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## ***Pseudoperomyia* gen. n. from Malaysia and the phylogeny of the Micromyidi**

**(Diptera: Cecidomyiidae, Lestremiinae)**

With 10 figures

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### **Summary**

A new cecidomyiid genus *Pseudoperomyia* gen. n. is described from Malaysia, with 8 new species: *P. acutistyla* sp. n., *P. bidentata* sp. n., *P. humilis* sp. n., *P. parvolobata* sp. n., *P. intermedia* sp. n., *P. longicornis* sp. n., *P. macrostyla* sp. n., and *P. platistyla* sp. n. *Pseudoperomyia* belongs to the lestremiine tribe Micromyini with *Anodontoceras* as its sister group. The result of a computerized parsimony analysis for the Micromyidi largely supports a recently-published hypothesis on the phylogeny of this taxon.

### **Zusammenfassung**

Die Gallmücken-Gattung *Pseudoperomyia* gen. n. wird für 8 Lestremiinen-Arten aus Malaysia begründet. Die neubeschriebenen Arten sind: *P. acutistyla* sp. n., *P. bidentata* sp. n., *P. humilis* sp. n., *P. parvolobata* sp. n., *P. intermedia* sp. n., *P. longicornis* sp. n., *P. macrostyla* sp. n. und *P. platistyla* sp. n. Innerhalb der Tribus Micromyini ist *Anodontoceras* die Schwestergruppe von *Pseudoperomyia*. Das Resultat einer Computeranalyse unterstützt weitgehend eine jüngst vorgeschlagene Hypothese zur Phylogenie der Micromyidi.

### **0 Introduction**

Present knowledge of the gall midges of the subfamily Lestremiinae with free-living larvae is largely restricted to the Holarctic Region. Except for a few occasional species records scattered in the literature, nothing more substantial has been published on tropical lestremiines. 26 species are recorded from the Oriental Region, most of them from India (GAGNÉ, 1977). They are associated with widespread Holarctic genera, but their true specific status is largely unrevised. The lestremiine fauna of South East Asia is completely unknown.

During our studies of Oriental Lestremiinae, we have discovered a group of very similar species which clearly belong to the Micromyidi, as it has recently been defined (JASCHHOF, 1998), but do not fit any of the recognized genera. We are assigning them to a new genus *Pseudoperomyia*.

The aims of the present work are to describe *Pseudoperomyia* and its eight included species, to demonstrate the monophyly of the group, to find its sister-group, and to show the interrelationships of its species. At the same time we test by computerized parsimony analysis the recently proposed hypothesis on the phylogeny of the whole Micromyidi (JASCHHOF, 1998).

## 1 Material and methods

Most of the specimens studied here were collected during an expedition to parts of the Malaysian Peninsula in February / March 1997. Additional material came from the holdings of the Swedish Museum of Natural History, Stockholm, from previous collecting trips to Malaysia in 1992 and 1994. The specimens were collected with Malaise traps, sweepnet and exhaustor, and were preserved in 70 % alcohol. To mount the specimens on microscope slides, they were first transferred from alcohol into a mixture of alcohol / formaldehyde (10 ml of 70 % alcohol mixed with 2-3 drops of 30 % formaldehyde) and then placed in creosote for 12-24 hours. On the slide, the hypopygium and (in some material) one wing were separately mounted in Canada balsam as well as the rest of the body. In some cases we dissected the male genitalia to scrutinize the structural details, but only when there was sufficient material available and when the hypopygium was large enough to manipulate with insect pins.

All the material discussed here is deposited in the Swedish Museum of Natural History, Stockholm. The drawings were made with the aid of a drawing tube attached to a Leitz Diaplan microscope. The measurements were made with a micrometer slide. The morphological terminology follows JASCHHOF (1998). Some of the characters used in the parsimony analysis are explained in Appendix 1.

The parsimony analysis was carried out using PAUP version 3.1.1. (SWOFFORD, 1993) in combination with MacClade version 3.06 (MADDISON & MADDISON, 1992). Bootstrap proportions were computed using PAUP and decay indices using PAUP in combination with AutoDecay version 3.0 (ERIKSSON & WIKSTRÖM, 1995).

## 2 Results

### 2.1 Genus *Pseudoperomyia* gen. n.

Type species: *Pseudoperomyia longicornis* sp. n.

#### Description

**Male.** Head: postfrons prominent, without setae or scales. Ocelli 3 in number or absent. Postocellar bristles present. Eye bridge complete, 2-7 facets wide, at vertex little wider than laterally. With 1 or 2 rows of postocellar bristles. Occiput and clypeus densely covered with scales and sometimes additionally with setae. Antennae 2 + 12-segmented. Scape and pedicel of same size, with scales and setae. 1<sup>st</sup> flagellomere slightly elongated and covered with scales basally. Neck of 4<sup>th</sup> flagellomere slightly shorter to slightly longer than node. Node of subglobular type, as long as wide or slightly longer; with setae and sensory hairs in specific irregular or whorl-like arrangements, without crenulate whorls (exceptionally with occasional indistinct traces); with sensory spines and characteristic small bottle-shaped or conical sensillae distally. Distal flagellomeral nodes becoming more slender and necks longer. Palpus with 3 segments; 1<sup>st</sup> segment shortest (despite the indistinct basal stem), with scattered sensory hairs, long setae and scales; distal segments more slender, terminal segment as long as to obviously longer than segment 2 and tapering distally, both segments with spine-like setae and scales, 2<sup>nd</sup> segment sometimes with a few additional sensory hairs. Thorax: anterior pronotum<sup>1</sup> with a row of long setae. Scutum with long setae laterally and along

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<sup>1</sup> The limits between the poorly sclerotized thoracic sclerites, i. e. posterior and anterior pronotum and episternum 1, are not clearly visible in the lestremini specimens that we have examined. But, when compared with the situation in the Sciaridae, the setae should insert on the anterior pronotum.

parapsidal sutures in well defined stripes; lateral setae irregularly arranged and numerous (extended type, Fig. 8D) or more or less row-like and few in number (reduced type, Fig. 2F). Scutellum with 1 transverse row of long setae interrupted medially.

Legs: densely covered with scales, among them additionally with a few setae; scales becoming increasingly shorter and broader on distal parts of legs. Claws crescent-shaped, those on middle legs with 2-4 small teeth mesally. Empodium narrow, as long as claws or slightly shorter.

Wing: membrane densely covered with small scales; macrotrichia ventrally on  $R$ ,  $R_1$  and 2/3 of  $CuA$ -stem proximally; pattern of sensory pores:  $R_1$  3 (occasionally 4),  $rs$  1,  $r-m$  1;  $Sc$  distinct, reaching level of  $R_1$ ; strong anterior part of  $C$  running approximately 7 times the vein width beyond the intersection with  $R_3$ , followed by distinct break;  $R_1$  up to 2 times the length of  $rs$ ;  $r-m$  short, usually about as long as  $rs$ ;  $CuA$ -fork with angle of 85-90°;  $M_{1+2}$  and  $CuA_2$  usually not reaching wing margin; anal margin slightly convex. Haltere with stem strong, half the length of the ovoid knob; knob densely covered with scales and with a few setae on stem.

Abdomen: segment 1 non-setose. Tergites 2-6 covered with scales, tergites 7-8 bare except for some lateral scales, and with strongly sclerotized anterior margin; intersegmental membrane with ovoid patch of scales; sternites densely covered with scales (exceptions: see under species descriptions).

Hypopygium: very diverse; in general gonocoxites united ventrobasally, with setae and scales ventrally; gonostylus usually with apical tooth-like structure; genital rod present; tegmen membranous except for parameral apodemes, partly with characteristic nose-shaped projections dorsally; tergite 9 stripe-like with 1 row of long setae or strongly modified with horn-like projections, narrowed distal margin and reduced number of setae; tergite 10 bilobed, ovoid or elongated, partly with sclerotized arc dorsally, usually with setae; sternite 10 weakly membranous, bilobed, without setae.

Body length: 1.0-1.4 mm.

Female: unknown.

### Biology

Largely unknown. All the specimens were collected along forest margins or inside lowland and mountainous primary forest up to 1750 m. It is very probable that one of the species emerged from humus soil (see *P. humilis*). Only one of the 8 species was at all common.

### Distribution

Oriental (Peninsular Malaysia).

### Etymology

With their small body size, together with the subglobular flagellomeral nodes, specimens of *Pseudoperomyia* resemble *Peromyia* in general appearance under the stereo microscope, and the generic name is derived from this.

### Discussion

*Pseudoperomyia* can easily be distinguished from other related genera of the Micromyidi by the combination of the following derived characters: 1. the lack of sensory pores on  $R_3$  (with simultaneous presence of 1 pore on  $r-m$ ), 2. the absence of macrotrichia on  $R_3$ , 3. the presence of subglobular flagellomeral nodes lacking crenulate whorls and with a rather centrally placed neck, 4. the occurrence of bottle-shaped and conical flagellomeral sensillae, 5. the lack of postfrontal setae, 6. the presence of nose-like and dorsad-directed projections of the tegmen in at least some of the

included species, and 7. the stripe-like shape of tergite 9 which is distinctly narrower than the distal margin of gonocoxites in some of the included species. The bottle-shaped and conical sensillae as well as the nose-like tegmen projections are unique characters found nowhere else within the Lestremiinae.

*Pseudoperomyia* differs from the other genera of the Micromyini (sensu JASCHHOF, 1998) by each of the characters 1, 2 and 4-7. The globularisation of the flagellomeral node with simultaneous reduction of crenulate whorls (character 3) also occurs in *Anodontoceras*. *Peromyia* species, which are superficially similar to *Pseudoperomyia* and share characters 2, 3 and 5 in some of the species, have 1 sensory pore on  $R_5$  (whilst lacking the  $r-m$ -pore).

## 2.2 Species of *Pseudoperomyia*

### Key to species

- |   |   |                              |
|---|---|------------------------------|
| 1 | Antennal flagellomeres with a regular whorl of setae basally and 1 bottle-shaped sensilla distally (Figs. 1D, 2D, 3E, 4C) .....                         | 5                            |
| - | Antennal flagellomeres with irregularly arranged and mixed setae and sensory hairs basally and 1 conical sensilla distally (Figs. 5D, 6E, 7F, 8C) ..... | 2                            |
| 2 | Gonostylus one-lobed, with apical tooth or tooth-like structure .....   | 3                            |
| - | Gonostylus bilobed (with additional small subbasal lobe), without apical tooth (Figs. 7A, E) .....  | <i>P. macrostyla</i> sp. n.  |
| 3 | Gonostylus compact, not distinctly flattened (Fig. 5A); distal margin of tergite 9 as wide as gonocoxites and without projections (Fig. 5C) .....       | <i>P. intermedia</i> sp. n.  |
| - | Gonostylus flattened; distal margin of tergite 9 narrower than gonocoxites and with sclerotized projections .....                                       | 4                            |
| 4 | Tegmen with waist-like constriction; genital rod very short, much shorter than tegmen; projections of tergite 9 very short (Fig. 8B) .....              | <i>P. platistyla</i> sp. n.  |
| - | Tegmen parallel-sided; genital rod as long as tegmen; projections of tergite 9 very long (Figs. 6B, C) .....  | <i>P. longicornis</i> sp. n. |
| 5 | Ocelli absent .....   | 6                            |
| - | Ocelli present .....  | 7                            |
| 6 | Apical tooth of gonostylus two-pointed; gonostylus only little broader basally than subapically; genital rod very broad (Figs. 2B, C) .....             | <i>P. bidentata</i> sp. n.   |
| - | Apical tooth of gonostylus fingernail-like; gonostylus much broader basally than subapically; genital rod narrow (Figs. 1B, C) .....                    | <i>P. acutistyla</i> sp. n.  |
| 7 | Lobes of tergite 10 distinct, elongated and with distal horn-like prolongations; gonostylus with subapical lobe (Fig. 4A) .....                         | <i>P. parvolobata</i> sp. n. |
| - | Lobes of tergite 10 indistinct, ovoid and without unusual modification; gonostylus evenly tapering to tip (Figs. 3A, C) .....                           | <i>P. humilis</i> sp. n.     |

### *Pseudoperomyia acutistyla* sp. n.

(Figs. 1A-D)

#### Material studied

Holotype: male, West Malaysia, Pahang, Cameron Highlands, Gunung Jasar, 1700 m, 20.-23.11.1994, by Malaise trap, T. PAPE. Paratypes: 1 male, same locality as holotype, but 24.-27.11.1994;



1 male, same locality as holotype, but 1500 m, 20.-26.11.1994; 2 males, Cameron Highlands, Brinchang, 1400-1600 m, 26.-31.03.1992, by sweepnet, H. & H. HIPPA & G. SELLERHOLM; 4 males, Pahang, Bukit Fraser, 1200 m, 14.-17.03.1997, by Malaise trap, H. HIPPA, M. JASCHHOF, B. VIKLUND.

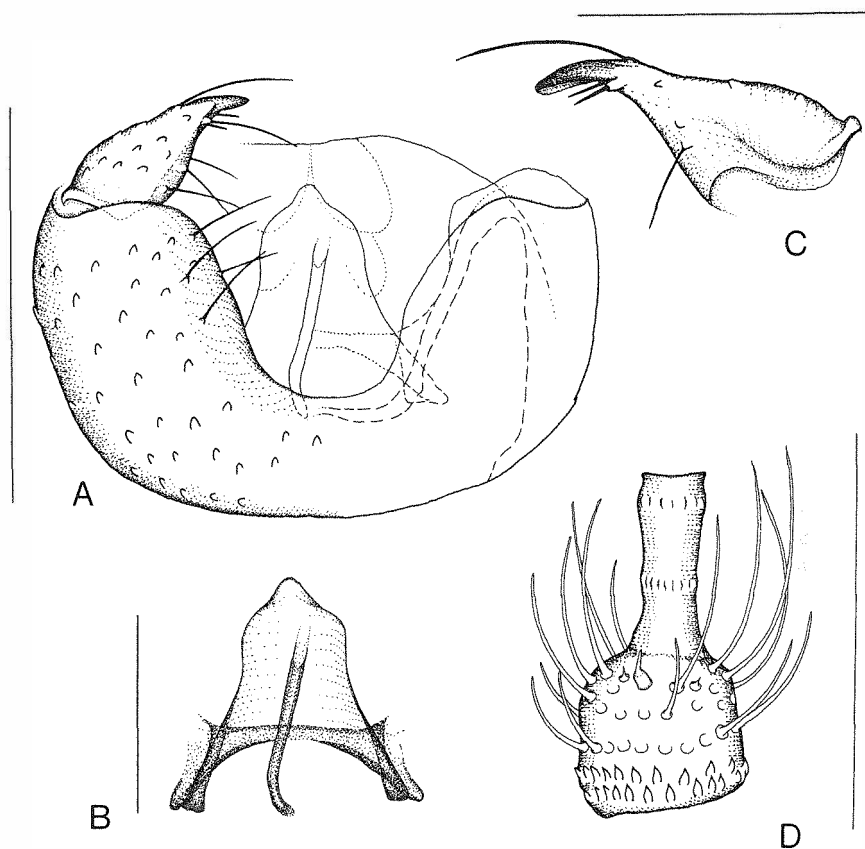


Fig. 1: *Pseudoperomyia acutistyla* sp. n.; A: hypopygium, ventral view (paratype from Gunung Jasar); B: tegmen and genital rod (same paratype from Gunung Jasar); C: gonostylus, dorsal view (paratype from Brinchang); D: flagellomere 4, mesal view (holotype). Scale for A and D 0.1 mm, for B and C 0.05 mm.

### Description

**Male.** Head: ocelli absent. Eye bridge 5-6 facets wide. With 1 row of postocular bristles, 1-2 weaker bristles in a short second row situated more ventrally. Occiput densely covered with scales or setae (totally absent in the specimens available). Flagellum with more than 11 segments (broken in the specimens available). Neck of flagellomere 4 longer than node (Fig. 1D); node with a double whorl of setae (or scales?, broken) basally and with irregularly arranged sensory hairs of different lengths, the most proximal sensory hairs shortest and forming a rather distinct whorl; among the hair-like sensillae with a few sensory spines and 1 inconspicuous bottle-shaped sensilla distally (lacking from flagellomere 6 on). Terminal palpal segment a little to obviously longer than segment 2; 2<sup>nd</sup> segment with a few sensory hairs basally.

Thorax: arrangement of lateral scutal setae of the reduced type (see Fig. 2F).

Legs: claws of middle legs with 2 small teeth mesally. Empodium approximately as long as claws.

Wing:  $R_1=1\frac{1}{2}-2\text{ rs}$ ; *CuA*-fork approximately rectangular.

Hypopygium: gonocoxites (Fig. 1A) setose ventrally (scales broken if present); distal margin with broadly U-shaped emargination. Gonostylus (Figs. 1A, C) widest in proximal third, strongly tapering to tip; with apical fingernail-like tooth (appears to be a pointed tooth in lateral view) and 2 subapical spines clearly shorter than tooth; with long setae. Tegmen (Fig. 1B) broadest at base, tapering to narrow tip; apex with a ventrally-directed, cap-like projection; parameral apodemes not reaching basal gonocoxal margin. Genital rod (Fig. 1B) sclerotized, narrow and with indistinct invagination near apex. Tergite 9 with broadly rounded distal margin and 1 transverse row of setae. Tergite 10 bilobed, ovoid, with a few weak setae. Sternite 10 indistinct, bilobed, without setae.

Body length: 1.2 mm.

#### Discussion

Within *Pseudoperomyia* only *P. acutistyla* and *P. bidentata* lack ocelli. Both species can easily be distinguished by the shape of gonostylus and tegmen (see Figs. 1B-C and 2B-C).

#### *Pseudoperomyia bidentata* sp. n.

(Figs. 2A-G)

#### Material studied

Holotype: male, West Malaysia, Selangor, Genting Highlands, Gunung Ulu Kali, 1750 m, primary forest, 04.03.1997, by sweepnet, M. JASCHHOF. Paratypes: 6 males, same data as holotype; 1 male, same locality, but 05.-12.03.1997, by Malaise trap, H. HIPPA, M. JASCHHOF, B. VIKLUND; 3 males, Pahang, Genting Highlands, 1200-1400 m, by Malaise trap, H. HIPPA, M. JASCHHOF, B. VIKLUND.

#### Description

**Male.** Head: ocelli absent; with a narrow sclerotized spot on vertex instead (Fig. 2E). Eye bridge 4-5 facets wide. With 1 row of postocular bristles, 2-3 weaker bristles in a very short second row situated more ventrally. Last flagellomere with small second node or not. Neck of flagellomere 4 little longer than node (Fig. 2D). Node slightly longer than wide, with a double whorl of long setae basally and with irregularly arranged sensory hairs of different lengths, the most proximal sensory hairs forming a rather distinct whorl; among the hair-like sensillae with a few sensory spines and 1 inconspicuous bottle-shaped sensilla distally. Terminal palpal segment a little to obviously longer than segment 2; 2<sup>nd</sup> segment with a few sensory hairs basally.

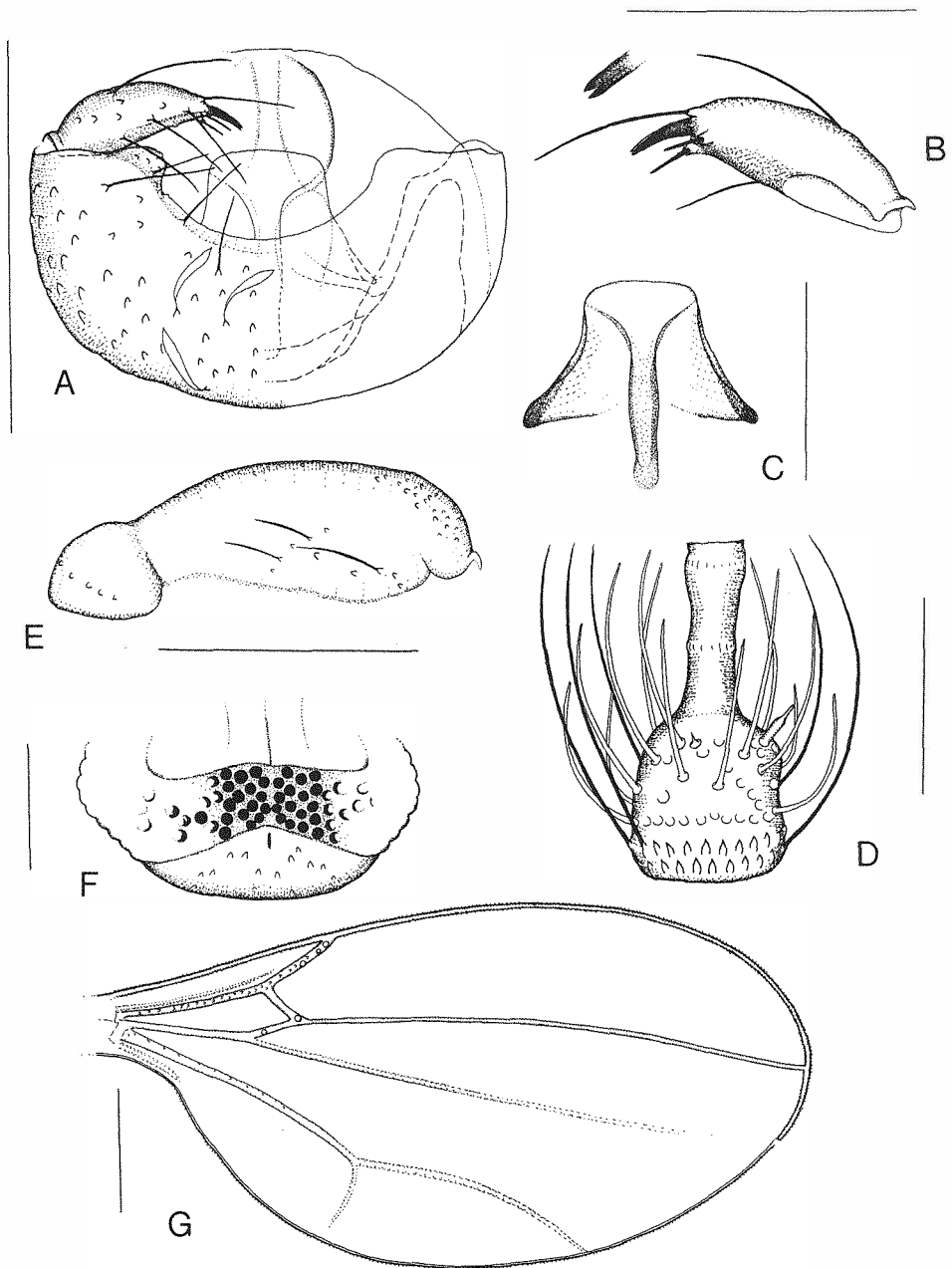
Thorax: arrangement of lateral setae of the reduced type (Fig. 2F).

Legs: claws of middle legs with 2 small teeth mesally. Empodium as long as claws.

Wing (Fig. 2G):  $R_1=1\frac{1}{2}\text{ rs}$ ; *CuA*-fork rectangular.

Hypopygium: gonocoxites (Fig. 2A) covered with setae and scales ventrally; distal margin with broadly U-shaped emargination. Gonostylus (Figs. 2A, B) slender, evenly tapering to tip; with apical tooth-like structure with 2 points (in lateral position often appearing to be a simple tooth) and 2 subapical spines little shorter than tooth; with long setae and some scales proximally. Tegmen (Fig. 2C) broad and short; distal margin truncate; parameral apodemes not reaching basal gonocoxal margin. Genital rod (Fig. 2C) weakly sclerotized, very broad and with broadly funnel-like invagination running into the distolateral margin of tegmen. Tergite 9 with broadly rounded distal margin and 1 transverse row of setae; anterior membranous area partly with additional long setae. Tergite 10 strong, especially distinct along lateral margins; bilobed and elongated, with weak setae. Sternite 10 indistinct, bilobed, without setae.

Body length: 1.2 mm.



**Fig. 2:** *Pseudoperomyia bidentata* sp. n.; **A:** hypopygium, ventral view (holotype); **B:** gonostylus, dorsal view (holotype); apical tooth from above (paratype); **C:** tegmen and genital rod (holotype); **D:** flagellomere 4, anterior view (holotype); **E:** vertex (holotype); **F:** mesonotum, lateral view (paratype); **G:** wing, scales on membrane and macrotrichia along margin omitted (paratype). Scale for A 0.1 mm, for B-E 0.05 mm, for G 0.2 mm.

## Discussion

*P. bidentata* is easily distinguished from the other species by the short, broadly truncate tegmen combined with a very broad genital rod with a wide funnel-shaped invagination. It is necessary to have a specimen in a suitable position on the slide to make out the two points of the apical tooth of the gonostylus.

### *Pseudoperomyia humilis* sp. n.

(Figs. 3A-F)

## Material studied

Holotype: male, West Malaysia, Selangor, Ulu Gombak, near University of Malaya Field Studies Centre, 250 m, primary forest, 25.02.-01.03.1997, by Malaise trap, H. HIPPA, M. JASCHHOF, B. VIKLUND. Paratypes: 30 males, same data as holotype. Additional material: 5 males, same data, but 22.-25.02.1997; 2 males, same data, but 23.-25.02.1997; 5 males, same data, but 25.02.-02.03.1997; 101 males, same data, but 24.02.-14.03.1997; 39 males, same data, but 02.-08.03.1997; 73 males, same data, but 08.-21.03.1997; 79 males, same locality, but 22.-24.02., 28.02., 01.03., 07.-08.03.1997, by net and exhaustor, M. JASCHHOF; 2 males, Pahang, Genting Highlands, Awana, 10.03.1997, by exhaustor, M. JASCHHOF; 1 male, Pahang, Cameron Highlands, Bala's Hotel, 1500 m, 25.-28.11.1994, T. PAPE.

## Description

**Male.** Head: 3 ocelli. Eye bridge 4-5 facets wide. With 1 row of postocular bristles, 2-4 weaker bristles in a short second row situated more ventrally. Last flagellomere constricted and with small second node. Neck of flagellomere 4 as long as or little longer than node (Fig. 3E). Node with a basal whorl of long setae consisting of 2-3 rows and with irregularly arranged sensory hairs of different lengths, the most proximal sensory hairs sometimes forming an irregular whorl being indistinctly crenulate posteriorly (Fig. 3F); among the hair-like sensillae with a few sensory spines and 1 inconspicuous bottle-shaped sensillum distally (lacking on distal 6 flagellomeres). Terminal palpal segment a little to obviously longer than segment 2; 2<sup>nd</sup> segment with a few sensory hairs basally.

Thorax: arrangement of lateral scutal setae of the reduced type (see Fig. 2F).

Legs: claws of middle legs with 2 small teeth mesally. Empodium approximately as long as claws.

Wing:  $R_1=1\frac{1}{2}rs$ ;  $CuA$ -fork rectangular.

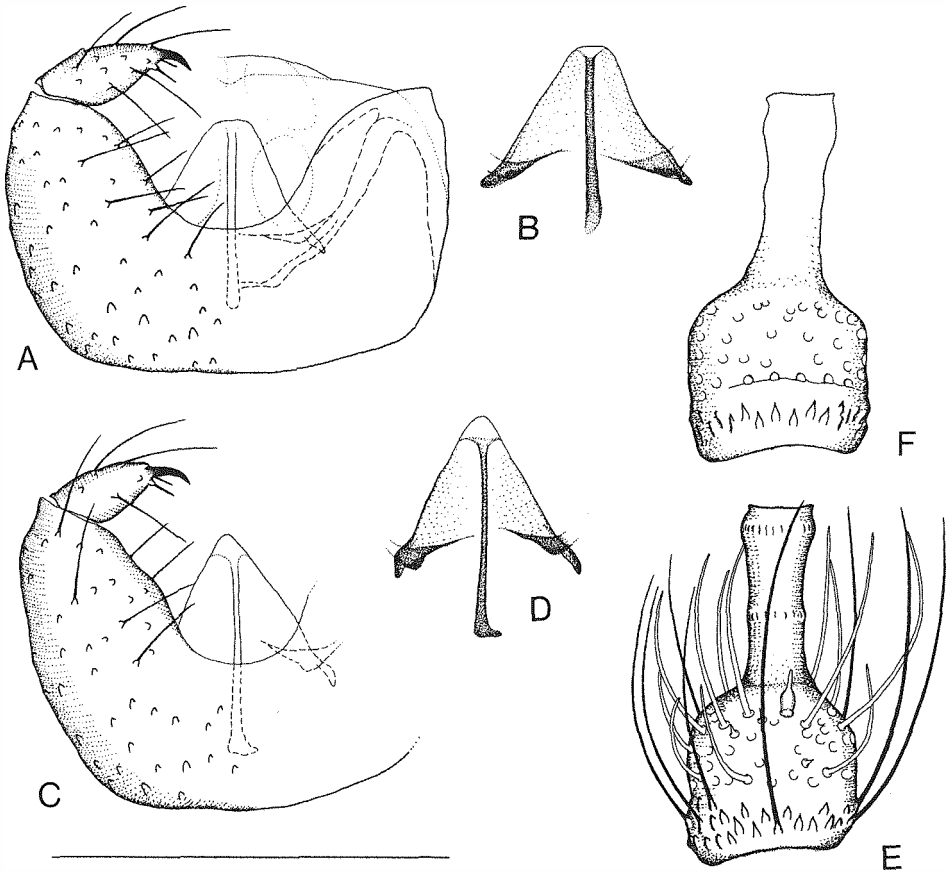
Hypopygium: gonocoxites (Figs. 3A, C) covered with setae and scales ventrally; distal margin with broadly U-shaped emargination. Gonostylus (Figs. 3A, C) rather small, a little flattened, tapering to tip; with a curved apical tooth and 2 subapical spines shorter than tooth; with long setae and some scales proximally. Tegmen (Figs. 3B, D) pyramid-shaped, with narrow apex (pointed or truncate); parameral apodemes not reaching basal gonocoxal margin. Genital rod (Figs. 3B, D) sclerotized, very narrow and just reaching tip of tegmen; with narrow funnel-shaped invagination apically; sometimes with a basal enlargement of various shapes. Tergite 9 with broadly rounded to straight distal margin with a slight depression medially (corresponding to weak sclerotization) and 1 transverse row of setae. Tergite 10 weak, bilobed, ovoid, with a few weak setae. Sternite 10 indistinct, bilobed, without setae (occasionally with 1 seta).

Body length: 1.1-1.3 mm.

## Discussion

*P. humilis* is the species of the genus that is most frequently encountered. Only males were observed (and collected in large numbers), forming loose swarms when flying in the morning over mixed accumulations of rotten leaves, wood and soil. The tegmen of *P. humilis* is evenly pyramid-

shaped and similar to that of *P. intermedia*, but broader basally. The apex of the membranous tegmen is not stable in shape and varies from pointed to truncate. The gonostyli differ in size and shape in a limited degree, and the apical tooth appears stronger, longer or more curved in some specimens. This is largely the result of different positions of these structures in the balsam mounts, but is probably also due in part to infraspecific variation.



**Fig. 3:** *Pseudoperomyia humilis* sp. n.; **A** and **C**: hypopygium, ventral view; **B** and **D**: tegmen and genital rod (**A** and **B** holotype, **C** and **D** paratype); **E**: flagellomere 4, mesal view (paratype); **F**: flagellomere 4, posterior view (paratype). Scale 0.1 mm.

***Pseudoperomyia parvolobata* sp. n.**  
(Figs. 4A-D)

**Material studied**

Holotype: male, West Malaysia, Selangor, Ulu Gombak, near University of Malaya Field Studies Centre, 250 m, primary forest, 02.-08.03.1997, by Malaise trap, H. HIPPA, M. JASCHHOF, B. VIKLUND. Paratypes: 1 male, same data as holotype.

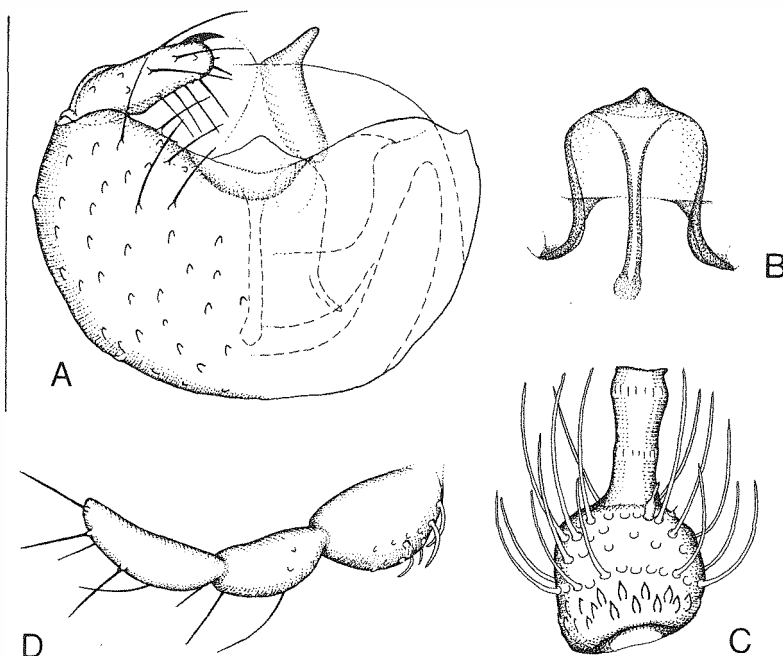


Fig. 4: *Pseudoperomyia parvolobata* sp. n.; A: hypopygium, ventral view (holotype); B: tegmen and genital rod (holotype); C: flagellomere 4, mesal view (paratype); D: palpus, lateral view (holotype). Scale 0.1 mm.

### Description

**Male.** Head: 3 ocelli. Eye bridge 3-4 facets wide. With 1 row of postocular bristles. Terminal flagellomere constricted and with small second node. Neck of flagellomere 4 little longer than node (Fig. 4C). Node with a double whorl of setae (or scales?, broken in both specimens) basally and with irregularly arranged sensory hairs of different lengths, the most proximal sensory hairs shortest and forming a rather distinct whorl; among the hair-like sensillae with a few sensory spines and 1 inconspicuous bottle-shaped sensilla distally (absent on distal 6-7 flagellomeres). 3<sup>rd</sup> palpal segment little longer than 2<sup>nd</sup> (Fig. 4D).

Thorax: arrangement of lateral scutal setae of the reduced type (see Fig. 2F).

Legs: claws of middle legs with 2 small teeth mesally. Empodium as long as claws.

Wing:  $R_1=1\frac{1}{2}rs$ ; *CuA*-fork rectangular.

Hypopygium: gonocoxites (Fig. 4A) covered with setae (and scales?) ventrally; united for almost its whole length medioventrally (resulting in a very shallow emargination). Gonostylus (Fig. 4A) with subbasal lobe dorsolaterally, near apex with a small lobe-like projection ventrally; with a slightly curved apical tooth shifted somewhat dorsad, and 2 inconspicuous subapical spines shorter than tooth. Tegmen (Fig. 4B) short and broad, parameral apodemes not reaching basal gonocoxal margin, nearly parallel-sided, with pointed apex forming a nose-shaped, dorsally-directed projection. Genital rod (Fig. 4B) weakly sclerotized, with a wide funnel-shaped invagination apically running into margin of tegmen. Tergite 9 with slightly and broadly rounded distal margin and 1 transverse row of setae. Tergite 10 distinct, bilobed, elongated with horn-like projections distally and some weak setae. Sternite 10 indistinct, bilobed, without setae.

Body length: 1.0 mm.

### Discussion

This is the only species of *Pseudoperomyia* with such distinct distal projections on tergite 10. The widely opened funnel-like genital rod is similar to that in *P. bidentata*, probably indicating a closer relationship between these two species than is shown by the cladogram. We did not use this character (shape of opening of genital rod) for the cladistic analysis as the definition of clear character states is not possible because of intermediate forms connecting the extremes.

### *Pseudoperomyia intermedia* sp. n.

(Figs. 5A-D)

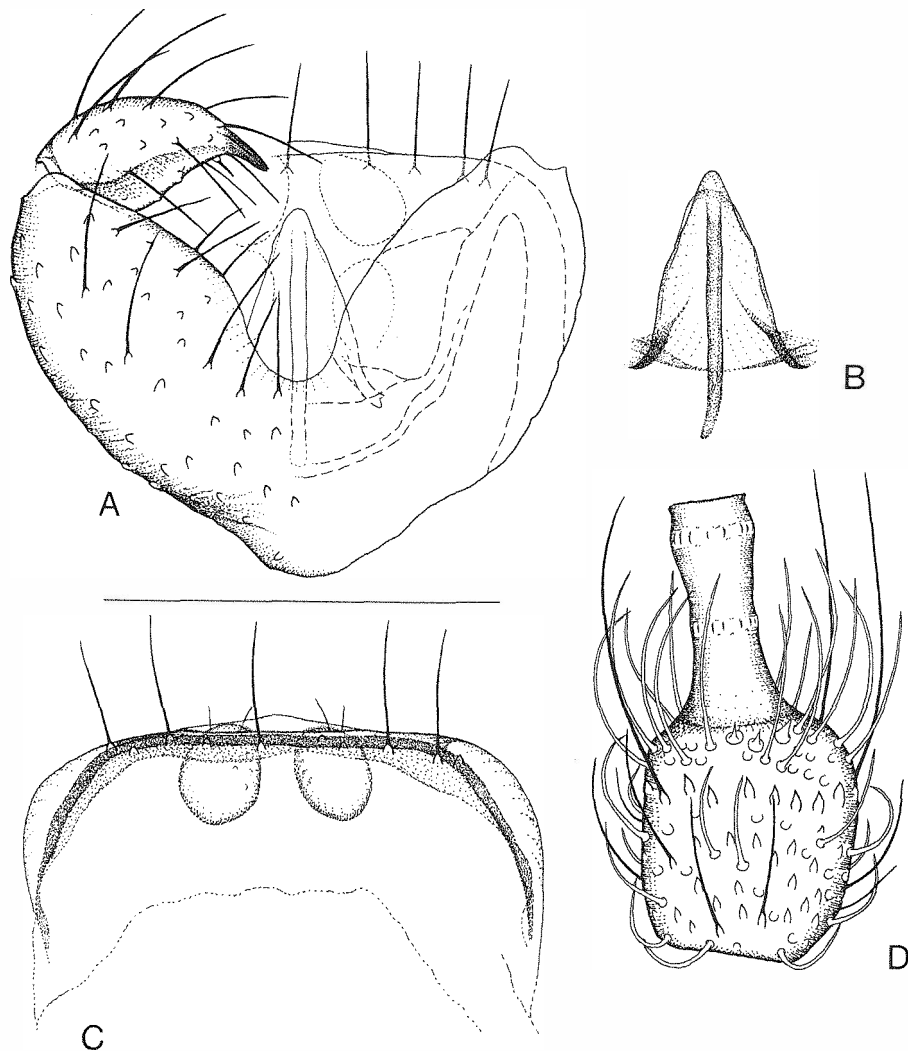


Fig. 5: *Pseudoperomyia intermedia* sp. n. (holotype); A: hypopygium, ventral view; B: tegmen and genital rod; C: tergites 9 and 10, dorsal view; D: flagellomere 4, lateral view. Scale 0.1 mm.



# Material studied

Holotype: male, West Malaysia, Selangor, Ulu Gombak, near University of Malaya Field Studies Centre, 250 m, primary forest, 25.02.-01.03.1997, by Malaise trap, H. HIPPA, M. JASCHHOF, B. VIKLUND.

# Description

**Male.** Head: 3 ocelli. Eye bridge 5-7 facets wide. With 2 rows of postocular bristles. Occiput mainly covered by setae and with only a few scales. Terminal flagellomere not constricted, apically pointed. Neck of flagellomere 4 (Fig. 5D) shorter than node. Node slightly longer than wide; with irregularly arranged short setae and short sensory hairs basally, with a double whorl of long setae beyond medial circumference, and distally with irregularly arranged sensory hairs longer than those basally; additionally with a few sensory spines and 1 inconspicuous small conical sensilla distally (absent on distal flagellomeres). 3<sup>rd</sup> palpal segment as long as 2<sup>nd</sup>.

Thorax: arrangement of lateral scutal setae of the extended type (see Fig. 8D).

Legs: claws of middle legs with 2-3 small teeth mesally. Empodium approximately as long as claws.

Wing:  $R_1=2-2\frac{1}{2}$   $rs$ ;  $r-m$  slightly longer than  $rs$ ;  $CuA$ -fork approximately rectangular.

Hypopygium: gonocoxites (Fig. 5A) covered ventrally with setae (and scales?, broken if present), distal margin with narrow and deep U-shaped emargination; basal margin projecting medially.

Gonostylus (Fig. 5A) compact, broadest in proximal third and tapering to tip; with strong apical tooth appearing to be two-pointed. Tegmen (Fig. 5B) narrow, pyramid-shaped; parameral apodemes not reaching basal gonocoxal margin. Genital rod (Fig. 5B) sclerotized, about as long as tegmen; without distinct apical modification. Tergite 9 (Fig. 5C) with straight distal margin with a row of setae; inner (anterior) margin strongly sclerotized; with indistinct, bare, stripe-like membrane beyond distal margin. Tergite 10 (Fig. 5C) distinct, bilobed, ovoid; with a few setae. Sternite 10 membranous, rather indistinct, bilobed, without setae.

Body length: 1.4 mm.

# Discussion

*P. intermedia* is characterized by the combination of a compact gonostylus with strong apical tooth, a narrow pyramid-shaped tegmen and a rather broad and long genital rod. It has the widest eye-bridge of all congeners. Since only the type-specimen is known, it is not possible to decide if the projecting basal gonocoxal margin is a stable character (or an artefact).

## *Pseudoperomyia longicornis* sp. n.

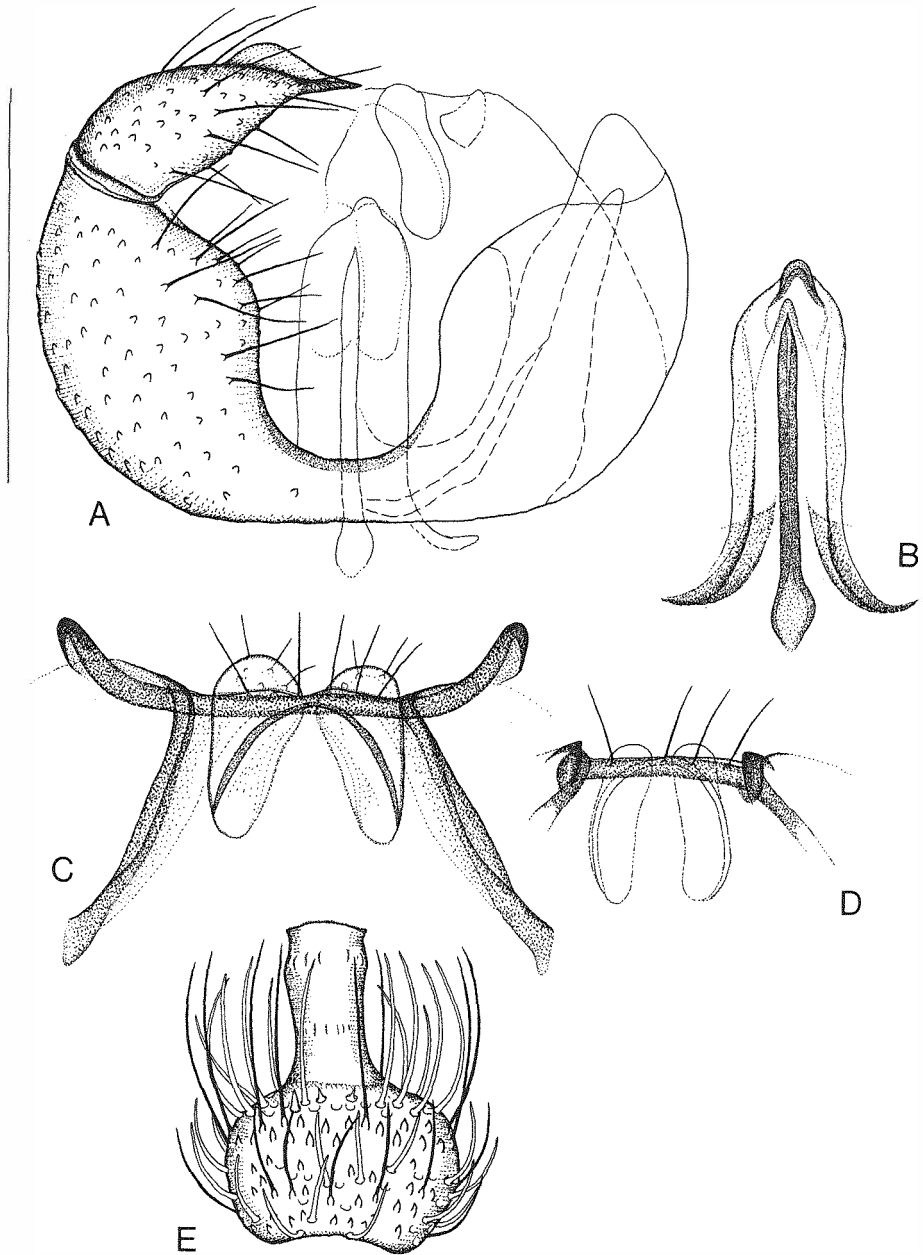
(Figs. 6A-E)

# Material studied

Holotype: male, West Malaysia, Selangor, Ulu Gombak, near University of Malaya Field Studies Centre, 250 m, primary forest, 25.02.-01.03.1997, by Malaise trap, H. HIPPA, M. JASCHHOF, B. VIKLUND. Paratypes: 1 male, same data as holotype, but 24.02.-14.03.1997; 5 males, same data, but, 08.-21.03.1997; 1 male, same locality, but 26.02.1997, by sweepnet, M. JASCHHOF; 1 male, West Malaysia, Kelantan, Gua Musang, <200 m, 12.-14.11.1992, by Malaise trap, T. PAPE.

# Description

**Male.** Head: 3 ocelli. Eye bridge 2-3 facets wide. With 2 rows of postocular bristles. Terminal flagellomere not constricted. Neck of flagellomere 4 as long as node, and node as long as wide (Fig. 6E illustrating flagellomere 1). Node with irregularly arranged short setae and short sensory hairs basally, with a double whorl of long setae distad of medial circumference, and distally with irregularly arranged sensory hairs longer than those basally; furthermore with a few sensory spines and 1 inconspicuous small conical sensilla distally (sometimes lacking). 3<sup>rd</sup> palpal segment longer than segment 2; 2<sup>nd</sup> segment with a few sensory hairs basally.



**Fig. 6:** *Pseudoperomyia longicornis* sp. n.; **A:** hypopygium, ventral view (holotype); **B:** tegmen and genital rod (holotype); **C:** tergites 9 and 10, dorsal view, slightly compressed (paratype from Gua Musang); **D:** same structures, in natural position (holotype); **E:** flagellomere 1, anterior view (paratype from Gua Musang). Scale 0.1 mm.

Thorax: arrangement of lateral scutal setae of the extended type (see Fig. 8D)

Legs: claws of middle legs with 3 small teeth mesally. Empodium  $\frac{3}{4}$  length of claws.

Wing:  $R_1=1\frac{1}{2} rs$ ;  $CuA$ -fork rectangular.

Hypopygium: gonocoxites (Fig. 6A) covered with setae and scales ventrally, distal margin with a deep U-shaped emargination, its inner margin slightly sclerotized. Gonostylus (Fig. 6A) flattened (when in lateral view); widest in proximal third and tapering to tip; in distal third with rather large tooth-like plate inserted dorsally and reaching apex of gonostylus. Tegmen (Fig. 6B) nearly parallel-sided, with rounded and hardly visible distal margin; at apex with nose-like projection directed dorsad; parameral apodemes running beyond basal gonocoxal margin. Genital rod (Fig. 6B) sclerotized, rather broad and with membranous cap apically, sometimes with an irregularly-shaped enlargement basally. Tergite 9 (Figs. 6C, D) with a straight and narrowed distal margin, with a row of setae and 2 long horn-like projections disto-laterally united by a sclerotized bridge (horns directed ventrad in natural conditions [Fig. D] and more laterad when the tergite is under pressure of the glass cover-slip [Fig. C]); inner (anterior) margin strongly sclerotized. Tergite 10 (Fig. 6C) very distinct, elongated, bilobed and both lobes connected by a horseshoe-shaped sclerotization dorsally; with a few short setae distally. Sternite 10 membranous, rather indistinct, bilobed, without setae.

Body length: 1.2 mm.

#### Discussion

The species is easily distinguished from its congeners by the very long distolateral horns of tergite 9, but these are not at all clearly visible in some positions. Further specific characters are the large and distinct lobes of tergite 10 running beyond the distal margin of tergite 10 and united by a strong sclerotized arc, and the broad, plate-like apical tooth of the gonostylus. *P. longicornis* appears to be the sister species of *P. platistyla*, mainly because they share the inner sclerotization of the gonocoxal emargination. But the structure of gonostylus, tegmen, genital rod and tergite 9 of both species differ greatly (see Figs. 6A and 8A, 6B and 8B, 6C and 8B).

#### *Pseudoperomyia macrostyla* sp. n.

(Figs. 7A-F)

#### Material studied

Holotype: male, West Malaysia, Selangor, Ulu Gombak, near University of Malaya Field Studies Centre, 250 m, primary forest, 25.02.-01.03.1997, by Malaise trap, H. HIPPA, M. JASCHHOF, B. VIKLUND. Paratypes: 1 male, same data as holotype, but 24.02.-14.03.1997; 10 males, same data, but 02.-08.03.1997.

#### Description

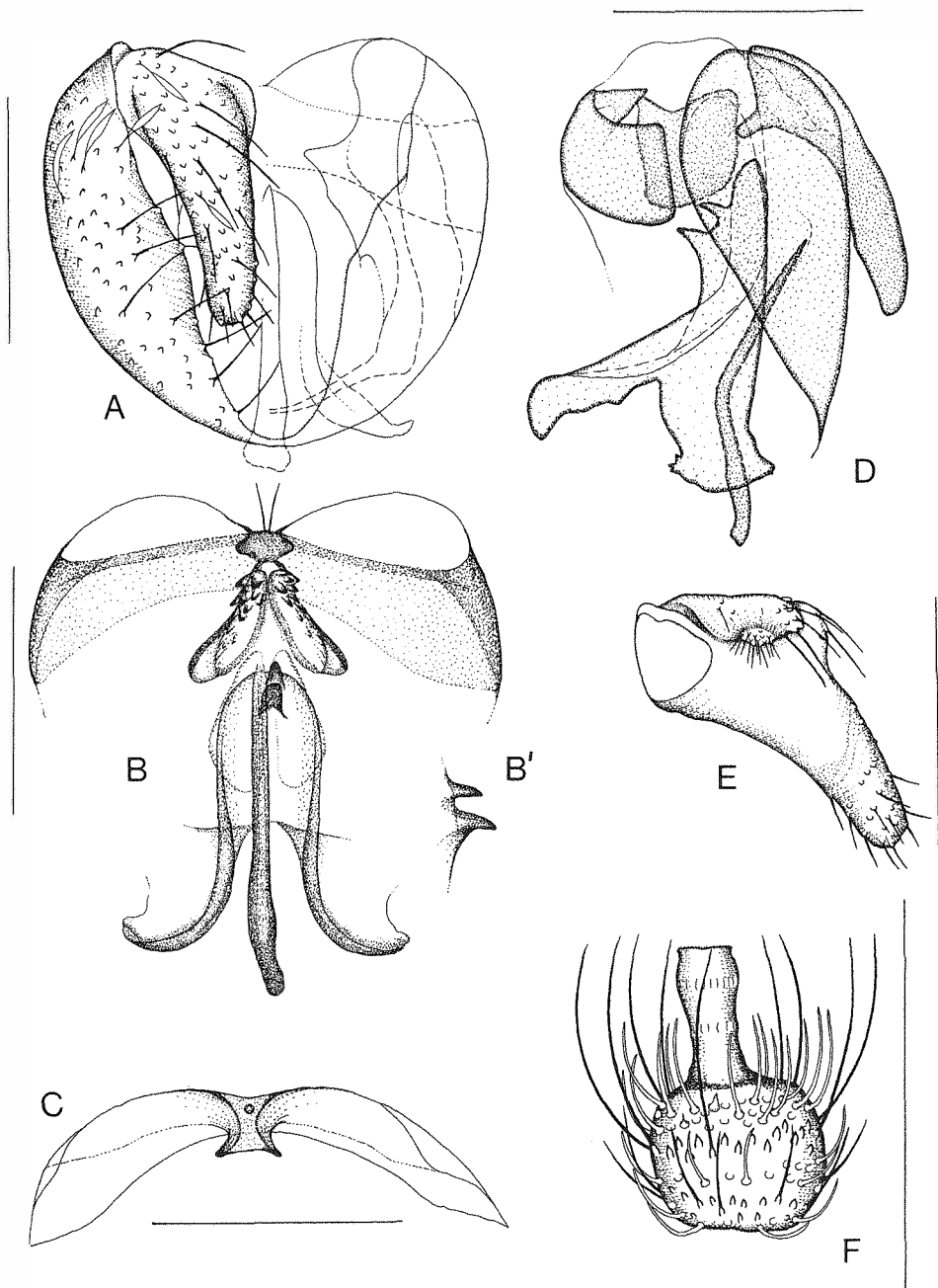
**Male.** Head: 3 ocelli. Eye bridge 2-3 facets wide. With 2 rows of postocular bristles. Terminal flagellomere egg-shaped, not constricted. Neck of flagellomere 4 little shorter than node (Fig. 7F). Node with irregularly-arranged short setae and short sensory hairs basally, with a double whorl of long setae medially, and distally with irregularly arranged sensory hairs little longer than those basally; additionally with a few sensory spines and 1 inconspicuous small conical sensilla distally (sometimes absent). 3<sup>rd</sup> palpal segment slightly to obviously longer than segment 2; 2<sup>nd</sup> segment with a few sensory hairs basally.

Thorax: arrangement of lateral scutal setae of the extended type (see Fig. 8D).

Legs: claws of middle legs with 3-4 small teeth mesally. Empodium  $\frac{3}{4}$  length of claws.

Wing:  $R_1=1\frac{1}{2}$ -2  $rs$ ;  $CuA_2$  exceptionally reaching wing margin;  $CuA$ -fork rectangular.

Abdomen: tergites 6-8 with strongly sclerotized anterior margin.



**Fig. 7:** *Pseudoperomyia macrostyla* sp. n.; **A:** hypopygium, ventral view (holotype); **B:** tegmen, genital rod, tergite 9 and 10, ventral view (paratype); **B':** nose-shaped projections of tegmen, lateral view (paratype); **C:** tergite 9 from above (paratype); **D:** hypopygium, lateral view (paratype); **E:** gonostylus, mesal view (paratype); **F:** flagellomere 4, lateral view (paratype). Scale 0.1 mm.

Hypopygium: much extended in 3<sup>rd</sup> dimension (Fig. 7D); gonocoxites (Fig. 7A) narrow, covered with setae and scales ventrally and almost completely divided basoventrally; inner bridge of gonocoxites prolonged inwards forming a pointed lobe with setae; dorsal gonocoxal link with a complicated looped structure. Gonostylus (Figs. 7A, E) very long and flattened, with its apex directed proximad; with small subbasal lobe dorsolaterally and an additional lobe directed inwards, latter with a group of spine-like setae; gonostylus bare inside, but exceptionally the distal fourth covered with short spine-like setae. Tegmen (Fig. 7B) almost parallel-sided, with hardly visible membranous distal margin; with 2 nose-like subapical projections directed dorsad, the distal a little smaller than the proximal (clearly visible only in lateral view, Fig. 7B'); parameral apodemes running up to basal gonocoxal margin. Genital rod (Fig. 7B) sclerotized, rather broad and reaching tip of tegmen; with membranous cap apically. Tergite 9 (Fig. 7B) strongly modified: distal margin strongly narrowed, with 2 large distolateral membranous lobes connected to distal gonocoxal margins; without setae, but exceptionally 2 weak median setae arising from a common insertion which is situated on a sclerotized lobe prolonged inwards (clearly visible only from above, Fig. 7C). Tergite 10 (Fig. 7B) very distinct (in lateral view appearing as a large sclerotized plate, Fig. 7D) and elongated, bilobed, surface with a pine-cone-like structure distally and without setae. Sternite 10 membranous, rather indistinct, bilobed, without setae.

Body length: 1.2-1.3 mm.

#### Discussion

The hypopygium of *P. macrostyla* is very remarkable because of the unusual modifications of the gonocoxites (Fig. 7A), gonostyli (Figs. 7A, E), tegmen (Figs. 7B, B'), and tergites 9 and 10 (Figs. 7B, C). No other species resembles this. In particular, the structure and shape of the gonostyli is completely different from all its congeners, what makes it difficult to understand the homologies.

#### *Pseudoperomyia platistyla* sp. n.

(Figs. 8A-D)

#### Material studied

Holotype: male, West Malaysia, Selangor, Gunung Ulu Kali, 1750 m, 03.-12.03.1997, by Malaise trap, H. HIPPA, M. JASCHHOF, B. VIKLUND. Paratypes: 2 males, same data as holotype, but 03.-22.03.1997.

#### Description

**Male.** Head: 3 ocelli. Eye bridge 2-3 facets wide. With 2 rows of postocular bristles. Terminal flagellomere not constricted, ovoid and with short apical neck. Neck of flagellomere 4 (Fig. 8C) as long as node. Node with irregularly arranged setae (or scales?, broken) and short and weak sensory hairs in basal half, with a double whorl of stronger setae (or scales?) in distal half, and distally with irregularly arranged sensory hairs a little longer than those basally; additionally with a few sensory spines and 1 inconspicuous small conical sensilla distally (absent on distal flagellomeres beginning with 5<sup>th</sup>). Terminal palpal segment longer than segment 2; 2<sup>nd</sup> segment with a few sensory hairs basally.

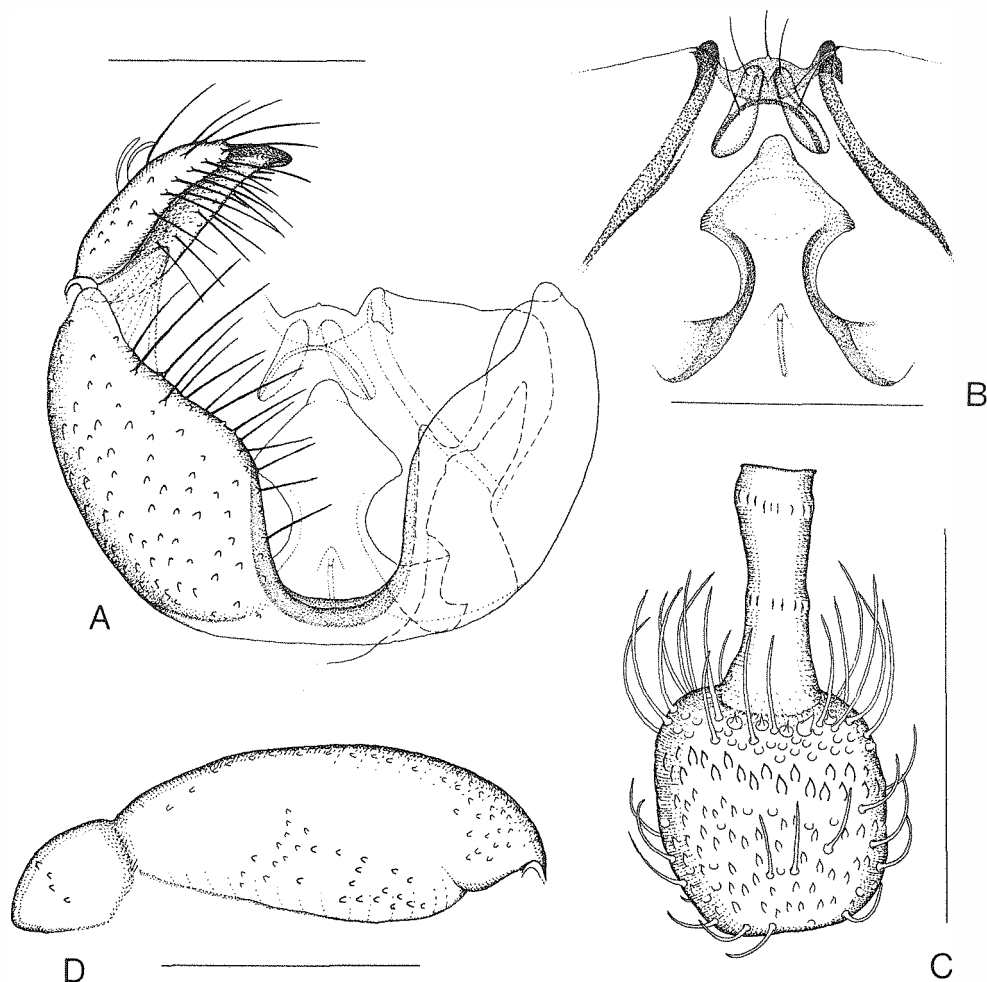
Thorax: arrangement of lateral scutal setae of the extended type (Fig. 8D).

Legs: claws of middle legs with 3 small teeth mesally. Empodium approximately as long as claws.

Wing:  $R_1=2\text{ rs}$ ;  $CuA$ -fork rectangular.

Hypopygium: gonocoxites (Fig. 8A) covered with setae and (probably) scales ventrally, with stronger and longer setae along distal margin; distal margin with a very deep U-shaped emargination (basomedial link narrow), its inner margin distinctly sclerotized; dorsal gonocoxal link looped in a complicated manner. Gonostylus (Fig. 8A) strongly flattened and broad (appears narrow and

slender in lateral view); densely covered with setae outside and inside and with scales in proximal half; apically with flattened tooth-like structure inserted rather dorsally, with 2 short spines inside subapically.



**Fig. 8:** *Pseudoperomyia platystyla* sp. n. (holotype); **A:** hypopygium, ventral view; **B:** tegmen, genital rod, tergites 9 and 10, ventral view; **C:** flagellomere 4, mesal view; **D:** mesonotum, lateral view. Scale of A-C 0.1 mm, of D 0.2 mm.

Tegmen (Fig. 8B) with characteristic shape: parameral apodemes directed outwards and reaching basal gonocoxal margin, followed distally by a waist-like medial constriction, distal half with triangular enlargement with rounded apex, latter appearing as an indistinct nose-like projection directed dorsad. Genital rod (Fig. 8B) membranous and very short, reaching 1/3 of tegmen length, with membranous cap. Setae of tergite 9 (Fig. 8B) few in number (up to 3?) and reduced in extension to a small central area, on both sides of that area 1 very short sclerotized horn-like projection directed ventrad; inner (anterior) margin of tergite 9 strongly sclerotized; 2 large disto-

lateral membraneous lobes linked with the distal gonocoxal margins. Tergite 10 (Fig. 8B) distinct, elongated, bilobed and both lobes connected by horseshoe-shaped sclerotization dorsally; with a few rather long setae distally. Sternite 10 not visible. Body length: 1.3 mm.

#### Discussion

*P. platistyla* is easily distinguished from its congeners by the constricted shape of tegmen, the strongly flattened gonostyli and the extremely short genital rod.

### 2.3 Phylogeny of *Pseudoperomyia* and the Micromyi

There is no doubt that the species of *Pseudoperomyia* are correctly placed within the supertribe Micromyi. The Micromyi are a monophylum well supported by a number of synapomorphies such as the forked *CuA*, the reduction of *CuP* and *A*, the reduction of ventral macrotrichia on *R*<sub>2</sub>, the presence of scales, the number of male flagellomeres reduced to 12, and the usually close connection of the lobes of tergite 10 with tergite 9 (KLEESATTEL, 1979; JASCHHOF, 1998).

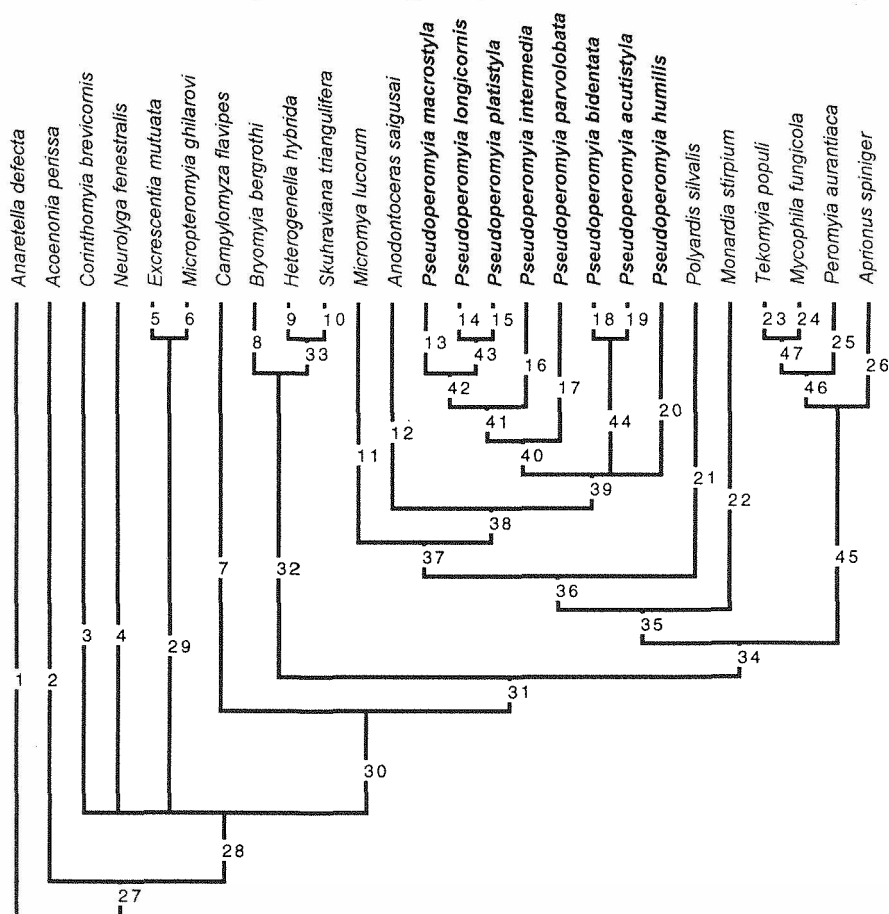


Fig. 9: Phylogeny of the Micromyi: interrelationship of the genera and *Pseudoperomyia* species. A strict consensus tree of 4 equally parsimonious trees (length 150 steps; CI 0.45; RI 0.66). Branch numbers refer to Appendix 3.



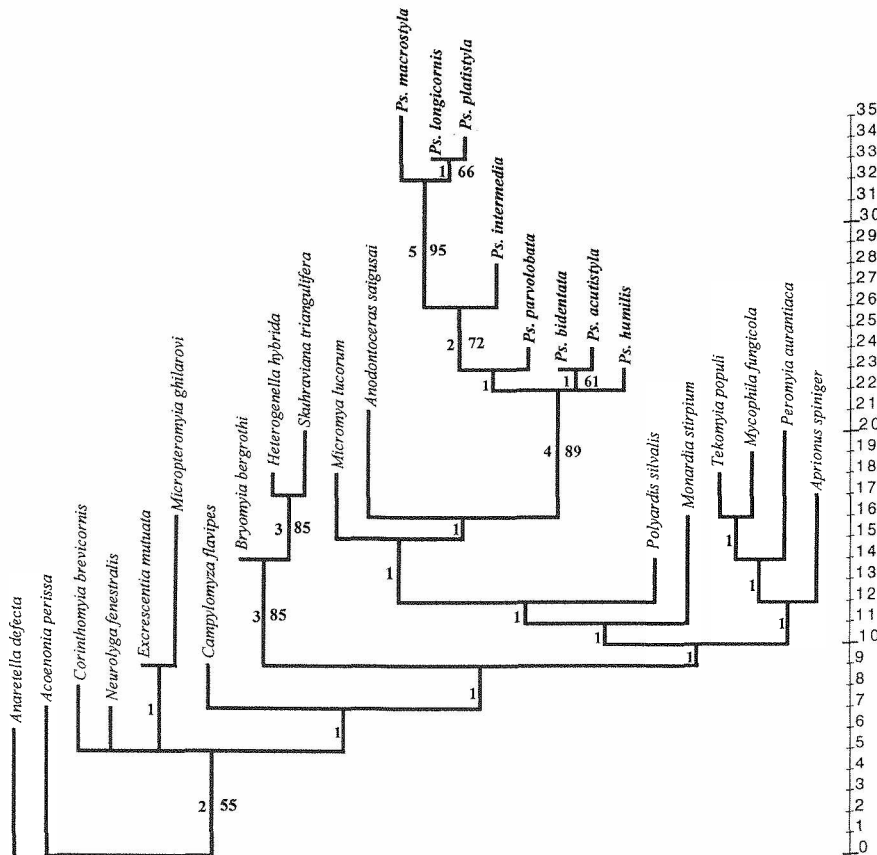


Fig. 10: Phylogeny of the Micromyiidae; cladogram as in Fig. 9 with branch length proportional to the number of characters that change unambiguously on branch (see scale); decay index on the left side and bootstrap proportion on the right side of each branch. Note that the number of changes involving the terminal taxa is not comparable with that elsewhere, since their autapomorphies were excluded from the analysis.

In addition, all micromyiids have a pattern of sensory pores on the wing veins which differs from group to group but which is stable within each species and within each group of related species. *Pseudoperomyia* shares all these derived characters, which contrast with the plesiomorphous conditions of the outgroup.

Questions concerning the monophyly and sister group of *Pseudoperomyia* were incorporated into a test of the recently-proposed hypothesis on the phylogeny of the supertribe Micromyiidae (JASCHHOFF, 1998).

For the parsimony analysis, we considered a total of 47 adult male characters (Append. 1) for all the known *Pseudoperomyia* species and for the type species of each genus of the Micromyiidae (Tab. 1). *Peromyia levellei* (type species of *Peromyia*) was replaced by *Peromyia aurantiaca* (type species of the synonym *Joannisia*), since the former is too incompletely known so far as the

morphological details needed for the analysis are concerned. *Anaretella defecta* was selected as the outgroup. It represents the tribe Lestremiini and has mainly plesiomorphous characters within the Cecidomyiidae (KLEESATTEL, 1979; JASCHHOF, 1998).

The characters used for the computer analysis were for the most part those traditionally used for taxonomic studies within the Lestremiinae. We redefined some of them to get clear character states (see character no. 28 or 43), and we added a few characters by considering homologous structural details of the same body part independently (see, for example, 10 and 11 or 12 and 14). The obvious lack of a good number of comparable characters with precisely defined character states does not permit well-supported monophyletic groups and sister group relationships, i. e. a more stable cladogram. Adding only one additional character with obviously incorrectly evaluated states into the matrix resulted in the replacement of many dichotomies by polytomies in such a poorly supported tree. Basic comparative studies to identify homologous structures are needed in order to achieve a substantial improvement in evaluating characters such as, for example, the large number of different types of flagellomeral sensillae or the confusing structural diversity of gonostylus and tegmen. So far as these characters are concerned (no. 13, 31-35 and 36-38), we were unable to find a more objective system of structural types on the basis of the information available, based on real homologies rather than on independent superficial similarities. Without any doubt there is still a large amount of information left in these structures, as is probably the case with other character complexes that have been entirely overlooked so far.

Tab. 1: Ingroup taxa included in the cladistic analysis of Micromyidi.

Acoenoniini	<i>Monardia stirpium</i> KIEFFER, 1895
<i>Acoenonia perissa</i> PRITCHARD, 1947	<i>Polyardis silvalis</i> (RONDANI, 1840)
Campylomyzini	<i>Pseudoperomyia acutistyla</i> sp. n.
<i>Campylomyza flavipes</i> MEIGEN, 1818	<i>Pseudoperomyia bidentata</i> sp. n.
<i>Corinthomyia brevicornis</i> (FELT, 1907)	<i>Pseudoperomyia humilis</i> sp. n.
<i>Excrescentia mutuata</i> MAMAEV & BEREST, 1991	<i>Pseudoperomyia intermedia</i> sp. n.
<i>Micropteromyia ghilarovi</i> MAMAEV, 1960	<i>Pseudoperomyia longicornis</i> sp. n.
<i>Neurolyga fenestralis</i> RONDANI, 1840	<i>Pseudoperomyia macrostyla</i> sp. n.
Bryomyiini	<i>Pseudoperomyia parvolobata</i> sp. n.
<i>Bryomyia bergrothi</i> KIEFFER, 1895	<i>Pseudoperomyia platistyla</i> sp. n.
<i>Heterogenella hybrida</i> MAMAEV, 1963	Aprionini
<i>Skuhraviana triangulifera</i> MAMAEV, 1963	<i>Aprionus spiniger</i> (KIEFFER, 1894)
Micromyini	<i>Mycophila fungicola</i> FELT, 1911
<i>Anodontoceras saigusai</i> YUKAWA, 1967	<i>Tekomyia populi</i> MÖHN, 1960
<i>Micromyia lucorum</i> RONDANI, 1840	Peromyiini
	<i>Peromyia aurantiaca</i> (KIEFFER, 1894)

A heuristic search by PAUP (random addition sequence with 1000 replicates, TBR, COLLAPSE and MULPARS options in effect, steepest descent option not in effect, all characters unweighted) resulted in the same 4 minimum length trees when all the characters were unordered (150 steps, CI 0.45, RI 0.66) and when the multiple state characters (7, 8, 9, 14, 19, 20, 32, and 43) were ordered (156 steps, CI 0.44, RI 0.69). In all the trees (strict consensus tree Figs. 9 and 10), the species of *Pseudoperomyia* appear as a well supported monophyletic group (bootstrap proportion in 1000 replicates 89, decay index 4). The internal phylogeny of *Pseudoperomyia* is only partly resolved, as there is a basal trichotomy. Only two of the internal clades (41 and 42) have both the bootstrap proportion over 50 and decay indices more than 1.

*Pseudoperomyia* appears in all 4 trees as the sister-group of *Anodontoceras* within the tribe Micromyini (sensu JASCHHOF, 1998). The sister-group relationship is rather poorly supported (bootstrap proportion < 50, decay index 1), as is the case with most of the interrelationships of supraspecific taxa within the Micromyidi.

Within the Micromyini both *Anodontoceras* and *Pseudoperomyia* share the globular / subglobular type of flagellomeral node as a synapomorphous character, which also occurs through convergence in *Skuhraviana* (tribe Bryomyiini) and in *Peromyia* (tribe Peromyiini).

Without discussing all the results in detail, it is apparent that the result of the present parsimony analysis is in rather good agreement with the relevant part of a recent hand-made cladogram for the entire Lestremiinae (JASCHHOF, 1998). The main differences between the two analyses involve the position of *Campylomyza*, previously referred to a group of genera including *Neurolyga*, *Micropteromyia* and *Excescentia* (together forming the tribe Campylomyzini), and the position of *Aprionus*, previously assigned to the Aprionini together with *Tekomyia* and *Mycophila*. *Peromyia* (the only genus of the Peromyiini) was previously considered to be the sister-group of the Bryomyiini + (Micromyini + Aprionini).

### Acknowledgements

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**Appendix 1:** Characters and character states used in the phylogenetic analysis

1. Number of palpal segments: 4 (0); 3 (1).
2. Shape of 1<sup>st</sup> palpal segment: normal (0); tumid (1). Normal and tumid are relative terms; tumid in this context means disproportionately swollen compared with the distal segments. There are intermediate expressions, but not among the species included in this analysis.
3. Tip of terminal palpal segment: rounded (0); pointed (1).
4. Clypeus: small (0); large (1). Small in this context means that a distinct prefrons is visible; a large clypeus also occupies the prefrons-area. Intermediate conditions do not exist.
5. Postfrons: setose or with scales (0); non-setose (1)
6. Number of ocelli: 3 (0); 2 (1); absent (2)
7. Eye bridge laterally: normal (0); without facets or facets very few in number and widely separated (1). Normal means that there is a minimum of 1 row of facets arranged as densely as in the ventral part of the compound eyes.
8. Postocular bristles: absent (0); poorly developed (1); strongly developed in 1 row (2); strongly developed in 2 rows (3). Poorly developed means that the row consists of only 3-5 bristles that are not much stronger than the strongest postcranial setae. In some cases of 1 row, there are 2-4 weaker postocular bristles forming the elements of a 2<sup>nd</sup> row, but we count as a 2<sup>nd</sup> row only those cases where the posterior row reaches at least 2/3 the length of the anterior row.
9. Number of male flagellomeres: >12 (0); 12 (1); <12 (2). In general, males belonging to species of the Micromyidi have 12 flagellomeres, whilst those belonging to more primitive groups (including the outgroup chosen for the analysis) have 14. But exceptions exist even within the Micromyidi, when the number of flagellomeres is increased to more than 12 or reduced to less than 12.
10. Male flagellomeral neck: posteriorly placed (0); intermediate (1); at the centre of node (2).
11. Male flagellomeral node: barrel-shaped, longer than wide (0); globular / subglobular, about as long as wide (1). When the node is about as long as wide it is often difficult to make a clear decision about its shape, since intermediate cases occur even within closely related groups. We propose only one alternative state (globular / subglobular) to the normal (barrel-shaped) expression.
12. Arrangement of setae on male flagellomeral node basally: whorl-like (0); irregular and mixed with sensory hairs. See, for example, Figs. 1D (state 0) and 5D (state 1).
13. Subapical sensillae on male flagellomeral node: simply hair-like (0); branched hair-like (1); bottle-shaped (2); conical (3); flattened, arising from single round pore (4); flattened, arising from 2 or more round pores or a single elongated pore (5). Much more information is needed about the homology of the different types of flagellomeral sensillae. There are some indications that outer appearances alone do not reflect real structural types (= character states). But this character is undoubtedly too significant for classification for it to be totally ignored.
14. Crenulate whorls on male flagellomeral nodes: present (0); vestiges present (1); absent (2). Vestiges means: only 1 of the whorls of setae or a part of it indistinctly shows the crenulate expression. In these cases the relevant setae appear much like sensory hairs.
15. Empodium: well developed, about as long as or longer than claws (0); reduced to a hair-brush (1). We consider all expressions to belong to the well developed type when the hairs do not form just a short brush but are inserted on an elongated stem.
16. Claws: evenly curved or rectangular, both angles of approximately same length (0); distal angle distinctly longer than proximal (1).
17. Scales: absent (0); present (1). This character involves all body parts, but is most obvious on the legs, especially the tarsomeres.
18. Dorsal macrotrichia on  $R_5$ : present (0); absent (1).
19. Number of sensory pores on  $R_1$ : >3 (0); 3 (1); 2 (2).
20. Number of sensory pores on  $R_5$ : >3 (0); 3 (1); 2 (2); 1 (3); absent (4).
21. Length of strong anterior part of C: ending near the point where C meets  $R_5$  (0); extending beyond that point more than 4 times the vein width (1).

22. Length of  $R_7$ : longer than 4  $rs$  (0); shorter than 4  $rs$  (1).
23. Length of  $R_5$ : ending distinctly before apex (0); running to apex (1).
24. Angle between  $CuA_1$  and  $CuA_2$ : acute (0); 85-90° (1).
25. Length of  $r-m$ : longer than  $rs$  (0); about as long as  $rs$  (1). About as long as  $rs$  means:  $r-m$  less than 1 1/2 times as long as  $rs$ .
26. Anterior margin of posterior abdominal tergites (tergites 5 or 6 to 8): membranous (0); with arc-shaped sclerotized stripe (1).
27. Pleural membrane of abdomen: non-setose (0); setose or with scales (1).
28. Distal margin of gonocoxites ventrally: with V-shaped deep emargination, basal connection narrow and membranous (0); with shallow U-shaped emargination, connection broad (1); with deep U-shaped emargination reaching 2/3 of gonocoxite length, connection narrow (2); gonocoxites without basal connection (3). We are not sure whether the observed structural differences are primary or are dependent upon the internal architecture of the gonocoxites.
29. Sclerotization of gonocoxal emargination: absent (0); present (1).
30. Dorsal transverse bridge of gonocoxites: with apodemes prolonged anteriorly (0); without prolonged apodemes (1).
31. Connection between gonocoxites and gonostyli: membranous, unmodified (0); linked by a sclerotized joint (1).
32. Tip of gonostylus: without modification (0); with modified setae or a group of spines (1); with tooth or tooth-like modification (2). We consider the diversity of tooth-like apical structures of the gonostylus to be homologous. There are also indications that densely arranged spines have the same origin, but more comparative studies are needed to arrive at a better understanding of the structure and architecture of the gonostylus. This latter conclusion applies to characters 33 to 35 as well.
33. Subapical part of gonostylus: without spines (0); with spines (1).
34. Base of gonostylus: unmodified (0); with a subbasal lobe dorsolaterally (1).
35. Gonostylus: compact (0); flattened (1). We considered a gonostylus to be flattened when the flattening influences the entire shape, so that the gonostylus appears much broader / longer than thick. When flattening involves only a part of the gonostylus, or when there is only an excavation inside, we refer it to the compact type.
36. Length of tegmen: short, parameral apodemes not reaching basal gonocoxal margin (0); long, parameral apodemes extending to or beyond basal gonocoxal margin (1).
37. Distodorsal nose-like projection(s) of tegmen: absent (0); present, directed ventrad or apicad (1); present, directed dorsad (2).
38. Tegmen with teeth-bearing lobes distolaterally: absent (0); present (1).
39. Genital rod: present (0); absent (1).
40. Length of genital rod: as long as tegmen or longer (0); distinctly shorter than tegmen (1).
41. Genital rod with double stripe-like modification distally: absent (0); present (1).
42. Aedeagal teeth: present (0); absent (1). The expression of aedeagal teeth ranges from minute microtrichia-like to tooth-like. Further studies are needed to avoid misinterpretations on the homology of the apical structures of the aedeagus / genital rod complex.
43. Shape of tergite 9: plate-like (0); stripe-like, as wide as gonocoxites distally (1); stripe-like, distinctly narrower than distal margin of gonocoxites (2).
44. Sclerotized projections of tergite 9: absent (0); present (1).
45. Tergite 10: free (0); fused with tergite 9 (1).
46. Sclerotized arc of tergite 10 dorsally: absent (0); present (1).
47. Spine-like hairs on sternite 10: absent (0); present (1).

**Appendix 2:** Observed character states. Explanation of symbols: 0-5 = monomorphic states; / = polymorphism; ? = character state unknown. For characters and character states, see Appendix 1.

Character	1	6	11	16	21	26	31	36	41	46
Taxon										
<i>Anaret. defecta</i>	0000 0	10000	0000 0	00 0 20	000?1	00000	02100	0?000	01000	00
<i>Acoen. perissa</i>	1000 1	01010	0001 1	00 0 22	1100?	01101	12000	0?000	00000	00
<i>Corinth. brevic.</i>	0000 1	00110	0000 0	00 0 11	10110	10100	00001	00000	00001	00
<i>Neur. fenestr.</i>	0100 1	01010	0000 0	00 0 11	10100	10100	00100	0?100	00001	00
<i>Excr. mutuata</i>	0000 1	00110	0050 1	00 0 11	1110?	?0100	00100	0?100	01001	00
<i>Micr. ghilarovi</i>	1110 1	01022	1052 1	00 0 11	11101	?0100	00100	0?100	01001	00
<i>Camp. flavipes</i>	0000 1	01110	0050 0	01 0 11	11100	10101	00100	0?000	00101	00
<i>Bryom. bergr.</i>	0001 0	00210	00000/1	01 0 12	11100	10101	10001	0?001	11001	00
<i>Heter. hybrida</i>	1011 1	00210	0010 0	01 0 12	11100	?0101	10001	0?001	11001	01
<i>Skuhr. triang.</i>	0011 1	00212	1012 0	010/112	11100	?0101	10001	0?001	11001	01
<i>Micr. lucorum</i>	1011 0	0022?	0052 0	01 0 13	11111	?1001	02100	00001	01001	00
<i>Pol. silvalis</i>	1011 0	00200	0000 0	01 0 13	11100	01001	02100	00000	01001	00
<i>Mon. stirpium</i>	1101 0	00110	0040 1	00 0 13	1110?	11001	02100	00000	01001	00
<i>Anod. saigusai</i>	1011 0	00310	1?02 0	01 0 13	11111	10301	01000	10000	01001	00
<i>Tek. populi</i>	1011 0	00220	0040 1	11 1 13	1110?	?0201	02?00	0001?	01101	00
<i>Myc. fungicola</i>	10110/1	00220	0040 0	01 1 24	1110?	10001	02?00	0001?	01101	00
<i>Apr. spiniger</i>	0001 0	00210	0000 1	11 1 13	11100	10211	02101	1?01?	01001	00
<i>Per. aurantiaca</i>	1011 1	00212	1002 0	01 1 13	01100	10201	01000	0?01?	01101	00
<i>Ps. macrostyla</i>	1011 1	00311	1132 0	01 1 14	11111	11201	01011	12000	01211	10
<i>Ps. longicornis</i>	1011 1	00311	1132 0	01 1 14	11111	11211	02?01	12000	01211	10
<i>Ps. platistyla</i>	1011 1	00311	1132 0	01 1 14	11111	11211	02101	12001	01211	10
<i>Ps. intermedia</i>	1011 1	00311	1132 0	01 1 14	11110	11101	02100	01000	01101	00
<i>Ps. bidentata</i>	1011 1	20211	1022 0	01 1 14	11111	11101	02100	00000	01101	00
<i>Ps. acutistyla</i>	1011 1	202?1	1022 0	01 1 14	11111	11101	02100	01000	01101	00
<i>Ps. humilis</i>	1011 1	00211	1021 0	01 1 14	11111	11101	02100	00000	01101	00
<i>Ps. parvolobata</i>	1011 1	00211	1022 0	01 1 14	11111	11101	02110	02000	01101	00

**Appendix 3:** Unambiguous character changes on the different branches. Branch number followed by character change. Same symbols as in Appendix 2.

- 1: 5(1→0); 6(0→1); 9(1→0); 21(1→0); 28(1→0); 42(→1).
- 2: 1(0→1); 14(0→1); 15(0→1); 27(0→1); 30(0→1); 31(0→1); 33(1→0).
- 3: 24(0→1); 33(1→0); 35(0→1).
- 4: 2(0→1); 38(0→1).
- 5: no unambiguous changes.
- 6: 1(0→1); 2(0→1); 3(0→1); 9(1→2); 10(0→2); 11(0→1); 14(0→2).
- 7: 13(0→5); 43(0→1).
- 8: no unambiguous changes.
- 9: 1(0→1).
- 10: 10(0→2); 11(0→1); 14(0→2).
- 11: 9(1→2); 13(0→5); 40(0→1).
- 12: 8(2→3); 27(1→0); 32(2→1); 33(1→0); 36(0→1).
- 13: 32(2→1); 33(1→0); 34(0→1).
- 14: no unambiguous changes.
- 15: 40(0→1).
- 16: 25(1→0); 37(2→1).
- 17: 34(0→1).

- 18: no unambiguous changes.  
 19: 37(0→1).  
 20: 14(2→1).  
 21: 9(1→0); 26(1→0).  
 22: 2(0→1); 8(2→1); 13(0→4); 15(0→1); 17(1→0).  
 23: 15(0→1); 16(0→1).  
 24: 19(1→2); 20(3→4); 28(2→0).  
 25: 5(0→1); 10(0→2); 11(0→1); 14(0→2); 21(1→0); 32(2→1).  
 26: 15(0→1); 16(0→1); 29(0→1); 35(0→1); 36(0→1).  
 27: no unambiguous changes.  
 28: 19(2→1); 23(0→1); 26(0→1); 32(2→0); 45(0→1).  
 29: 13(0→5); 15(0→1); 38(0→1); 42(0→1).  
 30: 17(0→1); 30(0→1).  
 31: 4(0→1); 42(0→1).  
 32: 31(0→1); 33(1→0); 35(0→1); 40(0→1); 41(0→1).  
 33: 3(0→1); 13(0→1); 47(0→1).  
 34: 32(0→2).  
 35: 27(0→1).  
 36: 3(0→1).  
 37: 14(0→2); 24(0→1); 25(0→1).  
 38: 11(0→1).  
 39: 5(0→1); 10(0→1); 13(0→2); 18(0→1); 20(3→4); 43(0→1).  
 40: 37(0→2).  
 41: 8(2→3); 12(0→1); 13(2→3).  
 42: 28(1→2); 35(0→1); 36(0→1); 43(1→2); 44(0→1); 46(0→1).  
 43: 29(0→1).  
 44: 6(0→2).  
 45: 18(0→1); 39(0→1).  
 46: 3(0→1); 43(0→1).  
 47: 9(1→2); 13(0→4).



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