesilau differ in genital shape (fig. 23d) and are more similar to *M. simrothi* in this respect. The taxonomic position of this population remains to be investigated.

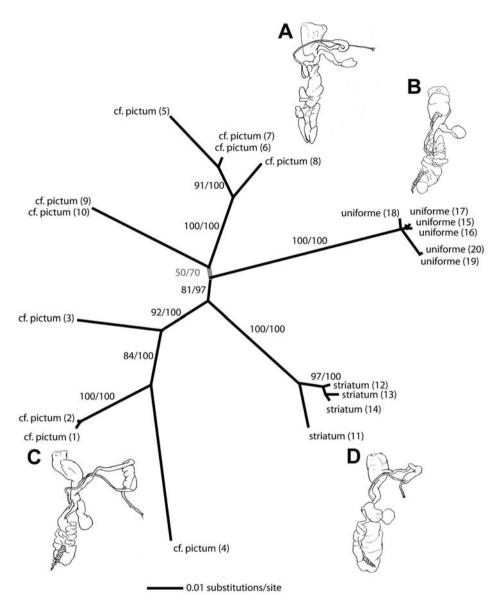


Fig. 21 Meghimatium molecular phylogeny. Unrooted maximum likelihood tree of the combined dataset (a single best tree in heuristic search, likelihood score: 5108.3897) with Bayesian posterior probability values (left) and MP bootstrap support (right) on the branches. Asterisk indicates a node supported by low posterior probability and bootstrap values. Refer to Table 1 for the annotated specimen numbers and genitalia.

Microparmarion simrothi Collinge & Godwin Austen, 1895 (figs 10, 11, 23c)

Microparmarion simrothi Collinge & Godwin Austen, 1895: 246 (Borneo, Sabah, Mount Kinabalu).

Material studied. – Mount Kinabalu, 1400 m alt. (BOR/MOL 3446); Mount Kinabalu, 1450 m alt. (BOR/MOL 5453); Mount Kinabalu, 1500 m alt. (BOR/MOL 3445); Mount Kinabalu, 1850 m, alt. (BOR/MOL 5455); Mount Kinabalu, 1900 m alt. (BOR/MOL 3428); Mount Kinabalu, 2000 m alt. (BOR/MOL 3442, 4511); Mount Kinabalu, 2200 m alt. (BOR/MOL 4515, 5458); Mount Kinabalu, 2300 m alt. (BOR/MOL 5459); Mount Kinabalu, 2300 m alt. (BOR/MOL 5459); Mount Kinabalu, 2350 m alt. (BOR/MOL 5454); Mount Kinabalu, 2400 m alt. (BOR/MOL 3424); Mount Kinabalu, 2500 m alt. (BOR/MOL 5456, 5460); Mount Kinabalu, 2550 m alt. (BOR/MOL 5457); Mount Kinabalu, 2700 m alt. (BOR/MOL 2879), Mount Kinabalu, 2800 m alt. (BOR/MOL 3443); Mount Kinabalu, 2900 m alt. (BOR/MOL 2875); Mount Trus Madi, 1400 m alt. (BOR/MOL 3429, 3434); Mount Trus Madi, 1800 m alt. (BOR/MOL 3422); Mount Trus Madi, 2300 m alt. (BOR/MOL 3830); Mount Alab, 1800 m alt. (BOR/MOL 5452)

Diagnosis. – Semislug. As *M. pollonerai*, but animal ranging from yellow (fig. 10) to dark brown (fig. 11), mottled with darker specks, especially striking in preserved specimens, in which the ground colour fades to white. Head with three longitudinal dark bands. The mantle carries numerous small tubercles. Where it encircles the shell, several larger tubercles are present, but no keels. Shell with almost two whorls. Body length up to 45 mm. Width up to 15 mm. Genitalia: fig 23c.

Biology and distribution. – Fairly common in primary montane forest of the west coast mountains (Crocker Range, Kinabalu, Trus Madi).

Microparmarion spec. (fig. 7)

Material studied. - Long Pa Sia, 1200 m alt. (BOR/MOL 5469)

Diagnosis. — Animal pale, with irregular brownish blotting. Head with three longitudinal darker brown lines and a darker brown line on the tail. Semi-transparent anterior mantle lobe with light brown, irregular, widely—spaced reticulate lines. A narrow, yellowish carina runs around the posterior part of the shell mantle, carrying 7 notches. Body length 30 mm.

Biology and distribution. - Only recorded in forest near Long Pa Sia (Upper Padas).

Parmarion Fischer, 1855

Semislugs. Shell reduced to a thin plate, in which whorls can hardly be recognised. Body large, tail with a distinct caudal horn. Mantle encircles the shell, carrying a keel all the way round, except at the front.

Parmarion martensi Simroth, 1893 (fig. 4)

Parmarion martensi Simroth, 1893: 107 (Cambodia).

Material studied. – Sukau (BOR/MOL 3447); Kota Kinabalu (BOR/MOL 3448); Bukit Padang (near Kota Kinabalu) (BOR/MOL 3449)

Diagnosis. – Body pink, leading to darker grey above. Tentacles black, mantle keels and dorsal keel on tail yellowish. Body length: up to 50 mm. Otherwise: see genus description.

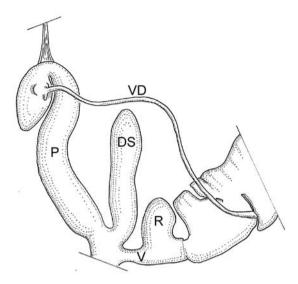


Fig. 22. Genitalia of *Ibycus rachelae* nov. spec., paratype (Mount Trus Madi, 1400 m alt.). Abbreviations: P, penis; V, vagina; VD, vas deferens; R, receptaculum; DS, dart sac.

Biology and distribution. – Introduced from its natural range (probably mainland Southeast Asia) into many areas around Southeast Asia and the Pacific (Cowie, 1997). In Sabah found in disturbed vegetation near human habitation; to be expected in and around most villages, towns, and cities.

Remarks. – The species can only be distinguished with certainty from another widely introduced species, *P. pusillus* Humbert, 1864, by the relative lengths of dart sac and dart gland. All anatomically examined Sabah material belongs to *P. martensi*, but it is possible that *P. pusillus* is also present.

Parmarion spec. (fig. 5)

Material studied. – Two diapositive slides of an adult animal made by Dr. Ravi Mandalam (Sabah Medical Centre) on Mount Kinabalu, near Marai-Parai in 2001.

Diagnosis. – Mantle and tail brown, dark grey at the edge of the foot. Dorsum bluish grey, head and tentacles black.

Biology and distribution. – in montane vegetation on ultramafic soil.

Remarks. – Probably an undescribed species, but until specimens for dissection become available, we refrain from naming it.

Philippinella von Moellendorf, 1899

Slugs with the mantle covering the shell entirely; shell completely internal. Mantle weakly keeled. Tail relatively short.

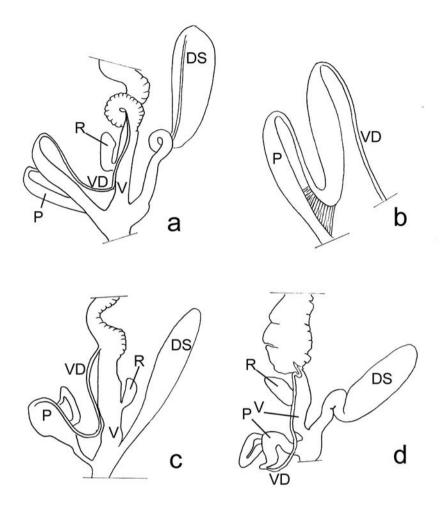


Fig. 23. Genitalia of *Microparmarion*; **a**, genitalia of *M. pollonerai* (after Collinge, 1895); **b**, penis of *M. pollonerai* (after Laidlaw, 1937); **c**, genitalia of *M. simrothi* (after Collinge, 1895); **d**, genitalia of *M. pollonerai* from Mesilau. Abbreviations: P, penis; V, vagina; VD, vas deferens; R, receptaculum; DS, dart sac.

Philippinella moellendorffi (Collinge, 1899)

Philippinella möllendorffi Collinge, 1899 (Philippines: Mindoro)

Material studied. – Kota Kinabalu (BOR/MOL 3421); Lower Kinabatangan (BOR/MOL 3425), Kinabalu Park, Poring Hot Springs, 500 m alt. (BOR/MOL 3441); Sepilok (BOR/MOL 3433)

Diagnosis. – In preserved state, body pale brown, often with a seam of vertical marks along the edge of the foot, the sides of the tail, and some specks on the mantle dark grey.

Tail shorter than the rest of the body. Shell internal, resembling a miniature unionid shell: flat, calcified, with a slightly raised 'spire'. A minute pore at the posterior part of the dorsum provides access to the shell. Dorsum carries two unpigmented, lightly raised longitudinal keels on either side, which almost touch posteriorly. These keels appear to be more pronounced in juveniles than in adults. Body length: up to 50 mm.

Biology and distribution. – In disturbed vegetation near towns and villages. Given its habitat, possibly a non-native species.

Family: Limacidae Rafinesque, 1815

Description. – Slugs. Dorsum keeled. Mantle oval, covered with concentric wrinkles in living individuals. Pneumostome postmedial.

Deroceras Rafinesque, 1820

Slugs. Mantle encloses a small, asymmetric internal shell. Tail only keeled at the tip. No caudal horn.

Deroceras cf. laeve (Müller, 1774) (fig. 12)

Limax laevis Müller, 1774: 1 (Denmark)

Material studied. – Kinabalu Park Headquarters, 1500 m alt. (BOR/MOL 3431); Kinabalu Park, Mesilau, 1800 m alt. (BOR/MOL 3836)

Diagnosis. – Small slug, glassy, chestnut to dark brown, dorsum often lighter, with coarse concentric circles. The area surrounding the pneumostome often somewhat unpigmented. Body length: up to 25 mm.

Biology and distribution. – Introduced; disturbed vegetation near human habitation in cool, montane environment. Around buildings in Kinabalu park, in the Headquarters area and at Mesilau. Introduced from its natural Holarctic range into many areas around the world, including various parts of Southeast Asia and the Pacific (e.g. Hawaii; Cowie, 1997).

Family: Philomycidae Gray, 1847

Slugs without any internal shell. Body more or less cylindrical. Dorsal side fully enclosed in the notum, foot with a broad central sole that is separated from the notum by a pedal groove. The animals feed on lichen and fungi.

Meghimatium Van Hasselt, 1824

Slugs, body white or pale yellowish brown, often with an attractive pattern of black stripes and dots. *Meghimatium* species are mainly classified on the basis of pigmentation, penis shape, and the arrangement of spermatheca, vagina, and atrium (Wiktor *et al.*, 2000; Tsai *et al.*, 2005). Although in our Sabah material we could tentatively identify *Meghimatium uniforme* and *M. striatum* by their unique and relatively consistent mantle pigmentations and genitalia, the rest of the taxa (many of which resembled *M. pictum*) presented us with a confusing mix of colour forms, while lack of adults (see Table 1) lim-

ited the extent to which we could rely on genital characters. To delineate the species and to ascertain their identity, we performed a molecular phylogenetic analysis (see above under Materials & Methods). We used 20 samples that had been collected between 2004 and 2008 (table 1).

Our preliminary results (sequences and alignments may be obtained from T.-S. L. on request), supplemented with unpublished COI data kindly provided by Tsai C.-L., suggested that the Borneo species form a monophyletic group relative to other Asian species. However, since we observed saturation in the COI locus, we did not include any outgroup taxa in the present analysis. The length of the combined data matrix was 1693 bp (ITS = 625 bp, COI = 567 bp, and 16S = 501 bp). All different datasets (Table 2) showed similar topologies both under MP and BA. Thus, we used the tree resulting from the combined dataset in the following discussion. The ML heuristic search found a single best tree with likelihood score 5108.3897. Both Meghimatium uniforme and M. striatum form respective monophyletic groups with high posterior probability and bootstrap supports. However, the polymorphic M. cf. pictum form two major groups, of which one group consists of M. cf. pictum '1' to '4' (western slopes of the Crocker Range and Mount Kinabalu) and the other of M. cf. pictum '5' to '8', deriving from the eastern slopes of the same massifs (fig. 21; Table 1), whereas M. cf. pictum '9' and '10' from Tawau form a third clade. Our analysis thus suggests that M. uniforme and M. striatum are well-characterised, clearly defined species, whereas *M. pictum* consists of at least two or three subspecies (see further below).

Meghimatium striatum (Van Hasselt, 1824) (fig. 18)

Meghimatium striatum Van Hasselt, 1824: 82 (Java)

Material studied. – Mount Kinabalu, southern slope, 2350 m alt. (BOR/MOL 2878); Mount Kinabalu, eastern slope, 2000 m alt. (BOR/MOL 3412); Mount Kinabalu, southern slope, 2500 m alt. (BOR/MOL 3417); Mount Kinabalu, southern slope, 2400 m alt. (BOR/MOL 5433); Mount Kinabalu, eastern slope, 2050 m alt. (BOR/MOL 5436); Mount Kinabalu, eastern slope, 2400 m alt. (BOR/MOL 5437)

Diagnosis. – Slender, orange-yellow, usually with five regular and straight black longitudinal bands, of which the outermost two are often dissolved into separate dots or have completely disappeared. Upper tentacles dark. Body length up to 45 mm, width up to 7 mm. Genitalia: see anatomy "D" in fig. 21.

Biology and distribution. — Primary montane forest on Mount Kinabalu, at 2000-2500 m alt. (Note added in proof: we have recently been given material from the Crocker Range as well.) Widespread throughout East Asia, from Japan down to Java.

Remarks. – Our material of *M. striatum* appears conspecific with other East and Southeast Asian material of this species. However, since preliminary data (not shown) indicate that it forms a clade together with other Bornean *Meghimatium* species, which does not include Taiwanese forms of the genus, it is possible that multiple unrelated species with a convergent colour pattern have been subsumed under this name.

Meghimatium uniforme Laidlaw 1937 (figs 15-17)

Meghimatium uniforme Laidlaw, 1937: 177 (Borneo, Sabah, Mount Kinabalu).

Material studied. – Mount Kinabalu, southern slope, 3100 m alt. (BOR/MOL 2870, 3413); Mount Kinabalu, southern slope, 3200 m alt. (BOR/MOL 3416, SP12510); Mount Kinabalu, southern slope, 3300 m alt. (BOR/MOL 2868, 5428, 5430); Mount Kinabalu, eastern slope, 3100 m alt. (BOR/MOL 5431); Mount Slope, 3100 m alt. (BOR/MOL 5431); Mount

Kinabalu, eastern slope, 3300 m alt. (BOR/MOL 5423, 5424, 5432); Mount Kinabalu, eastern slope, 3400 m alt. (BOR/MOL 3419, 5425, 5427); Mount Kinabalu, eastern slope, 3500 m alt. (BOR/MOL 5426)

Diagnosis. – Moderately slender, with uniform colouration that can range from pale bluish grey to yellowish orange, occasionally with scattered small black specks. Upper tentacles black. Body length: up to 30 mm. Body width: up to 8 mm. Penis extremely short (see anatomy "B" in fig. 21).

Biology and distribution. – Very common in primary montane forest on Mount Kinabalu, at 3000-3500 m alt.

Meghimatium pictum (Stoliczka, 1872) (figs. 14, 19, 20)

Philomycus pictus Stoliczka, 1872 (Penang)

Material studied. – Crocker Range, eastern slope, 1200 m alt. (SP12654, SP12728, SP12836, SP12887); Crocker Range, western slope, 500 m alt. (BOR/MOL 3837); Crocker Range, western slope, 1200 m alt. (SP12656); Mount Kinabalu, eastern slope, 1200 m alt. (BOR/MOL 5434); Mount Kinabalu, southern slope, 1450 m alt. (BOR/MOL 3414, 5435); Mount Kinabalu, northern slope, 1200 m alt. (SP12886); Mount Trus Madi, 1400 m alt. (BOR/MOL 3415); Tawau Hills, Mount Magdalena, 1300 m alt. (SP12898)

Diagnosis. – Similar to *M. striatum*, but ground colour of the body white. Tentacles may be pale or dark. Also, the (three) dark stripes do not contrast as strongly with the background, and are interspersed with a more or less regular zigzag patterning, which often makes the lines confluent and can result in almost the entire dorsal side having a mottled dark colouration. Upper tentacles dark. Body length: up to 45 mm. Body width: up to 7 mm. Genitalia either with a coiled or a non-coiled epiphallus (see anatomies 'A' and 'C' in fig. 21).

Biology and distribution. – Throughout Sabah in primary lowland and lower montane forest, 500-1500 m alt.

Remarks. – The substantial phylogeographic divergence, great diversity in body colour pattern, and differences in the genitalia in the two dissected individuals suggest that at least two or three subspecies exist. These may possibly be distinguished by their anatomy, but more adult material is needed to confirm this. Until then, we refrain from describing infraspecific taxa.

ACKNOWLEDGEMENTS

We thank Jaap Vermeulen, Wim Maassen, Ravi Mandalam, and the staff of Sabah Parks and the Institute for Tropical Biology and Conservation for assistance. This paper is dedicated to Edi Gittenberger, who, 20 years ago, introduced the first author to malacology, and, indirectly, should be credited with laying the foundation for the second author's career in malacology.

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