# Phylogeny of the Manotinae, with a review of *Eumanota* EDWARDS, *Paramanota* TUOMIKOSKI and *Promanota* TUOMIKOSKI (Diptera, Mycetophilidae)

[Phylogenie der Manotinae, nebst einem Überblick der Gattungen *Eumanota* EDWARDS, *Paramanota* TUOMIKOSKI und *Promanota* TUOMIKOSKI (Diptera, Mycetophilidae)]

by

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**Abstract** The phylogeny of the Manotinae and related genera was studied by parsimony analysis. The cladistic analysis of 60 morphological characters from the adults of 27 (extant) or 29 (extant and fossil) ingroup species and one outgroup species produced three shortest cladograms. In the analysis excluding the fossils, the most parsimonious solution confirmed the monophyly of the Manotinae sensu TUOMIKOSKI. In the cladograms obtained by analysing the extant and fossil taxa together, one fossil species, *Alavamanota burmitina* BLAGODEROV & GRIMALDI, appeared as the sister-group of *Manota* WILLISTON, whereas the other fossil, *Alavamanota hispanica* BLAGODEROV & ARILLO, was placed outside the Manotinae clade. In both analyses, the genus *Procycloneura* ENDERLEIN, traditionally classified in the Leiini, appeared as the sister-group of the Manotinae. Unlike the Manotinae, the genera of the Leiini sensu EDWARDS analysed here did not form a monophyletic group. The Leiini appear to be highly polyphyletic, and our results thus confirm the doubts of many previous authors concerning the monophyly of this tribe.

Five new species from the Oriental region are described: ***Eumanota hilleviae* spec. nov.**, ***E. kambaiti* spec. nov.**, ***Paramanota awanensis* spec. nov.**, ***P. peninsulae* spec. nov.** and ***P. sumatrana* spec. nov.** *Promanota malaisei* TUOMIKOSKI, 1966 is redescribed and the genera *Eumanota*, *Paramanota* and *Promanota* are redefined. The females of *Eumanota* and *Paramanota* are described for the first time.

**Key words** Phylogeny, morphology, Mycetophilidae, Manotinae, new species, Oriental region

**Zusammenfassung** Die Phylogenie der Manotinae und verwandter Gattungen wurde mittels Parsimonie-Analyse untersucht. Die kladistische Analyse von 60 morphologischen Merkmalen der Imagines von 27 (rezenten) bzw. 29 (rezenten und fossilen) Arten der Innengruppe und einer Art in der Außengruppe ergab drei kürzeste Kladogramme. Im Ergebnis der Analyse ohne Fossilien wird die Monophylie der Manotinae sensu TUOMIKOSKI bestätigt. In den Kladogrammen unter Einschluss von Fossilien ist die eine fossile Art, *Alavamanota burmitina* BLAGODEROV & GRIMALDI, Schwestergruppe von *Manota* WILLISTON, während die andere, *Alavamanota hispanica* BLAGODEROV & ARILLO, außerhalb der Manotinae-Stammlinie erscheint. In beiden Analysen erscheint die Gattung *Procycloneura* ENDERLEIN, traditionell zu den Leiini gestellt, als Schwestergruppe der Manotinae. Im Gegensatz zu den Manotinae bilden die hier analysierten Gattungen der Leiini sensu EDWARDS kein Monophylum. Unsere Resultate kennzeichnen die Leiini als Polyphylum, womit frühere Autoren in ihrem Zweifel an der Monophylie dieser Gruppe bestätigt werden.

Fünf neue Arten aus der Orientalis werden beschrieben: ***Eumanota hilleviae* spec. nov.**, ***E. kambaiti* spec. nov.**, ***Paramanota awanensis* spec. nov.**, ***P. peninsulae* spec. nov.** und ***P. sumatrana* spec. nov.** *Promanota malaisei* TUOMIKOSKI, 1966 wird nachbeschrieben und die Gattungsdiagnosen von *Eumanota*, *Paramanota* und *Promanota* werden ergänzt. Die Weibchen von *Eumanota* und *Paramanota* werden erstmalig charakterisiert.

**Stichwörter** Phylogenie, Morphologie, Mycetophilidae, Manotinae, neue Arten, Orientalische Region

## Introduction

The Manotinae sensu Tuomikoski (1966) is now usually treated as a distinct subfamily of the Mycetophilidae (Vockeroth 1981, Zaitzev 1990, Söli 1997, see also Söli 1993, 2002). However, since Tuomikoski (1966), the question of the monophyly and proper systematic rank of the Manotinae has seldom been discussed. There are various reasons for this. Firstly, the type-genus, *Manota* Williston, 1896, is so strikingly different from most other mycetophilids that a subfamily status seems amply justified. Secondly, *Manota* is the only reasonably common manotine genus present in fungus gnat collections, and in at least parts of the tropics *Manota* is rich in both individuals and species (Hippa, Jaschhof, pers. obs.). All other manotines are exceedingly rare, a fact reflected in their sparse occurrence in the literature and in the paucity of specimens in museum collections. Consequently, references to the Manotinae often mean only *Manota*. As regards the Manotinae other than *Manota*, Edwards (1933) described the genus *Eumanota*, which he found "somewhat closely related" to *Manota* but also "to connect the Manotinae with the Leiini". It was indeed the discovery of *Eumanota* which raised the questions of the delimitation and monophyly of the Manotinae, mainly in relation to the Leiini as defined by Edwards (1925). Tuomikoski (1966) described his *Paramanota* and *Promanota*, two monotypic genera closely related to *Manota* and *Eumanota*. He re-defined the Manotinae "more sharply than before" and eventually concluded that "the Manotinae, if at all closely related to the Leiini, at most represent a sister group of the latter subfamily". Subsequent authors did not explicitely doubt the monophyly of the Manotinae, but continued to stress its close affinities to certain genera of the Leiini (Zaitzev 1990, Söli 1997, 2002, Söli et al. 2000). The monophyly of the Leiini is thus crucial for resolving the phylogenetic problems of the Manotinae. *Allactoneura* de Meijere, 1907, *Sticholeia* Söli, 1994, and several other genera of Leiini show a close resemblance to manotines. A recently described fossil genus *Alavamanota* Blagoderov & Arillo, 2002, from Cretaceous amber, was classified in the Manotinae (Blagoderov & Arillo 2002, Blagoderov & Grimaldi 2004).

The present study was prompted by material of several undescribed Manotinae other than *Manota* which we have collected over many years. In the light of these new species, we felt it necessary to test by parsimony analysis the monophyly of most of the extant and fossil taxa currently classified in the Manotinae, and to study the phylogenetic relationships among them and the relevant genera traditionally placed in the Leiini. In addition, we describe two new species of *Eumanota* and three of *Paramanota*.

Our paper was ready for submitting to the journal when we became aware of the most recent publication on Manotinae by Papp (2004). The new taxa published therein we took into consideration for the purpose of species comparison, but we did not include them in our cladistic analysis.

## Material and methods

### Taxonomy

Most specimens of the newly described species were picked from Malaise trap samples taken during various expeditions to Peninsular Malaysia and Sumatra in the 1990s. Specimens of *Promanota malaisei* Tuomikoski and *Eumanota kambaiti* spec. nov. were found in the original material collected by René Malaise in Burma in 1934. The ethanol-preserved remnants of this material, very pale and fragile in condition, are kept in the Swedish Museum of Natural History, Stockholm (NRM). Type specimens of the new species, as well as the specimens of *Promanota malaisei*, were dissected and slide-mounted in Euparal. Additional specimens of

*Paramanota peninsulae* spec. nov. are preserved in 70 % ethanol. This material, including all the types, is deposited in NRM. As regards other Manotinae, we studied the holotypes of *Eumanota leucura* EDWARDS and *Eumanota humeralis* EDWARDS. The genus *Manota* WILLISTON was represented in our study by slide-mounted specimens of two undescribed species, from New Zealand and Costa Rica respectively.

The material studied is deposited in the following collections (see Appendix 1): Swedish Museum of Natural History, Stockholm (NRM); The Natural History Museum, London (BMNH); New Zealand Arthropod Collection, Auckland (NZAC); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBIO).

Illustrations were made with the help of a drawing tube attached to a Leitz Diaplan compound microscope. Morphological terminology follows that in SÖLI (1997), with the addition of the term 'postocular bristles' which we use for peculiar bristles along the hind margin of the eyes (see character 3 in Appendix 2).

## The phylogenetic analysis: characters, procedure and terminals

For the analysis, 60 adult morphological characters (Appendix 2) were coded for 27 extant and 2 fossil species in the ingroup, and for one outgroup species (Appendix 1). The data matrix for analysis (Appendix 3) was constructed and manipulated with the computer programme WinClada, version 1.00.08 (NIXON 2000). Phylogenetic relationships were studied by parsimony analysis with the computer programme NONA, version 2.0 (GOLOBOFF 1999), and Ratchet (NIXON 2000), together with WinClada, to search for the most parsimonious cladograms. The search parameters used with NONA were 'hold100000; hold/1000; mult* 1000; max*; sswap*;'. With these commands and settings, the programme makes a heuristic search and swaps branches with 'tree bisection-reconnection'. The Ratchet search was done using 1000 iterations, with 100 trees to hold per iteration, 25 characters to sample. The unsupported nodes were collapsed to accept only unambiguous support for the nodes in the strictest sense. The resulting cladograms and their strict consensus cladograms (Figs 1, 2) and character optimizations were studied with WinClada; to show synapomorphies in the cladograms, the looser homoplasy setting in WinClada ("state") was applied. This alternative allows a synapomorphic state to occur as unique regardless of possible further reversals. The characters were equally weighted for the analysis, and the multistate characters were analyzed unordered. The character states were coded as (-) when the character involved was absent from a terminal and as (?) when the state was not known. The programmes used do not differentiate these cases.

Two analyses were performed, one with the extant taxa only and the other with the addition of the fossils. Selected species from the genera were used as terminals. From the *Manota* group of genera, *Promanota malaisei*, four species of *Paramanota* (including three new species to be described here), two undescribed species of *Manota*, and eight species of *Eumanota* (including two new species to be described here and one undescribed species) were included in our analysis. The fossil taxa included were *Alavamanota burmitina* BLAGODEROV & GRIMALDI and *Alavamanota hispanica* BLAGODEROV & ARILLO, both from Lower Cretaceous amber (Appendix 1). The ingroup included also representatives of the Mycetophilini, namely the genus *Mycetophila* MEIGEN, and the main lineages of the Leiini. The included taxa of Leiini were: *Allactoneura* DE MEIJERE spec. indet. (from Malaysia); *Aphrastomyia* COHER & LANE spec. indet. (from Costa Rica); *Docosia gilvipes* (HALIDAY) (from Finland); *Ectrepesthoneura hirta* (WINNERTZ) (from Finland); *Greenomyia baikalica* ZAITZEV (from Finland); *Leia cylindrica* MEIGEN (from Finland); *Leiella* ENDERLEIN spec. indet. (from Costa Rica); *Mohelia* MATILE spec. indet. (from South Africa); *Procycloneura* EDWARDS spec. indet. (from Costa Rica); *Ron-*

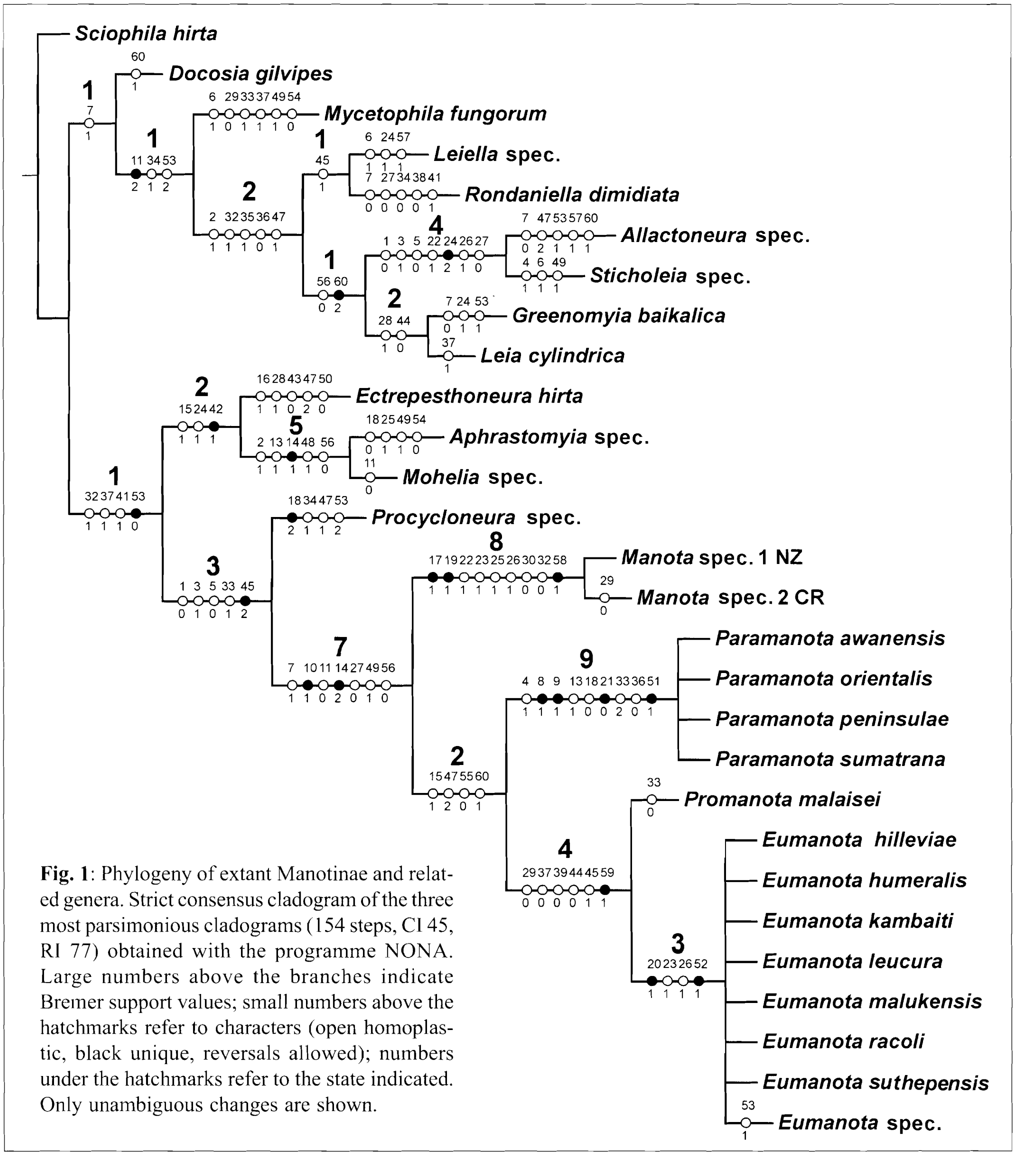


**Fig. 1**: Phylogeny of extant Manotinae and related genera. Strict consensus cladogram of the three most parsimonious cladograms (154 steps, CI 45, RI 77) obtained with the programme NONA. Large numbers above the branches indicate Bremer support values; small numbers above the hatchmarks refer to characters (open homoplastic, black unique, reversals allowed); numbers under the hatchmarks refer to the state indicated. Only unambiguous changes are shown.

*daniella dimidiata* (MEIGEN) (from Finland); *Sticholeia* SÖLI spec. indet. (from Papua New Guinea). Specimens of these species were examined both in ethanol and on slide preparations. These taxa were selected for the ingroup because genera of the Leiini and Mycetophilini appeared in the same major clade as *Eumanota* in the analysis by SÖLI (1997). The extant genus *Sciophila* MEIGEN, represented by *Sciophila hirta* MEIGEN (from Finland), appears outside the *Manota* clade in SÖLI's (1997) analysis, and was chosen as the outgroup for our analysis. Our study is based mainly on males because females of the taxa in question are poorly known. We did not include female characters in the analysis because we could not always be certain that males and females belonged to the same species, even though they usually originated from the same sample.

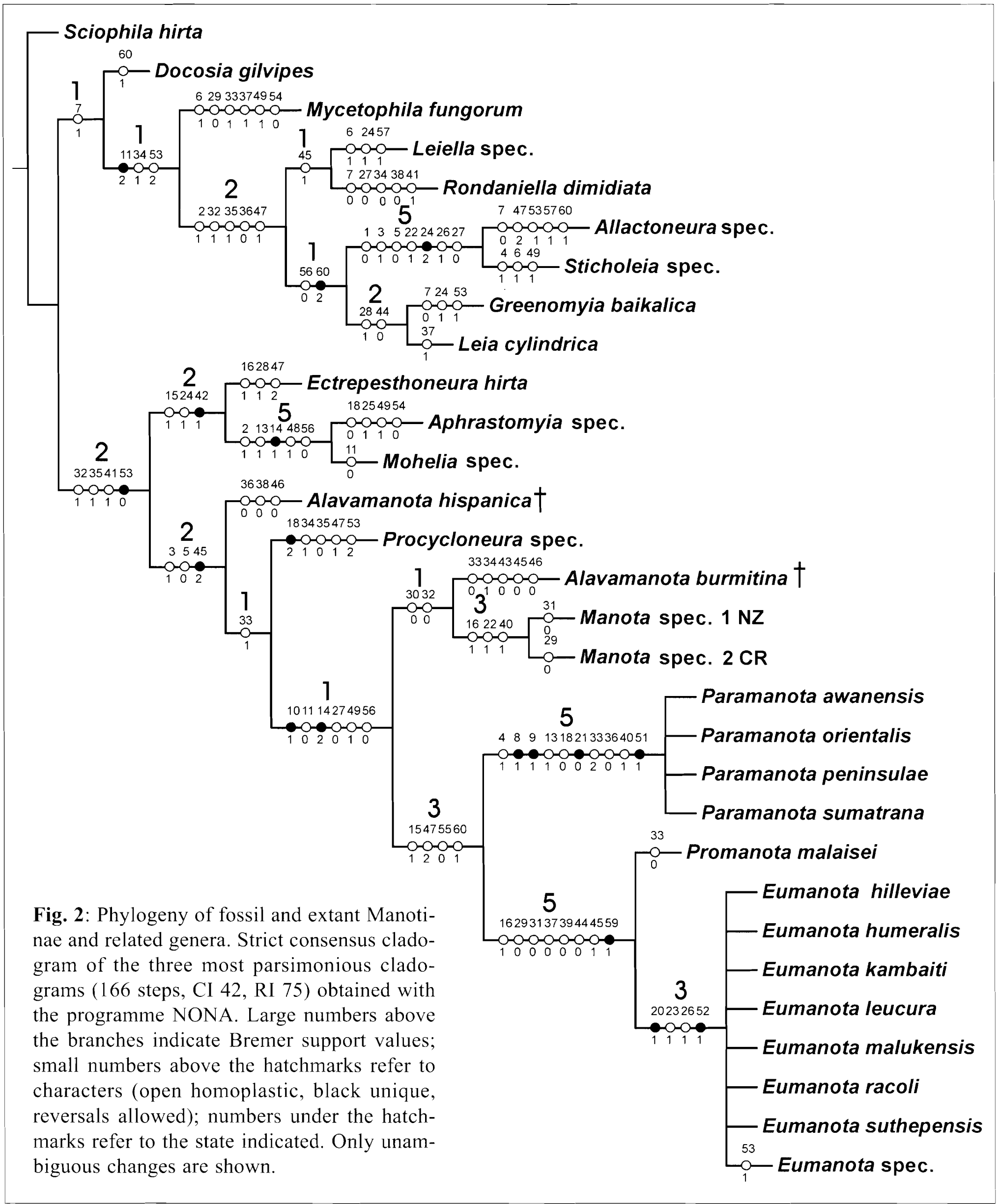


**Fig. 2**: Phylogeny of fossil and extant Manotinae and related genera. Strict consensus cladogram of the three most parsimonious cladograms (166 steps, CI 42, RI 75) obtained with the programme NONA. Large numbers above the branches indicate Bremer support values; small numbers above the hatchmarks refer to characters (open homoplastic, black unique, reversals allowed); numbers under the hatchmarks refer to the state indicated. Only unambiguous changes are shown.

## Phylogeny of the Manotinae

The parsimony analysis with NONA with the extant taxa produced only three most parsimonious cladograms (154 steps, CI 45, RI 77). Of these, the strict consensus cladogram was fully resolved except for the apical clades including the species of *Paramanota* and *Eumanota* (Fig. 1). The second analysis, with the addition of the two fossils, also produced three most parsimonious cladograms (166 steps, CI 42, RI 75). The consensus cladogram was identical with the previous one, except for the fossils (Fig 2). The Ratchet searches did not find alternative solutions.

In the analysis excluding the fossils, the basal clades were fully resolved (Fig. 1). Based on seven character state changes, two of which were unique (10: 1, distinctly compressed male antennal flagellomeres; and 14: 2, premental apodeme with a single, short prolongation), the Manotinae clade appeared monophyletic, with the relationships *Manota* + [*Paramanota* + (*Promanota* + *Eumanota*)]. Strongly supported by nine character state changes, three of which were unique (17: 1, finger-like, rounded apical extension of the third palpomere; 19: 1, presence of thick sensilla on the third palpomere; and 58: 1, absence of male tergite 9), the *Manota* clade, with two undescribed species, was monophyletic. The three new species of *Paramanota* formed a monophyletic group with *Paramanota orientalis*, this clade being supported by nine character states, four of which were unique (8: 1, median ocellus divided into two; 9: 1, complete eye bridge present; 21: 0, setose postpronotum; and 51: 1, absence of fore tibial antero-apical depression). The sister-group relationhip *Promanota* + *Eumanota* was based on six character states, one of which was unique (59: 1, elongated outline of male tergite 9 and cerci). Finally, the monophyly of the *Eumanota* species was based on four character states, two of which were unique (20: 1, extremely long terminal palpomere; and 52: 1, hind tibia with a sensory groove). The Bremer support values for the nodes, ranging from 1 to 9, are also shown in Fig. 1.

Unlike the Manotinae, the genera of the Leiini that were analysed did not form a monophyletic group. In one of the main clades of the cladogram, *Docosia* appeared as the sister-group of *Mycetophila* + six leiine genera, including *Leia*. In the other main clade, *Ectrepesthoneura*, *Aphrastomyia* and *Mohelia* together appeared as the sister-group of *Procycloneura* + Manotinae (Fig. 1). Our conclusion regarding the non-monophyly of the Leiini agrees with that of Söli (1997), whereas the Leiini were considered as monophyletic by Blagoderov & Grimaldi (2004), based mainly on fossil data. It must be noted, however, that not all the genera currently placed in the Leiini (e.g. Bechev 2000) have been included in a cladistic analysis.

The cladograms obtained by analysing extant and fossil taxa together (Fig. 2) showed *Alavamanota burmitina* as the sister-group of *Manota* (based on two homoplastic character states, 30: 0, setose pre-episternum; and 32: 0, setose episternum). The other fossil, *Alavamanota hispanica*, appeared more basally on the same major clade, indicating that the current concept of *Alavamanota* should be re-assessed.

## Descriptions

### Genus *Eumanota* Edwards, 1933

The two new species described below are undoubtedly congeneric with the type-species, *Eumanota leucura* Edwards. In addition, we describe for the first time, but do not name, a female individual belonging to *Eumanota*. We also add a few characters not explicitly mentioned in Söli's (2002) diagnosis of the genus, which are present in all the species we have seen.

**Supplementary description** (see Edwards 1933, Söli 2002)

**Head.** Lacinia very weak or absent. Palpomeres 3–5 inside with numerous erect, blunt-tipped, hair-like sensilla that are sometimes curved apically.

**Wing.** In addition to the dorsal setae, with ventral setae on R distally, R1, tb, ta, R5, and sometimes the M-stem proximally. M1 basally weakly sclerotised or obsolete. **Legs.** In male, hind tibia inside in basal half with a groove of fine, pale, densely-set trichia ('hind tibial organ'); in female, presence of hind tibial organ unknown.

**Abdomen.** Sternite 1 non-setose. **Terminalia.** Male. Sternite 9 not discernible as a distinct sclerite. Gonocoxites longer than wide, broadly fused ventro-proximally and emarginated slit-like distally, with or without interior lobes. Gonostylus flattened dorso-ventrally, with non-setose portions usually on inner (dorsal) surface, with more strongly sclerotised projections terminally and/or subbasally. Aedeagus without sclerotised portions. Parameres in two pairs; ventral pair fused to form a tegmen; dorsal pair with ventral portions projecting finger-like and bearing a brush or row of setae distally, and with dorsal portions more stout and usually bearing a small group of setae subbasally. Tergite 9 very long, roughly trapezoid. Tergite 10 (if correctly identified) present as setose, weak, rather membraneous lobes on either side of tergite 9 disto-laterally. Cerci and hypoproct long, extending far beyond tergite 9. Female. See *Eumanota* spec. (below).

## *Eumanota leucura* Edwards, 1933

(Figs 3d, e, 5c, d)

**Supplementary description** (see Edwards 1933, Söli 2002)

**Male. Head.** Flagellomeres (Fig. 3d) with trichia arranged in irregular transverse rows; bases of trichia interconnected by weak lines and slightly raised, resulting in a serrated outline to the rims of the flagellomeres; trichia interspersed with tiny sensilla and, on flagellomeres 1–6, with a very few small socketed setae ventrally. In lateral view, node of fourth flagellomere 1.5 times as long as wide. Palpomeres 3–5 inside with numerous erect, blunt-tipped, hair-like sensilla. **Legs.** Hind tibia with tibial organ and 3 setae basally (Fig. 3e). **Terminalia.** Gonocoxites (Fig. 5d) interiorly with 2 elongate setose lobes of uncertain position. Gonostylus (Fig. 5d) flattened dorso-ventrally; short-setose on outer surface, almost non-setose on inner surface; terminally with a short, dark, triangular, ventrally directed projection bearing a very few setulae; subbasally with a long, dark, bare projection directed ventrally. Aedeagus (Fig. 5d) consisting of a weak rod with a subrectangular shield-like head (ejaculatory apodeme?) and, more dorsally, a membraneous, trichiose cap tapering to its tip. Tegmen present, broadly rounded distally. Dorsal pair of parameres with a ventro-distal projection bearing a brush of curved setae subterminally and 3–4 setae dorso-subbasally (Fig. 5d). Tergite 9 (Fig. 5c) much longer than cerci. Hypoproct (Fig. 5c) shorter than cerci, with numerous strikingly long, dishevelled setae directed inwardly.

**Note on the holotype.** We slide-mounted several parts of the pinned specimen (one antenna, one hind leg, and terminalia) in order to recognise further morphological details. The rest of the specimen is still on its pin.

## *Eumanota hilleviae* spec. nov.

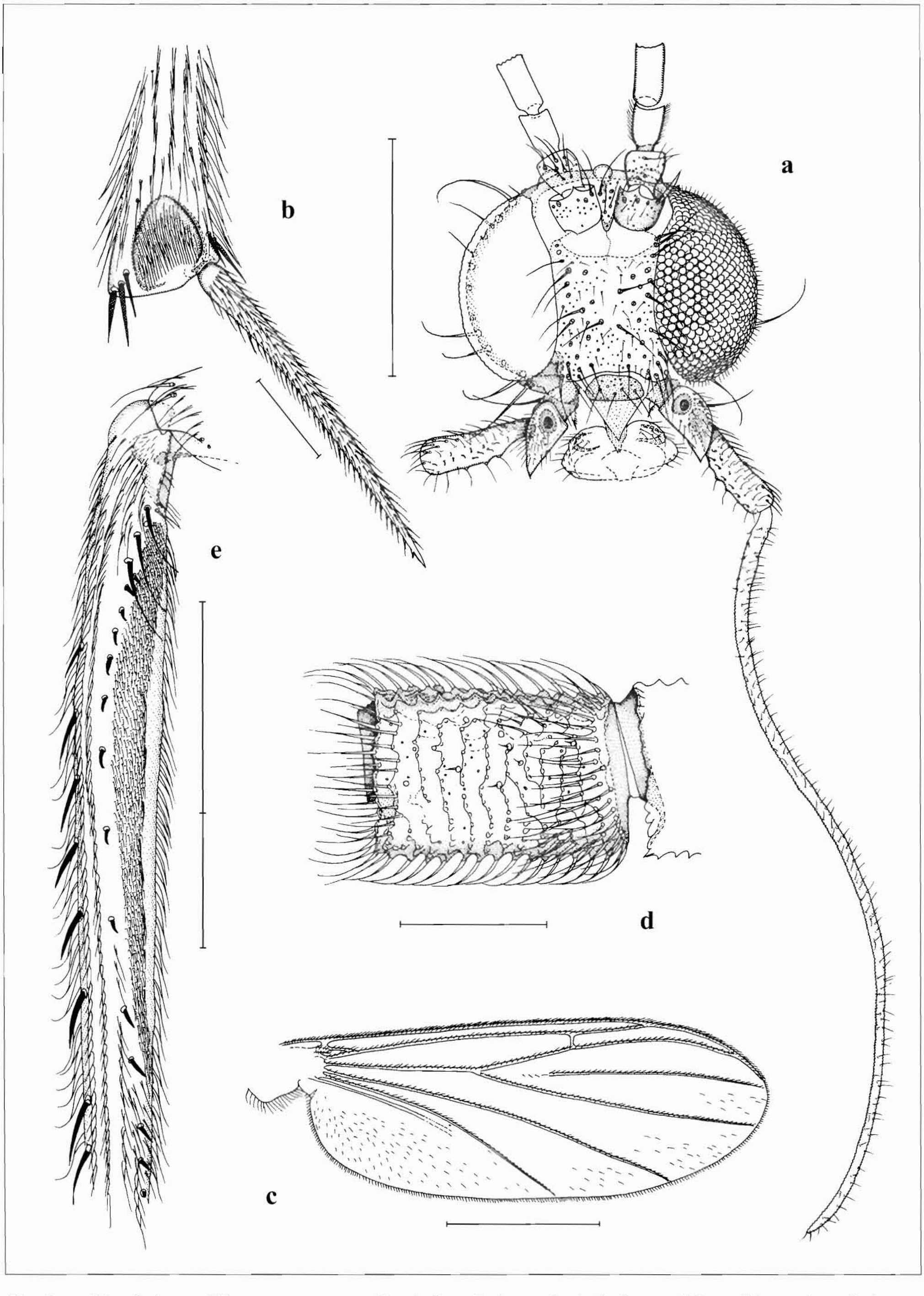
(Figs 3a–c, 4a, 5a, b)

### Description

**Male.** Wing length 3.2 mm. **Head** (Fig. 3a). Postocular bristles numbering 10 or more. Antennal flagellum as in *E. leucura*. Face 1.3 times as long as wide. Lacinia present, small, style-like. Maxillary palpomere 5 more than six times as long as preceding palpomere.

**Thorax.** See Fig. 4a. **Wing** (Fig. 3c). Membrane darkened in distal half (lightened again towards tip) and posterior of CuA2; with setae all over posterior portion, but most numerous in anal area. M-stem with ventral setae. **Legs.** Fore tibia with an antero-apical depression as in Fig. 3b. Mid tibia with the shorter spur half as long as the long spur. Hind tibia with the shorter spur almost two-thirds as long as the long spur. Hind tibia as in *E. leucura*.

**Abdomen.** Tergite and sternite 8 non-setose. **Terminalia.** Gonocoxites (Fig. 5a) fused ventro-basally for less than half their length; disto-ventrally with a setose lobe directed inwardly; dorso-distal margin setose; interior setose lobes present, but difficult to see in detail. Gonostylus (Fig. 5a) elongate, curved, dorso-ventrally flattened, short-setose on outer surface, almost non-setose on inner surface; subterminally with 1 megaseta next to 1 ordinary seta; subbasally with a long, dark projection bearing 2 setae apically and some 3 setae elsewhere. Aedeagus and ventral pair of parameres barely discernible, but apparently similar to those in *E. leucura*. Dorsal pair of parameres with a ventro-distal projection bear-



**Figs 3a–e**: Morphology of *Eumanota* spp. – **a**: Head, frontal view; – **b**: Apical part of front tibia, prolateral view; – **c**: Wing, dorsal view; – **d**: Antennal flagellomere 4, lateral view; – **e**: Basal part of hind tibia, prolateral view. **a–c**: *Eumanota hilleviae* spec. nov. (holotype); **d, e**: *E. leucura* EDWARDS (holotype). Length of scale bars: c = 1 mm; a = 0.5 mm; b, e = 0.1 mm; d = 0.05 mm.

ing a dense brush of curved setae subterminally; dorsal portions of parameres broadly shield-like and bearing 1–2 setae (Fig. 5a). Tergite 9 (Fig. 5b) little longer than cerci. Hypoproct (Fig. 5b) shorter than cerci, with several strikingly large, straight setae directed inwardly.

**Female.** Unknown.

**Diagnostic characters.** In this species, the gonostylus is unique in bearing both a subbasal projection, as found in *E. leucura*, and a subterminal megaseta, as found in *E. kambaiti* (see the next species).

**Etymology.** The species epithet is dedicated to Ms Hillevi SARTOLA-HIPPA who helped to collect the insect samples containing this species.

**Holotype.** Male (mounted on two slides), INDONESIA, Sumatra, Sumatera Utara, Semangat Gunung, 1300 m, in jungle, 18 March 1992, by Malaise trap, H. HIPPA.

## *Eumanota kambaiti* spec. nov.

(Fig. 4b)

### Description

**Male.** Wing length 4.0 mm. **Head.** Antennal flagella and distalmost portions of maxillary palpi missing; face distorted. **Wing.** Membrane with setae confined to anal area; no darkened area apparent in the single pale specimen available for study. M-stem with ventral setae. A1 setose. **Legs.** Mid tibia with only the long spur remaining. Hind tibia with the shorter spur almost two-thirds as long as the long spur. Hind tibia without setae basally; tibial organ with a row of setae on either side. **Terminalia** (Fig. 4b). Gonocoxites fused ventro-basally for less than half their length; disto-ventrally subtriangular; dorso-distal portion enlarged lobe-like and extensively setose; interior setose lobes not discernible. Gonostylus narrow basally, widened in distal half, dorso-ventrally flattened, short-setose on outer surface, almost non-setose on inner surface; terminally with a subtriangular projection darkened at tip, at base with 1 short, blunt megaseta. Aedeagus, parameral structures, tergite 9 and proctiger largely distorted in the only specimen available for study, but apparently similar to those in *E. hilleviae*.

**Female.** Unknown.

**Diagnostic characters.** In *E. kambaiti*, the shape of the gonostylus is reminiscent of that in *E. humeralis* EDWARDS, *E. racola* SÖLI, *E. suthepensis* SÖLI, *E. jani* PAPP and *E. parahumeralis* Papp, but it differs from all these species by the presence of a megaseta subterminally.

**Etymology.** The name refers to the type-locality, Kambaiti.

**Holotype.** Male, BURMA, Kambaiti, 2000 m, 12–17 June 1934, by Malaise trap, R. MALAISE.

## *Eumanota* spec.

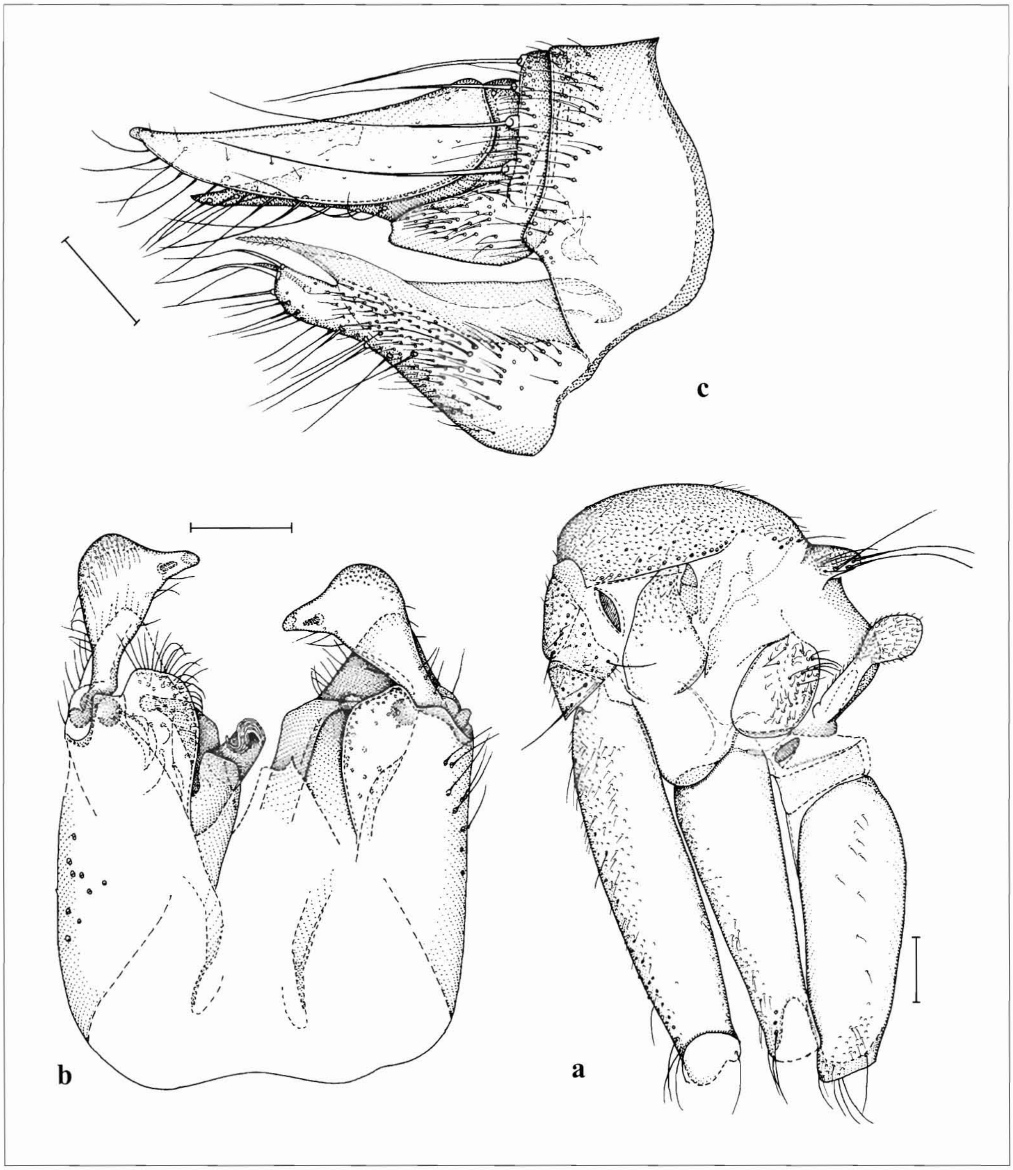
(Fig. 4c)

### Description

**Male.** Unknown.

**Female.** Wing length 3.3 mm. **Head.** Postocular bristles numbering 10 or more. Face 1.2 times as long as wide. Lacinia present, very short, style-like, fringed laterally and apically. Fifth palpomere 5.5 times as long as preceding palpomere. **Wing.** Membrane darkened in distal half (lighter again towards tip) and posterior of CuA2; with setae all over posterior portion, but most numerous in anal area. A1 setose. **Legs.** Mid tibia with the shorter spur almost two-thirds as long as the long spur. Hind legs missing. **Terminalia** (Fig. 4c). Tergite 8 well-developed, short-setose. Gonocoxite 8 setose, including 3 strikingly large setae posteriorly. Gonapophyses 8 extending beyond gonocoxites, finely trichiose. Tergite 9 very short; in addition to small setae, with a row of large setae along posterior margin. Gonocoxite 9 large, extending far posteriorly; short-setose. Gonapophyses 9 not identified. Tergite 10 very short and indistinct; with a few short setae. Sternite 10 long and pointed, with large setae. Cercus one-segmented, long, pointed posteriorly, on outer surface almost non-setose except for a few scattered setulae.

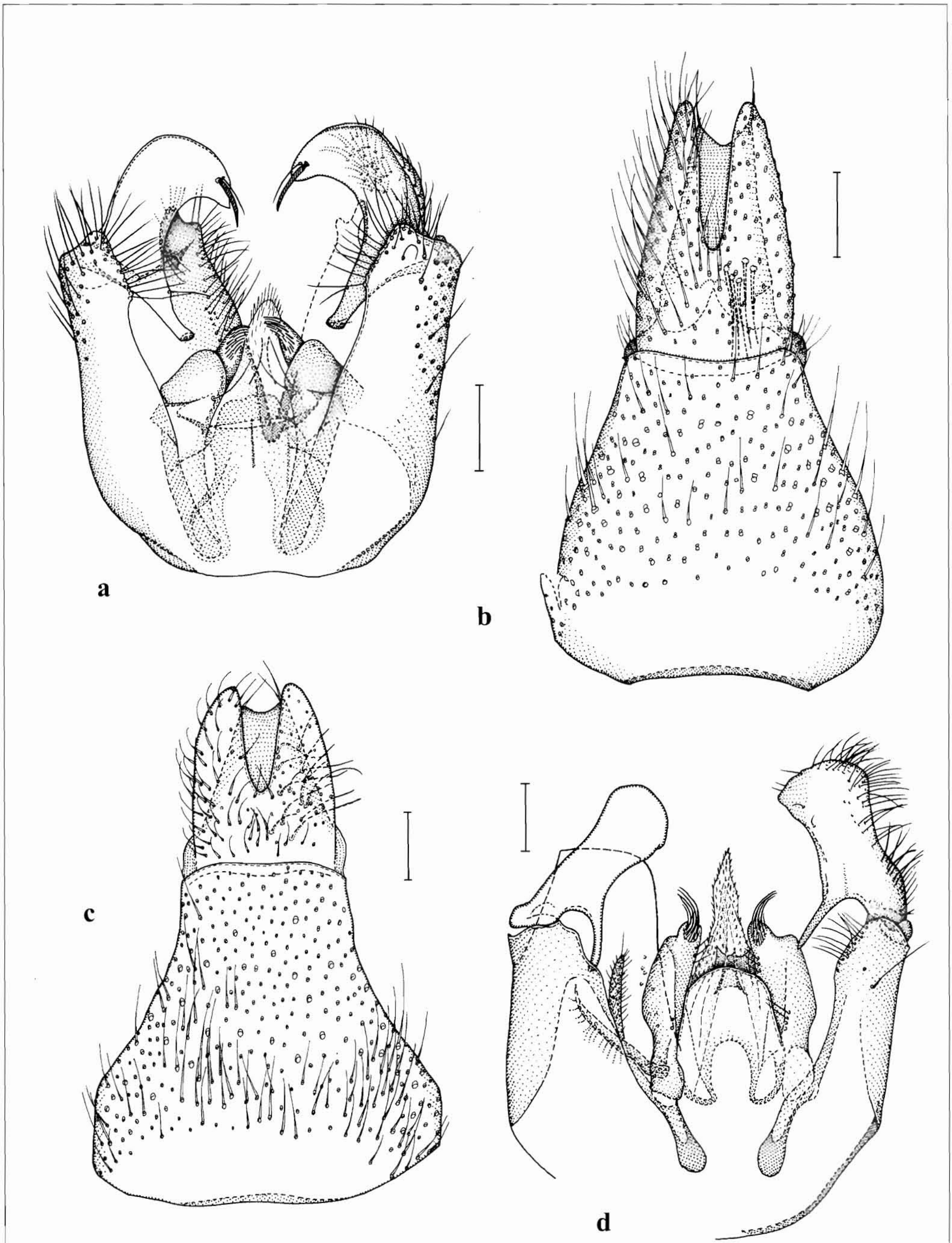
**Material studied.** Female, MALAYSIA, Pahang, Cameron Highlands, 1300 m, in jungle, by Malaise trap #3, 20–26 Nov. 1994, T. PAPE.



**Figs 4a–c**: Morphology of *Eumanota* spp. – **a**: Thorax, lateral view; – **b**: Male terminalia, dorsal view, tergite 9 and associated structures removed; – **c**: Female terminalia, lateral view. **a**: *Eumanota hilleviae* spec. nov. (holotype); **b**: *E. kambaiti* spec. nov. (holotype); **c**: *Eumanota* spec. Length of scale bars: a = 0.2 mm; b, c = 0.1 mm

## Genus *Promanota* TUOMIKOSKI, 1966

SÖLI (2002) took the view that the differences between *Promanota* and *Eumanota* were too slight for them to be considered as separate genera. However, he had not studied specimens of *Promanota malaisei* and consequently was able to base his decision only on the descriptions by TUOMIKOSKI (1966). After studying two males of *P. malaisei* from the type-locality, we



**Figs 5a–d**: Male terminalia of *Eumanota* spp. – **a, d**: Terminalia, dorsal view, tergite 9 and associated structures removed; – **b, c**: Tergite 9 and associated structures, dorsal view. **a, b**: *E. hilleviae* spec. nov. (holotype); **c, d**: *E. leucura* EDWARDS (holotype). Length of scale bars = 0.1 mm.

conclude that the generic status of *Promanota* must be revived, which agrees with the decision made by PAPP (2004). Our conclusion is based on the following differences between *Promanota* and *Eumanota* (in parentheses): (1) the face is very narrow (broader); (2) the clypeus is subtriangular and invades the ventral margin of the face (ovate and not invading); (3) the terminal segment of the maxillary palpus is comparatively short (extremely long and whip-like); (4) the epimeron 1 is present as a sclerite separate from the antepronotum (antepronotum and epimeron merged); (5) the lateral portions of the basisternum 1 are small (large); (6) the wing membrane is completely covered with setae (setae restricted to the posterior portions of wing); (7) the row-like arrangement of trichia on the tibia is obscured distally and is oblique on the tarsomeres (very pronounced and straight on both tibia and tarsomeres); (8) the hind tibia lacks the tibial organ (tibial organ present); and the genitalic structure differs markedly. In detail, these differences include: (9) the gonocoxites are equipped with spines (absent in *Eumanota* spp.); (10) the aedeagus has a distinct ejaculatory apodeme (absent in *Eumanota* spp.); (11) the completely different outline of the parameres (see below); and (12) the different outline of tergite 10 (see below). Some of these characters were applied in our phylogenetic analysis, with the result shown in Figs 1 and 2. PAPP (2004) recognized a number of differences between *Promanota* and *Eumanota*, some of which correspond with the characters we refer to above.

### *Promanota malaisei* TUOMIKOSKI, 1966

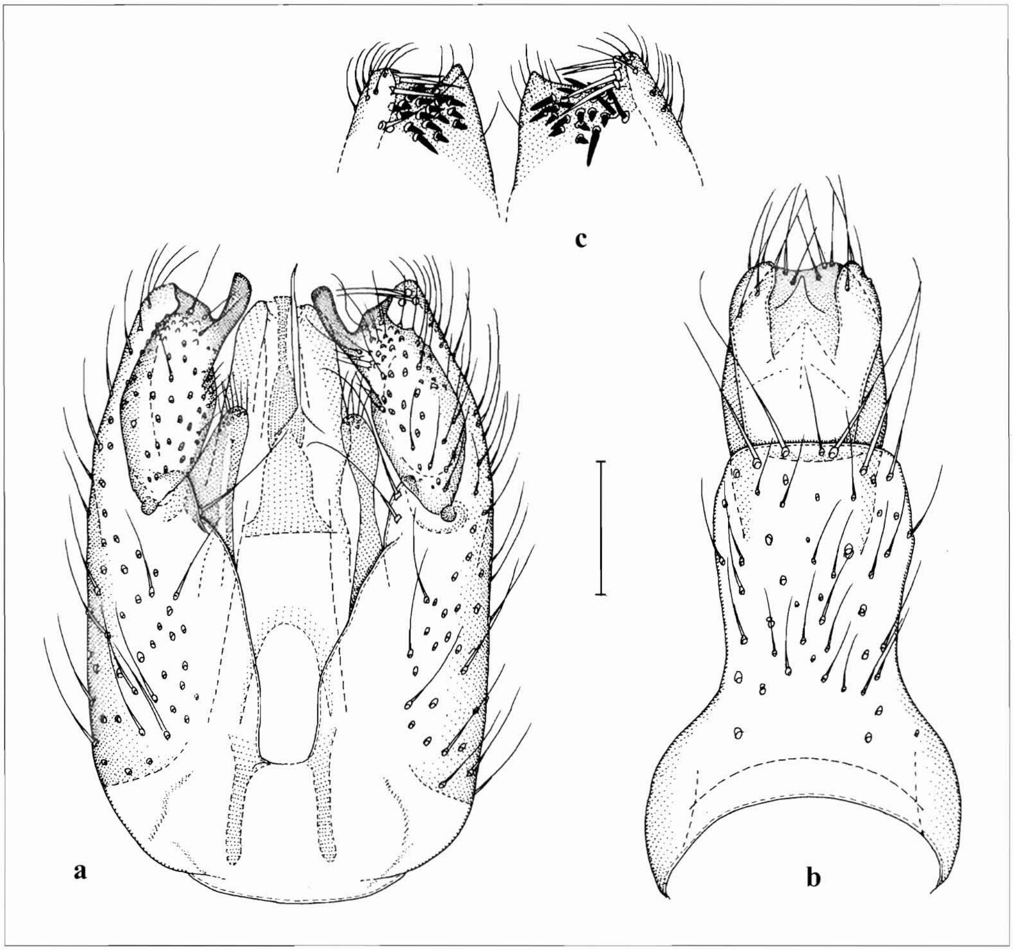
(Figs 6a–c)

**Supplementary description** (see TUOMIKOSKI 1966, SÖLI 2002).

**Head.** Postocular bristles numbering 4–5. Flagellomeres with a vestiture probably as in *Eumanota* spp. In lateral view, node of fourth flagellomere as long as wide. Face twice as long as wide. In one specimen (with a somewhat distorted head), median lobe of postgenae rather small and poorly sclerotised. Prementum with a short median apodeme. Lacinia present, style-like, as long as the most basal maxillary palpomere. Palpomeres 3–5 inside with numerous erect, blunt-tipped, apically-curved, hair-like sensilla, along with setae on palpomeres 3 and 4; basalmost palpomere with 1–2 short setae. Terminal palpomere twice as long as preceding palpomere.

**Thorax.** Scutum, in addition to short setae, with large setae scattered over lateral portions. Antepronotum larger than proepisternum, both separated by a thin suture and bearing setae and bristles. Proepimeron present, elongate. Basisternum with lateral portions comparatively small, the major portion situated in the frontal position, with setae and bristles. **Legs.** Front coxa 1.1 times as long as mid coxa (consequently not markedly shorter than in *Eumanota* spp. where the ratio is 1.2) Fore tibia with an antero-apical depression as in *Eumanota* spp. Mid and hind tibiae with the shorter spurs two-thirds as long as the long spurs. Tibial trichia comparatively fine, arranged in rows except distally where the arrangement becomes rather irregular. Tarsal trichia arranged in oblique rows. Tarsal claws and empodia as in *Eumanota* spp.

**Abdomen.** All sclerites, including sternite 1, setose. **Terminalia.** Sternite 9 not discernible as a distinct sclerite. Gonocoxites (Fig. 6a) fused ventro-basally for more than two-thirds of their length; disto-ventrally on inner surface with numerous rather short, irregularly arranged spines and, more laterally, with a row of 5–6 longer spines (Fig. 6c); dorso-distally inside with 2 large setae; interior setose lobes not discernible. Gonostylus (Fig. 6a) elongate, slightly flattened dorso-ventrally; dorsally (on outer surface) densely setose; ventrally (on inner surface) almost non-setose except for 1 large seta in proximal half and 1 seta in distal half; apically with two dark, bare projections, the long projection finger-like and directed ventrally, the short projection subtriangular and directed dorsally. Aedeagus (Fig. 6a) with a slender, vase-shaped ejaculatory apodeme and a finger-shaped, trichiose membraneous cap, both projecting beyond gonocoxites. Ventral pair of parameres fused to form a rounded tegmen, laterally each with 2 pairs of long, slender appendages, the shorter appendage terminating in 4–6 setae, the longer appendage finely trichiose all over. Dorsal pair of parameres with ventral portions consisting of 2 long,



**Figs 6a-c**: *Promanota malaisei* Tuomikoski (specimen from Burma): – **a**: Terminalia, dorsal view, tergite 9 and associated structures removed; – **b**: Tergite 9 with associated structures, dorsal view; – **c**: Apicoventral part of gonocoxites, dorsal view. Length of scale bar = 0.1 mm.

bare projections; dorsal portions consisting of a thin plate with a long, pointed process apically. Tergite 9 (Fig. 6b) very long, with a broad, rounded proximal portion and a narrower, subrectangular distal portion; with setae of various lengths. Tergite 10 apparently slightly sclerotised, largely hidden below tergite 9; with 2 large setae on either side. Cerci (Fig. 6b) clearly shorter than tergite 9, projecting little beyond hypoproct distally. Hypoproct (Fig. 6b) extending far proximally, longer than cerci; in addition to ordinary setae, with 1–2 large setae distally.

**Diagnostic characters.** *Promanota formosana* Papp appears to be extremely similar to, if not even identical with *P. malaisei*. According to the description by Papp (2004), differences between the two species lie mainly in the setation of various body parts, including wing veins, whereas male terminalia are practically identical.

**Material studied.** 1 male (on slide), BURMA, Kambaiti, 7000 ft., 13 April 1934, by Malaise trap, R. Malaise; 1 male (on two slides), same locality, but 2000 m, 15 April 1934.

## Genus *Paramanota* TUOMIKOSKI, 1966

Knowledge of this previously monotypic genus is here enlarged with three more species. The female of *Paramanota* is described for the first time. Based on this new information, the generic description by TUOMIKOSKI (1966) is revised.

**Supplementary description** (see TUOMIKOSKI 1966)

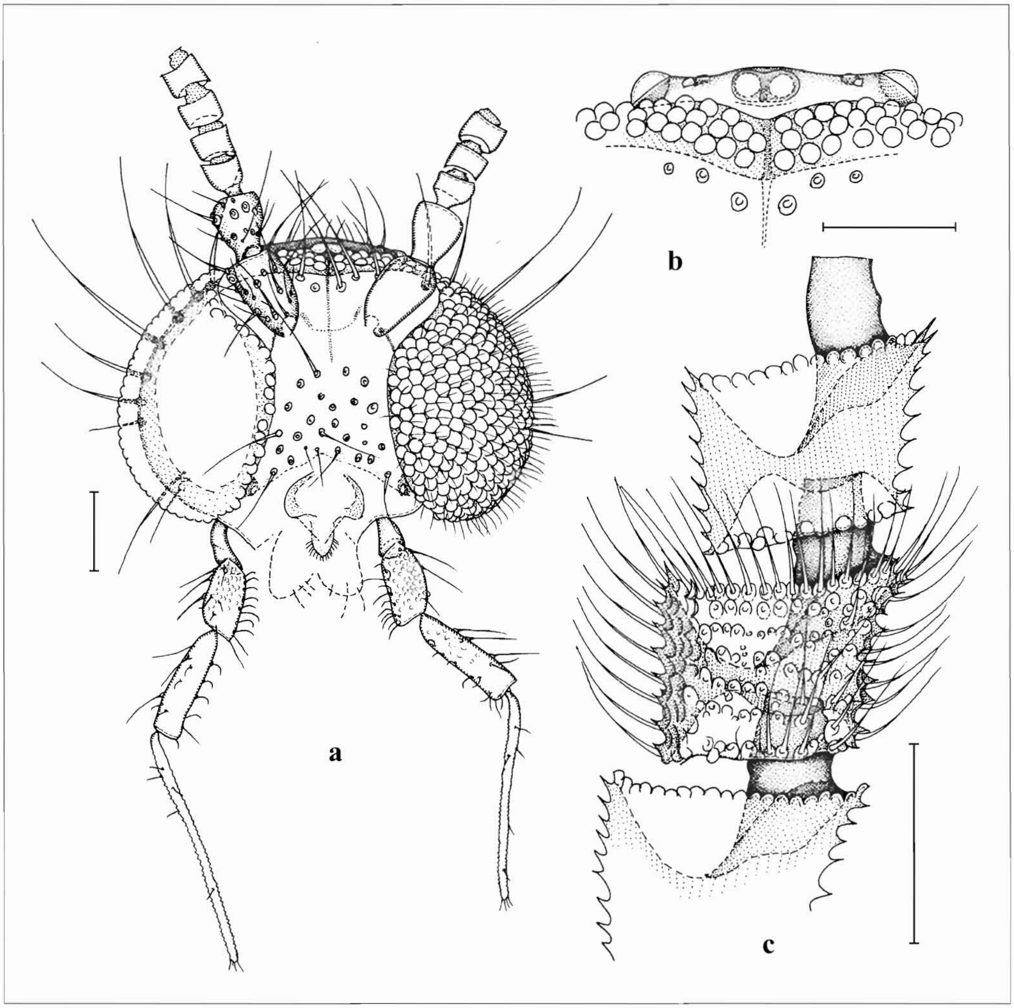
**Head.** Head capsule convex behind. Postocular bristles numbering 6–8. Antenna in male longer than in female; with 14 flagellomeres; distal flagellomeres more slender than proximal ones; each individual flagellomere with the stem one-third length of the node. Flagellum with a vestiture consisting of dense rows of trichia with large, raised bases, resulting in a strongly serrated outline to the rims of the flagellomeres. Three ocelli arranged in an almost straight line, median ocellus divided into two. Eyes with numerous, comparatively long interommatidial setulae. Frons on either side with 2–3 pairs of strong bristles; frontal tubercle absent. Median lobes of postgenae small and poorly sclerotised. Prementum with a short median apodeme. Labrum small, weakly sclerotised, subtriangular, non-setose. Lacinia absent. Labella small. Maxillary palpus with 4 palpomeres visible, probably due to the fusion, or loss, of palpomere 1 or 2. 'First' palpomere almost as long as third, non-setose. Third palpomere subcylindrical, somewhat thickened apically; in addition to the setae, with scattered peg-like sensilla medially. Palpomere 4 inserted slightly subapically on palpomere 3, longer than 3, somewhat thickened apically, setose. Palpomere 5 slender, almost twice as long as palpomere 4. Palpomeres 3–5 inside with numerous erect, blunt-ended, apically-curved hair-like sensilla.

**Thorax.** Antepronotum and proepisternum subequal in size, separated by a thin suture; the former with setae, the latter with setae and strong bristles. Proepimeron present, elongate-subtriangular. Basisternum with lateral portions comparatively small and narrow, its major portion situated in the frontal position; with setae and bristles. **Wing.** Membrane somewhat darkened along anterior margin. In addition to dorsal setae, with ventral setae sometimes on R1 and on distal half of R5. Rs present as an extremely short remnant of tracheae on the same level as Sc1.

**Legs.** Front coxa little shorter than mid coxa, mid coxa little shorter than hind coxa. Mid and hind tibiae with the shorter spurs two-thirds as long as the long spurs. Tarsal trichia arranged in oblique rows. Tarsal claws small, each claw deeply split into two branches that are subequal in size. Empodia reduced to a few short hairs.

**Abdomen.** Sternites 1 and 2 non-setose, all other sclerites setose. Sternite 1 pale, almost twice as long as tergite 1 and four times as long as sternite 2. **Terminalia.** Male. Rotated 180° in all specimens studied. Sternite 9 not discernible as a distinct sclerite. Gonocoxites shorter to little longer than wide, not fused ventro-basally, bearing spines, with interior lobes or not; dorsal gonocoxal apodemes very small. Gonostylus consisting of several lobes in a complicated three-dimensional structure; outwardly directed surfaces with portions of pale lamellae; an inwardly directed lobe with 1 or 2 comb(s) of black lamellae. Aedeagus with a sclerotised ejaculatory apodeme. Parameres in two pairs, ventral pair fused to form a tegmen, dorsal pair varying in outline. Tergite 9 comparatively short, subrectangular, slightly longer than wide, with setae of various lengths. Tergite 10 (if correctly identified) largely fused with, and visible as the pronounced disto-lateral edges of, tergite 9; setose. Cerci and hypoproct extending well beyond tergite 9; both with large setae.

**Female.** Terminalia rather short and small. Tergite 8 well-developed; setose, including several large setae marginally. Gonocoxite 8 setose, including several strong setae near apex. Gonapophyses 8 shorter than gonocoxites, finely trichiose. Tergite 9 with a strongly sclerotised hind margin; non-setose. Gonapophyses 9 present as sclerotized internal ribs. Tergite 10 very short, stripe-like; setose. Sternite 10 comparatively large; setose, including some large setae. Cercus



**Figs 7a–c**: *Paramanota peninsulae* spec. nov. (paratypes). – **a**: Head, frontal view; – **b**: Vertex, frontal view; – **c**: Antennal flagellomeres 3–5, lateral view. Length of scale bars = 0.1 mm.

two-segmented; in lateral view, anterior segment subrectangular, large; setose, including some large setae inserted on inner surface. With species-specific differences to be found in at least gonocoxite 9 and cerci.

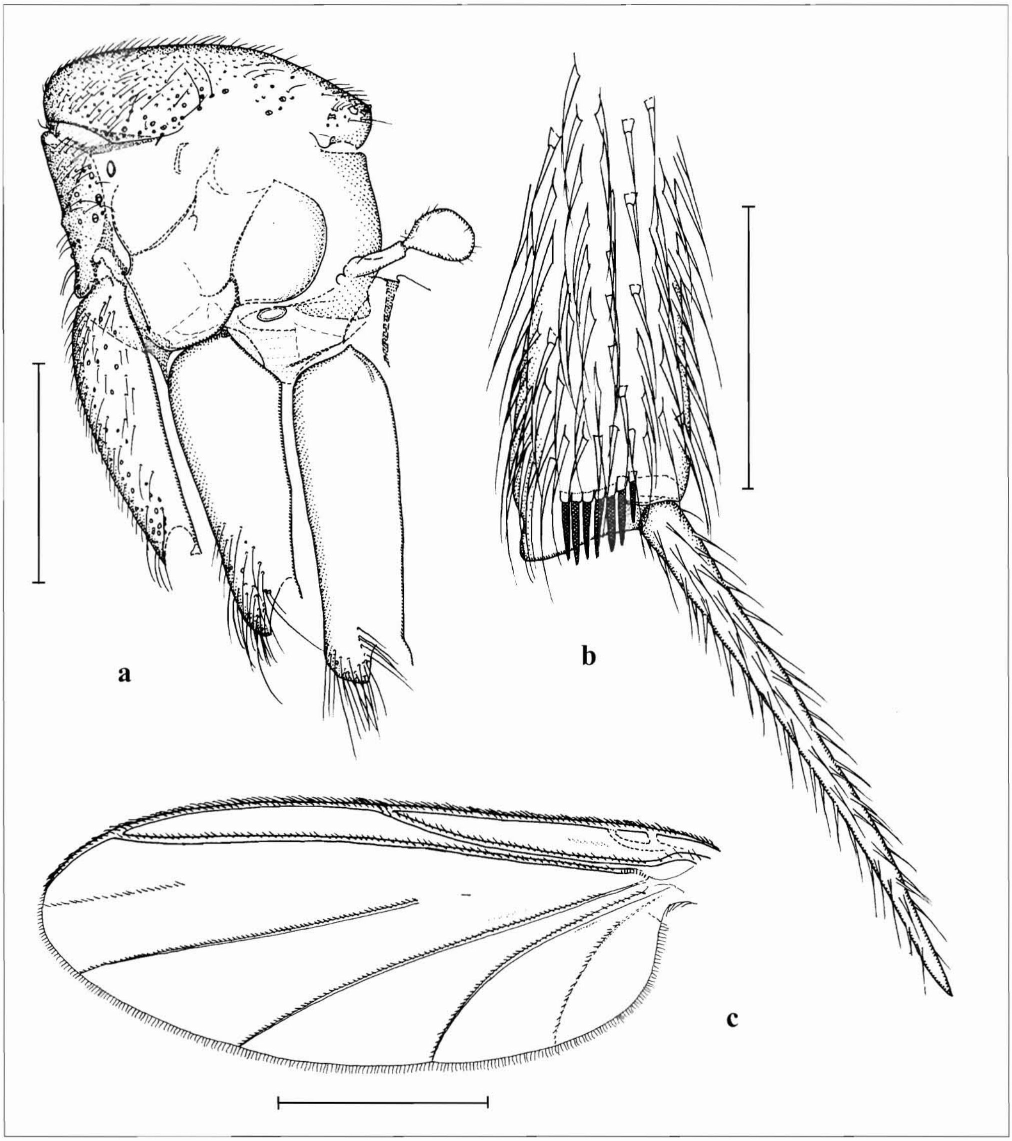
**Discussion.** The male terminalia in *Paramanota* species have a very complex structure that, on the basis of the material available for study, could not be worked out in every detail, let alone be clarified in terms of the homologies. The female terminalia seem to provide more species-specific characters than can be recognised in the few specimens known.

### *Paramanota peninsulae* spec. nov.

(Figs 7a–c, 8a–c, 9a–d, 11e)

#### Description

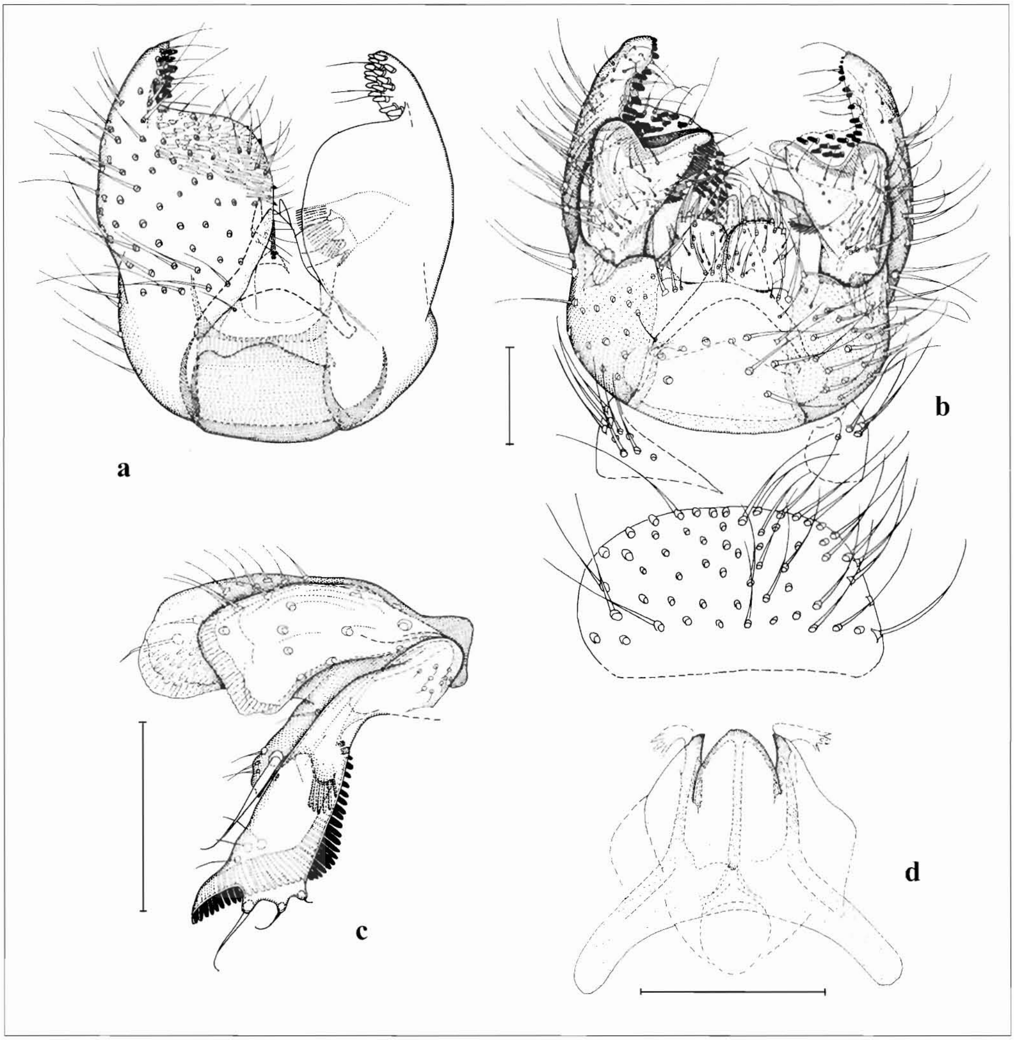
**Male.** Wing length 3.0–3.3 mm. **Head.** In lateral view, fourth flagellomere (Fig. 7c) 1.3 times as wide as long. **Thorax.** See Fig. 8a. **Wing.** See Fig. 8c. **Terminalia.** Gonocoxites (Figs 9a, b) ventrally with



**Figs 8a–c**: *Paramanota peninsulae* spec. nov. (paratypes): – **a**: Thorax, lateral view; – **b**: Apical part of front tibia, prolateral view; – **c**: Wing, dorsal view. Length of scale bars: a = 0.5 mm; b = 0.1 mm; c = 1.0 mm.

lobe-like extended disto-lateral edges, on interior surface with numerous short spines forming a broad stripe along disto-ventral margin including lobes; on outer surface with setae of various lengths. Gonostylus (Figs 9b, c) with interior lobe bearing a long, angled comb of black lamellae, overlapped by a thin lobe bearing 3 setae and accompanied by another lobe bearing a short comb of black lamellae plus 1 megaseta. Aedeagus and tegmen as in Fig. 9d. Dorsal parameres consisting of a pair of subtriangular sclerotised plates (Fig. 9d).

**Female.** Wing length 3.4 mm. **Head** (Fig. 7a). Eye bridge and ocelli as in Fig. 7b. Maxillary palpomere 3 with peg-like sensilla more numerous than in male; such sensilla also more sparsely distributed on palpomere 4. **Legs.** Apex of front tibia as in Fig. 8b. **Terminalia** (Fig. 11e). Gonocoxite 8 pointed.

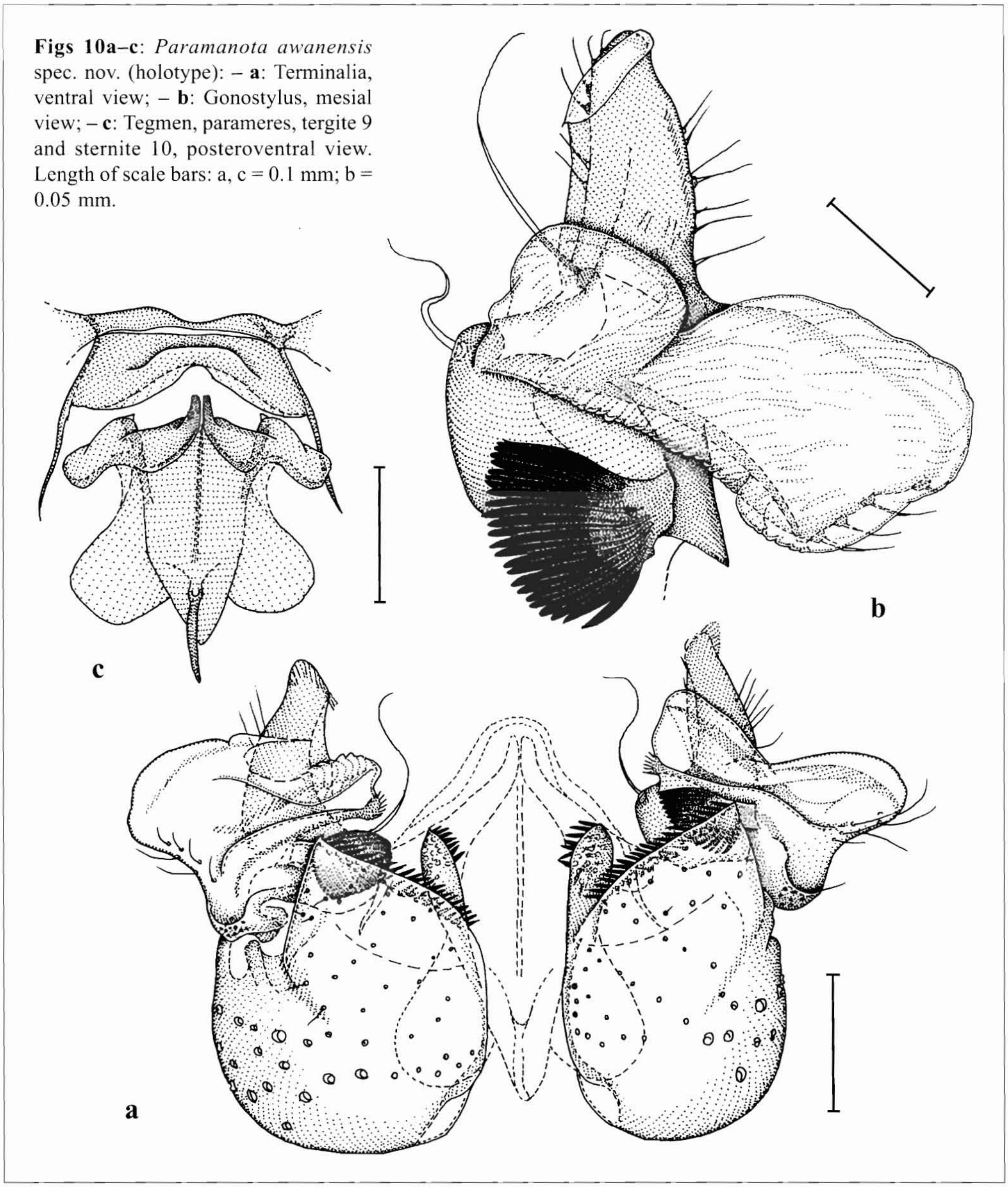


**Figs 9a–d**: *Paramanota peninsulae* spec. nov. (b: holotype; a, c, d: paratypes). – **a**: Terminalia, ventral view; – **b**: Terminalia with abdominal segments 7 and 8, dorsal view; – **c**: Gonostylus, mesial view; – **d**: Tegmen and parameres, ventral view. Length of scale bars = 0.1 mm.

Gonocoxite 9 indistinguishable from tergite 9. Sternite 10 setose, including some large setae. Anterior cercal segment completely sclerotised; posterior segment minute, knob-like, with setae of various lengths.

**Diagnostic characters.** As regards the male terminalia, this species is similar to *P. orientalis* Tuomikoski, which is known to us only from the original description (Tuomikoski 1966). In *P. peninsulae*, the gonocoxites are extended lobe-like disto-laterally, whereas this is not the case in *P. orientalis*. The gonostyli seem to differ between the two species, but their characterisation in *P. orientalis* is too poor to be certain about the details. *Paramanota schachti* Papp is even more similar to *P. peninsulae*, as in both species male gonocoxites are lobe-like extended disto-laterally. The two species differ in the outline of gonostyli (see Papp 2004: Fig. 30 versus Fig. 9c in this paper).

**Types. Holotype.** Male, MALAYSIA, Pahang, Cameron Highlands, 1500 m, in jungle, 15–20 Nov. 1994, by Malaise trap #1, T. Pape. **Paratypes.** 1 male, same locality as holotype, but 1400 m, 17–22 Nov. 1994, by Malaise trap #5;

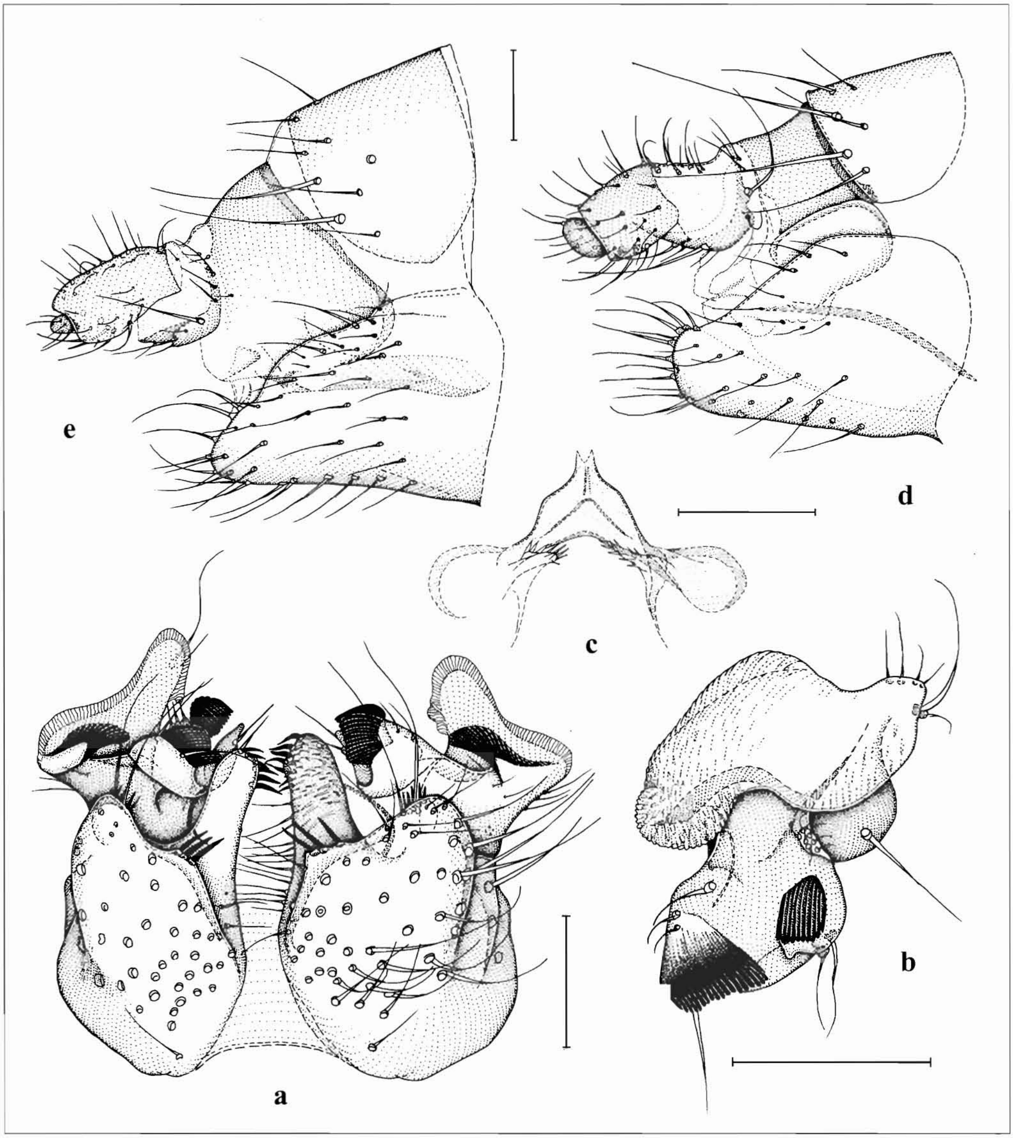


**Figs 10a–c**: *Paramanota awanensis* spec. nov. (holotype): – **a**: Terminalia, ventral view; – **b**: Gonostylus, mesial view; – **c**: Tegmen, parameres, tergite 9 and sternite 10, posteroventral view. Length of scale bars: a, c = 0.1 mm; b = 0.05 mm.

1 male (terminalia on slide, rest of body in ethanol), same locality, but 27 Nov. 1994, by Malaise trap #4; 1 female, same locality, Gunung Beremban, 1800 m, 20–26 Nov. 1994, by Malaise trap #4; 1 male, Pahang, Fraser's Hill, in jungle, 17 March 1997, by Malaise trap, H. Hippa, M. Jaschhof & B. Viklund; 1 male, Malaysia, Selangor, Genting Highlands, Gunung Ulu Kali, in jungle, 5725 ft, 27 Feb. –5 March 1997, by Malaise trap, H. Hippa, M. Jaschhof & B. Viklund; 1 female, same locality, but 12–22 March 1997.

**Further material studied.** 2 males (in ethanol), MALAYSIA, Selangor, Genting Highlands, Gunung Ulu Kali, 5725 feet, 27 Feb. –5 March 1997, Malaise trap, H. Hippa, M. Jaschhof & B. Viklund; 13 males (in ethanol), same locality, but 3–22 March 1997; 3 males (on slide), same data, but 5650 ft; 1 male, 1 female (in ethanol), Pahang, Cameron Highlands, 1400 m, 27 Nov. 1994, by Malaise trap #4, T. Pape; 3 males (in ethanol), same locality, but 17–22 Nov. 1994; 1 female (in ethanol), same locality, but 1300 m, 20–26 Nov. 1994, by Malaise trap #3.

**Etymology.** The name refers to the occurrence of this species in the Malay Peninsula.



**Figs 11a–e**: Morphology in *Paramanota* spp. – **a**: Male terminalia, ventral view; – **b**: Gonostylus, mesial view; – **c**: Tegmen and parameres, dorsal view; – **d, e**: Female terminalia, lateral view. **a–d**: *P. sumatrana* spec. nov. (a–c: holotype; d: paratype); **e**: *P. peninsulae* spec. nov. Length of scale bars = 0.1 mm.

## *Paramanota awanensis* spec. nov.

(Figs 10a–c)

### Description

**Male.** Wing length 2.9 mm. **Head.** In lateral view, fourth flagellomere 1.4 times as wide as long. **Terminalia.** Gonocoxites (Fig. 10a) on interior surface with numerous short spines in a row-like arrangement along the disto-ventral margin, on either side with a large finger-like lobe that is widened distally and bears numerous short, thick spines apically; with fine setae in distal half and larger setae elsewhere.

Gonostylus (Figs 10a, b) on inner lobe with a fan-like comb of black lamellae. Aedeagus and parameres as in Figs 10a, c.

**Female.** Unknown.

**Diagnostic characters.** *Paramanota awanensis* is most similar to *P. sumatrana* (see the next species), but is distinguished from the latter by structural details of the gonocoxites and gonostyli (for a species comparison, see under *P. sumatrana*).

**Etymology.** The name refers to the type-locality, Awana.

**Holotype.** Male, MALAYSIA, Pahang, Genting Highlands, Awana, in jungle, 10–23 March 1997, by Malaise trap, M. JASCHHOF, H. HIPPA & B. VIKLUND.

### *Paramanota sumatrana* spec. nov.

(Figs 11a–d)

#### Description

**Male.** Wing length 2.9 mm. **Head.** In lateral view, fourth flagellomere 1.2 times as wide as long. Peg-like sensilla present on palpomere 3, and such sensilla also present on palpomere 4. **Terminalia.** Gonocoxites (Fig. 11a) with 3 short spines at inner disto-ventral edge and more than 10 short spines on interior surface disto-laterally, on either side with a large thumb-like lobe bearing numerous short, thick spines apically and dorsally, with setae of various lengths elsewhere. Gonostylus (Figs 11a, b) with inner lobe bearing 2 separate combs of black lamellae; the larger comb accompanied by 1 large seta, the smaller comb by 2 large setae. Tegmen as in Fig. 11c. Hypoproct with 2 large setae apically.

**Female.** Wing length 2.9 mm. **Head.** Maxillary palpomere 3 with peg-like sensilla more numerous than in male, and such sensilla also present on palpomere 4. **Terminalia** (Fig. 11d). Gonocoxite 8 blunt-tipped. Gonocoxite 9 large and well-separated from tergite 9; non-setose. Tergite 10 setose, including large setae. Anterior cercal segment with only the distal portion sclerotized, but with setae also in the membraneous proximal portion; posterior segment broad but short, with setae of various lengths.

**Diagnostic characters.** The characters distinguishing *Paramanota sumatrana* and *awanensis* (in parentheses) include the gonocoxites bearing two separate groups of spines at the disto-ventral margins (one continuous row of spines), and the gonostylus with two combs of black lamellae (one such comb).

**Types. Holotype.** Male, INDONESIA, Sumatra, Sumatera Utara, Semangat Gunung, 18 March 1992, 1300 m, in jungle, by Malaise trap, H. HIPPA. **Paratype.** Female, same data as holotype.

**Etymology.** The name refers to the island of Sumatra, where the type-specimens were collected.

## Acknowledgements

We are most grateful to Dr Jevgeni JAKOVLEV, Finnish Forest Research Institute, Vantaa, for identifying and donating to us some study material of various Mycetophilidae. The following institutions and individuals are gratefully acknowledged for the loan of specimens: The Natural History Museum, London (Nigel WYATT); New Zealand Arthropod Collection, Auckland (Dr Trevor K. CROSBY); and Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (Manuel ZUMBADO). Dr Adrian PONT, Reading, kindly checked the English language.

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**Appendix 1**: Taxa used in the phylogenetic analysis.

*Sciophila hirta* MEIGEN (Finland; NRM)
*Alavamanota burmitina* BLAGODEROV & GRIMALDI (in BLAGODEROV & GRIMALDI 2004)
*Alavamanota hispanica* BLAGODEROV & ARILLO (in BLAGODEROV & ARILLO 2002)
*Allactoneura* DE MEIJERE (undescribed species, female) (Peninsular Malaysia; NRM)
*Aphrastomyia* COHER & LANE (undescribed species) (Costa Rica; INBIO)
*Docosia gilvipes* (HALIDAY) (Finland; NRM)
*Ectrepesthoneura hirta* (WINNERTZ) (Finland; NRM)
*Eumanota hilleviae* spec. nov. (Indonesia, Sumatra; NRM)
*Eumanota humeralis* EDWARDS (holotype) (Malaysia, Sabah; BMNH)
*Eumanota kambaiti* spec. nov. (Burma; NRM)
*Eumanota leucura* EDWARDS (holotype) (Malaysia, Sabah; BMNH)
*Eumanota malukensis* SÖLI (in SÖLI 2002)
*Eumanota racoli* SÖLI (in SÖLI 2002)
*Eumanota suthepensis* SÖLI (in SÖLI 2002)
*Eumanota* spec. (female) (Peninsular Malaysia; NRM)
*Greenomyia baikalica* ZAITZEV (Finland; NRM)
*Leia cylindrica* MEIGEN (Finland; NRM)
*Leiella* ENDERLEIN (undescribed species) (Costa Rica; INBIO)
*Manota* WILLISTON (undescribed species 1) (New Zealand; NZAC)
*Manota* WILLISTON (undescribed species 2) (Costa Rica; INBIO)
*Mohelia* MATILE (undescribed species) (South Africa; NRM)
*Mycetophila fungorum* DE GEER (Finland; NRM)
*Paramanota awanensis* spec. nov. (Peninsular Malaysia; NRM)
*Paramanota orientalis* TUOMIKOSKI (in TUOMIKOSKI 1966)
*Paramanota peninsulae* spec. nov. (Peninsular Malaysia; NRM)
*Paramanota sumatrana* spec. nov. (Indonesia, Sumatra; NRM)
*Procycloneura* EDWARDS (unidentified species) (Costa Rica; INBIO)
*Promanota malaisei* TUOMIKOSKI (Burma; NRM)
*Rondaniella dimidiata* (MEIGEN) (Finland; NRM)
*Sticholeia* SÖLI (unidentified species) (Papua New Guinea; NRM)

**Appendix 2**: The characters used in the phylogenetic analysis.

1. *Position of occipital foramen*: (0) centralised; (1) dorsalised.
2. *Median convexity of postgenae*: (0) present; (1) absent. This character is used following Söli (1997).
3. *Row of postocular bristles*: (0) absent; (1) present. Postocular bristles are arranged in a distinct row along the entire, or almost entire, hind margin of the eyes; they are erect or curved posteriorly; and they are of approximately the same size. There are enlarged setae, or bristles, present behind the eye margins in quite a number of the species in question; however, they are considered postocular bristles only when combining the three qualities described above.
4. *Frontal tubercle*: (0) present; (1) very weak or absent.
5. *Position of ocelli*: (0) on top of head; (1) frontalised.
6. *Number of ocelli*: (0) three; (1) two.
7. *Position of lateral ocelli relative to eye margin*: (0) far from eye margin; (1) close to eye margin. A distance from the eye margin greater than two times the diameter of the ocellus is coded 0.
8. *Outline of median ocellus*: (0) simple; (1) divided into two.
9. *Complete eye bridge*: (0) absent; (1) present.
10. *Shape of male antennal flagellomeres*: (0) cylindrical or subcylindrical; (1) clearly compressed.
11. *Size of face relative to clypeus*: (0) larger; (1) of approximately same size; (2) smaller.
12. *Shape of face*: (0) shorter than wide; (1) longer than wide; (2) more than two times longer than wide.
13. *Setosity of clypeus*: (0) setose; (1) non-setose.
14. *Outline of premental apodeme*: (0) with a pair of rod-like prolongations; (1) with a single, long prolongation; (2) with a single, short prolongation.
15. *Number of maxillary palpomeres basal of third palpomere*: (0) two; (1) one.
16. *Shape of third palpomere*: (0) normal; (1) with apical extension beyond attachment of fourth palpomere.
17. *Shape of apical extension of third palpomere*: (0) subtriangular, pointed; (1) finger-like, rounded.
18. *Position of peg-like sensilla on third palpomere*: (0) scattered over the surface; (1) concentrated in a pit.
19. *Thick sensilla on third palpomere*: (0) absent; (1) present. This morphotype of sensilla differs from the blunt-tipped, hair-like sensilla that are present on at least the third palpomeres in many species in being thicker and curved apically; these sensilla are confined to the apical extension of the third palpomere in *Manota* species.
20. *Length of terminal palpomere*: (0) long, i.e. at most two times as long as preceding palpomere; (1) extremely long, i.e. several times as long as preceding palpomere.
21. *Setosity of postpronotum*: (0) setose; (1) non-setose.
22. *Size of antepronotum*: (0) normal; (1) strongly enlarged. We coded as 1 only those conditions in which the antepronotum is both clearly enlarged in relation to the postpronotum and incises markedly the anterior edge of the scutum.
23. *Structure of epimeron 1 and episternum 1*: (0) normal, separate; (1) merged into a synsclerite.
24. *Size of epimeron 1*: (0) small, subtriangular; (1) large, extending dorsally as a narrow stripe; (2) very large, extending dorsally as a plate and partially covering anterior spiracle.
25. *Structure of basisternum 1 and episternum 1*: (0) normal, separate; (1) merged into a synsclerite.
26. *Size of basisternum 1*: (0) normal, not or marginally extending laterally; (1) enlarged, greatly extending laterally. In the enlarged condition, basisternum 1 lies like a shield or roof above coxa 1.
27. *Setosity of basisternum 1*: (0) setose; (1) non-setose.
28. *Setosity of lateral and dorso-lateral portions of scutum*: (0) evenly setose; (1) with non-setose stripes.
29. *Setosity of anepisternum*: (0) setose; (1) non-setose.
30. *Setosity of preepisternum 2*: (0) setose; (1) non-setose.
31. *Setosity of laterotergite*: (0) setose; (1) non-setose.
32. *Setosity of episternum 3*: (0) setose; (1) non-setose.
33. *Setosity of wing membrane*: (0) completely setose; (1) setae confined to posterior portions; (2) non-setose.
34. *Length of C*: (0) long, ending beyond R5; (1) short, ending at R5.

35. *Setosity of h*: (0) setose; (1) non-setose.
36. *Length of Sc*: (0) long, running into C; (1) short, ending free.
37. *Dorsal setosity of Sc*: (0) setose; (1) non-setose.
38. *Ventral setosity of Sc*: (0) setose; (1) non-setose.
39. *Sc-r*: (0) present; (1) absent.
40. *Length of R1*: (0) long, ending in distal half of wing; (1) short, ending in proximal half of wing.
41. *Length of R5*: (0) long, ending at level beyond tip of M2; (1) short, ending at level before tip of M2.
42. *Ventral setosity of R1 and R5*: (0) setose; (1) non-setose.
43. *Number of crossveins between R1 and R5*: (0) two; (1) one.
44. *Position of most basal crossvein*: (0) in distal half of wing; (1) in proximal half of wing.
45. *Outline of M*: (0) stem and fork complete; (1) fork incomplete due to detachment of base of M1; (2) stem and base of M1 reduced.
46. *Ventral setosity of M*: (0) setose; (1) non-setose.
47. *Outline of CuA*: (0) stem and fork complete; (1) fork incomplete due to detachment of CuA1; (1) CuA1 and CuA2 running separately to base of wing.
48. *Setosity of A1*: (0) setose; (1) non-setose.
49. *Arrangement of trichia on tibiae and tarsi*: (0) irregularly arranged; (1) arranged in rows.
50. *Length of fore tibia in relation to femur*: (0) longer; (1) shorter.
51. *Fore tibial antero-apical depression*: (0) present; (1) absent.
52. *Sensory groove on hind tibia*: (0) absent; (1) present.
53. *Size of setae on hind tibia*: (0) shorter or as short as tibial diameter; (1) up to one-and-a-half times the length of tibial diameter; (2) longer.
54. *Apical comb of pale setae on mid and hind tibiae*: (0) present; (1) absent. This structure should not be confused with dark, socketed setae arranged in a transverse row, with a distinct space between individual setae.
55. *Serrated rim of tibial spurs*: (0) absent; (1) present.
56. *Fold lines on abdominal sternites*: (0) absent; (1) present laterally and/or sublaterally; (2) present laterally and medially.
57. *Scales on abdomen*: (0) absent; (1) present.
58. *Male tergite 9*: (0) present; (1) absent.
59. *Outline of male tergite 9 and cerci*: (0) normal; (1) elongate. The elongate condition is characterised by the ninth tergite being longer than wide and the cerci extending far beyond the posterior margin of that tergite; this condition is met only in *Eumanota* and *Promanota*.
60. *Number of cercal segments in female*: (0) two; (1) one.

**Appendix 3**: Data matrix for phylogentic analysis. Fossil taxa shown shaded.

| | 111111111122222222223333333333444444444455555555556 |
|---|---|
| | 123456789012345678901234567890123456789012345678901234567890 |
| *Sciophila hirta* | 1000100000100000-000100000010000000000000000001010000000110100000 |
| ***Alavamanota burmitina*** | 0?1?000?01?????0-??0?0????00101001?1???01001000?11??????0??? |
| ***Alavamanota hispanica*** | ??1?0???00?????0-??0????????0??1?20100010100120000??0???0--0 |
| *Allactoneura* spec. | 011000000-200000-1001102010011012110010000110121010011101??1 |
| *Aphrastomyia* spec. | 1100100000101110-0001001101011012011110011110101110000100000 |
| *Docosia gilvipes* | 1000101000100000-10010000001011002001011000110100010011110001 |
| *Ectrepesthoneura hirta* | 100010000010001101001001001111112011110011 01?12000000111000? |
| *Eumanota hilleviae* | 00100010010102110101101-01000101101101001010112111010100001? |
| *Eumanota humeralis* | 00100010010102110101101-0100010110110100101011201 1??0100001? |
| *Eumanota kambaiti* | 00100010010102110101101-01000101101101001010112011010100001? |
| *Eumanota leucura* | 00100010010102110101101-01000101101101001010112111010100001? |
| *Eumanota malukensis* | 00100010010102110101101-0100010110110100101011211 1??01?0001? |

**Continuation of appendix 3.**

| | 1111111111222222222233333333334444444444555555555556 |
|---|---|
| | 123456789012345678901234567890123456789012345678901234567890 |
| *Eumanota racoli* | 001000100101021101011 01-0100010110110100101011 2011??01?0001? |
| *Eumanota suthepensis* | 00100010010102110101101-01000101101101001010112111??01?0001? |
| *Eumanota* spec. | 001000100-0102110101101-010001011011010010101120110?11000??1 |
| *Greenomyia baikalica* | 1100100000200000-10010010011110121100100001001100100111 0000? |
| *Leia cylindrica* | 1100101000200000-100100000111101211011000010011001002110000 2 |
| *Leiella* spec. | 1100111000200000-1001001001011012110011000111111010021111??0 |
| *Manota* spec. 1 NZ | 001?00100101020111101 11-11001000101111111011210011000110 01-0 |
| *Manota* spec. 2 CR | 00100010010102011110111-11000010101111111011210011000110 01-0 |
| *Mohelia* spec. | 1100100000001110-1001001001011012011110011110101010001100000 |
| *Mycetophila fungorum* | 1000111000200000-1001000001001001101111000110101110020120000 |
| *Paramanota awanensis* | 0011001111001210-0000000000011112010111110112120111001000001 |
| *Paramanota orientalis* | 0011001111001210-0000000000011112010111110112120111001000001 |
| *Paramanota peninsulae* | 0011001111001210-0000000000011112010111110112120111001000001 |
| *Paramanota sumatrana* | 0011001111001210-0000000000011112010111110112120111001000001 |
| *Procycloneura* spec. | 0010000000100000-2001000001011111101111010112110010021110000 |
| *Promanota malaisei* | 001000100102 0?1101001000000001010011010010101121110001 0?001? |
| *Rondaniella dimidiata* | 1100100000200000-1001000000110120100010101111110100211200 00 |
| *Sticholeia* spec. | 0111011000200000-1001102010011012110011000110110110021100002 |

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