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**On the systematic position of *Podopteroocus* Banks and *Dinopsocus* Banks, with a revised diagnosis of the genus *Sigmatoneura* Enderlein (Psocodea: 'Psocoptera': Psocidae)**

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**On the systematic position of *Podopteroocus* Banks and *Dinopsocus* Banks, with a revised diagnosis of the genus *Sigmatoneura* Enderlein (Psocodea: 'Psocoptera': Psocidae).** - The genus *Podopteroocus* Banks has been known only from male specimens and has been characterized by the thickened first antennal flagellomere and the expanded hind tibia. The genus *Dinopsocus* Banks has been characterized by the thickened first antennal flagellomere. Detailed morphological examinations and brief molecular-based identification (only for one species) suggest that both taxa are congeneric. Based on characters of female terminalia and fore wing venation, both taxa are furthermore considered to be closely related to the genus *Sigmatoneura* Enderlein. The discovery of two new species and observations on *Sigmatoneura* spp. reveal the limited significance of the diagnostic characters of *Podopteroocus* and *Dinopsocus*. Therefore we consider both *Podopteroocus* and *Dinopsocus* as junior synonyms of *Sigmatoneura*. Monophyly of the genus *Sigmatoneura*, including *Podopteroocus*, *Dinopsocus*, and the subgenus *Longifolia* Li, is well supported by the unique fore wing venation of females and by sexually dimorphic fore wing venation and coloration. Two new species, *Sigmatoneura kakisayap* sp. n. and *Sigmatoneura lehmsayap* sp. n., which would be classified under *Podopteroocus* or *Dinopsocus* by the previous generic definitions, are described. *Sigmatoneura longicornis* comb. n., the type species of *Podopteroocus*, is redescribed and transferred to *Sigmatoneura* and the female of this species is described for the first time. *Dinopsocus atratus*, the type species of *Dinopsocus*, is synonymized with *S. longicornis*. *Sigmatoneura semicolorata* comb. n. is redescribed and transferred from *Dinopsocus* to *Sigmatoneura*.

**Keywords:** Psocodea - Psocidae - *Sigmatoneura* - *Podopteroocus* - *Dinopsocus* - systematics - Malaysia - Indonesia - Brunei - Singapore.

## INTRODUCTION

*Podopteroecus* Banks, 1920 and *Dinopsocus* Banks, 1920 are enigmatic taxa of the family Psocidae. The former genus has been known only from one species, *Podopteroecus longicornis* Banks, 1920, and only from male specimens (see New, 1975) characterized by highly specialized, broadened hind tibiae (Figs 1D, 3C) and a thickened first antennal flagellomere (Fig. 1D). *Podopteroecus* was once treated as a subgenus of *Eremopsocus* McLachlan, 1866 by Roesler (1944) but is now regarded as a separate genus (Mockford, 1975) and is assigned to the tribe Cerastipsocini of the subfamily Psocinae (Lienhard & Smithers, 2002). The genus *Dinopsocus* on the other hand contains two species, which are also characterized by a thickened first antennal flagellomere. As *Podopteroecus*, *Dinopsocus* was once treated as a subgenus of *Eremopsocus* but is now regarded as a separate genus and assigned to the tribe Cerastipsocini (Lienhard & Smithers, 2002). However, a detailed examination of phylogenetically relevant characters of these genera has not yet been carried out. Therefore their exact taxonomic status and systematic position remained unclear. In addition, New (1978) tentatively suggested that *Podopteroecus* and *Dinopsocus* may represent the same taxon, closely related to the genus *Sigmatoneura* Enderlein, 1908, a member of the tribe Metylophorini (Lienhard & Smithers, 2002).

Recently we obtained some specimens that can be identified as *Podopteroecus* and/or *Dinopsocus* collected in Brunei, Indonesia (Sumatra), Singapore and Malaysia (peninsula and Sabah). By comparing these specimens and after having examined the type material of *D. atratus*, the type species of the genus *Dinopsocus*, we concluded that these two genera are actually congeneric and show extreme sexual dimorphism. Furthermore, extensive examination of specimens of *Sigmatoneura* revealed that the diagnostic characters for *Podopteroecus* and *Dinopsocus* are not clear-cut but rather continuous or homoplastic. In the following, we synonymize *Dinopsocus* and *Podopteroecus* with *Sigmatoneura* and discuss their systematic position based on a morphological examination of this material. We also describe two new species that would be assigned to *Podopteroecus* and/or *Dinopsocus* in the previous sense, based on specimens from Malaysia and Sumatra.

Methods of morphological examination follow Yoshizawa (2002). Specimens stored in 70% or 99.5% ethanol were used (except for dry preserved *Dinopsocus* types). Depositories of specimens are abbreviated as follow: MCZ - Museum of Comparative Zoology, Harvard University, USA (type specimens of *Dinopsocus*); MHNG - Muséum d'histoire naturelle, Genève, Switzerland; SEHU - Hokkaido University Insect Collection, Sapporo, Japan; UKM - Center for Insect Systematics, Universiti Kebangsaan Malaysia, Bangi, Malaysia.

## SYSTEMATICS

### *Sigmatoneura* Enderlein

*Sigmatoneura* Enderlein, 1908: 761. Type species: *Cerastipsocus subcostalis* Enderlein, 1903.  
*Podopteroecus* Banks, 1920: 308, **syn. n.**; Mockford, 1975: 251. Type species: *Podopteroecus longicornis* Banks, 1920. *Eremopsocus* (*Podopteroecus*): Roesler, 1944: 147.  
*Dinopsocus* Banks, 1920: 307, **syn. n.**; Mockford, 1975: 251. Type species: *Dinopsocus atratus* Banks, 1920. *Eremopsocus* (*Dinopsocus*): Roesler, 1944: 147.

*Revised diagnosis.* Large psocids, fore wing length about 6 mm in male and about 8 mm in female. Antenna very long, first flagellomere normal or sometimes thickened in both sexes (Fig. 1AB vs Fig. 1CDE). Male fore wing hyaline or sometimes with pale pigmentation or blackish brown markings, female fore wing blackish brown (Fig. 2); male fore wing venation normal, female fore wing R4+5 strongly sinuate; Rs and M fused for a short distance, meeting at a point, or connected by a cross vein of variable length in both sexes. Male hind tibia usually weakly flattened and somewhat enlarged, rarely paddle-shaped, on each side with a flat wing-like expansion (Fig. 3); female hind tibia of normal cylindrical shape (Fig. 1BE).

*Sigmatoneura kakisayap* Yoshizawa & Lienhard, sp. n. Figs 1AB, 2AB, 3A, 4, 5

*Podopterocus* sp. Johnson, Yoshizawa & Smith, 2004: 1774.

*Podopterocus* sp. KY240. GenBank (online database for gene sequences): accession number for 18S rDNA of holotype male is AY630557.

*Podopterocus* sp. KY329. GenBank (online database for gene sequences): accession number for 18S rDNA of paratype female is DQ116946.

*Holotype.* Male. MALAYSIA (peninsula), Gunung Berembun, Cameron Highlands, Pahang, 14. vii. 2003, leg. H. Kojima *et al.* (canopy fogging) (UKM).

*Paratypes.* MALAYSIA (peninsula): 2 males, same data as for holotype (SEHU and UKM); 1 male, from the type locality, 15. vii. 2003, leg. H. Kojima *et al.* (canopy fogging) (UKM); 1 female, Gunung Jasar, Cameron Highlands, Pahang, 14. iii. 2003, leg. K. Yoshizawa (beating dead branches) (SEHU); 1 female, from the type locality, 15. vii. 2003, leg. N. Takahashi (sweeping branches) (UKM). MALAYSIA (Sabah - West Coast Residency): 1 male (heavily damaged, lacking antennae and hind legs), Mt. Kinabalu, 1500 m, Liwagu Trail Section 2, 30. iv. 1987, leg. D. Burckhardt & I. Löbl (MHNG); 1 female, Mt. Kinabalu, 1750-1850 m, Liwagu Trail, 20. iii. 1983, leg. C. Lienhard (MHNG). INDONESIA (Sumatra): 1 male, Pematang Siantar, 1. vii. 1984 - 13. iv. 1985, leg. E. W. Diehl (MHNG).

*Description.* MALE (Fig. 1A). Head black, with narrow pale markings on frons along internal margins of eyes; gena white. Appendices blackish brown; first flagellomere not thickened. Eye small, IO/D=2.7. Thorax black, except for white membranous regions, propleuron, posterior margin of mesoscutum and metascutellum. Fore wing (Fig. 2A) hyaline, with blackish brown tinge along apical margin between veins R1 and M1, veins and pterostigma black; venation normal, Sc reaching C, Rs-M cross vein long, first section of CuA1 almost perpendicular to the anterior wing margin, CuA1+M connection long. Hind wing hyaline, with brownish tinge posteroproximally, veins black. Legs (Fig. 1A) blackish brown, distal ends of femora and basal ends of tibiae of front and middle legs brown, trochanter and basal end of tibia of hind leg white; hind leg long, hind tibia (Fig. 3A) with symmetrical wing-like expansions along distal 2/3. Abdomen whitish in ground color, dorsally black except for 7th and 8th segments, gray in distal ventral region.

*Terminalia.* Dorsal shelf of clunium absent (Fig. 4AB), dorsal region of clunium with round shallow concavity in the middle. Epiproct (Fig. 4B) without membranous region anteromedially. Paraproct as in Fig. 4AB. Hypandrium (Fig. 4C) covered with wrinkles, anterolaterally fused with clunium, anteromedially with semicircular membranous region, posteriorly with roughly trapezoidal projection and with longitudinal crest medially. Phallosome (Fig. 4D): parameres very weakly sclerotized; aedeagus gradually narrowing to truncated posterior end, posterior margin slightly rounded and

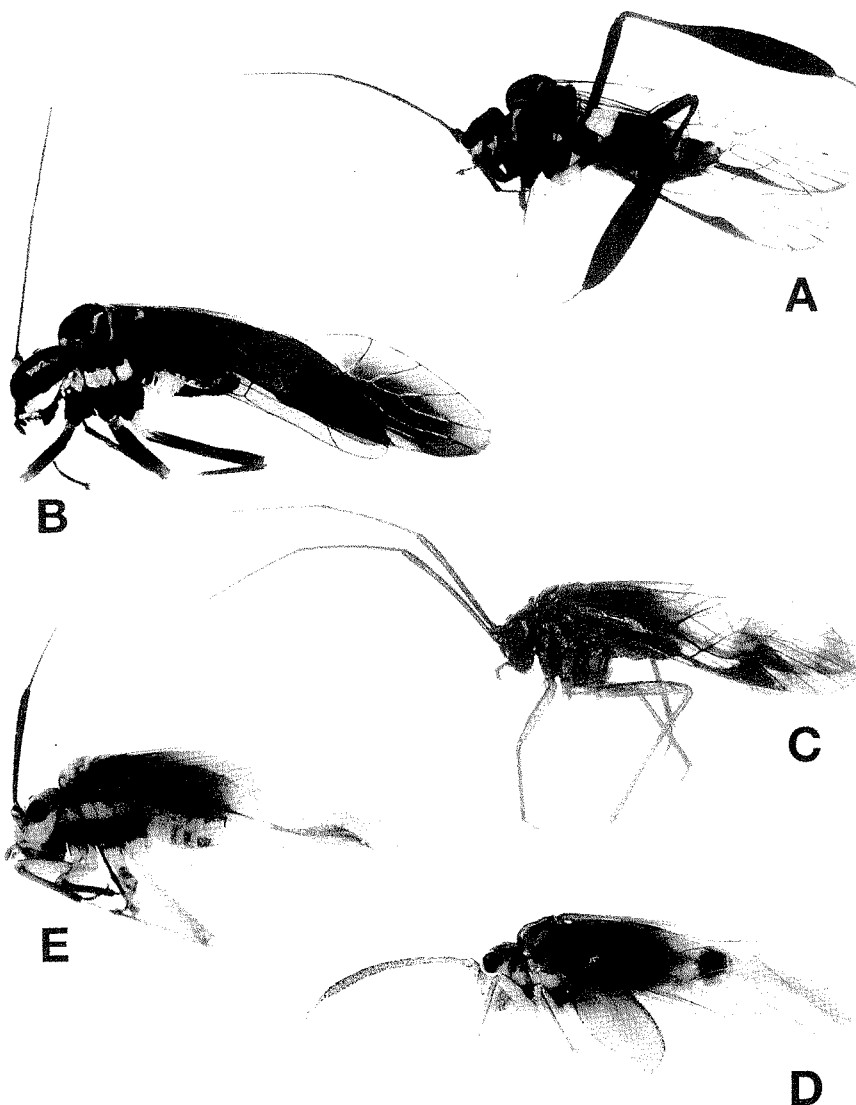


FIG. 1

Habitus of *Sigmatoneura* spp. (C dried specimen, others in alcohol). A: *S. kakisayap* sp. n., male paratype; B: *S. kakisayap* sp. n., female paratype; C: *S. semicolorata*, male holotype; D: *S. longicornis*, male from Brunei; E: *S. longicornis*, female from Singapore.

with tiny denticles laterally; phallobase gradually tapering anteriorly, with very short projection (anteriorly).

Length (in mm): body 4.3-4.5; fore wing 5.8-6.1; hind wing 3.6-3.8.

FEMALE. Almost as in male, except as follows. Head (Fig. 1B): white markings along eyes broad, expanded from antennal sockets to vertex. First and second

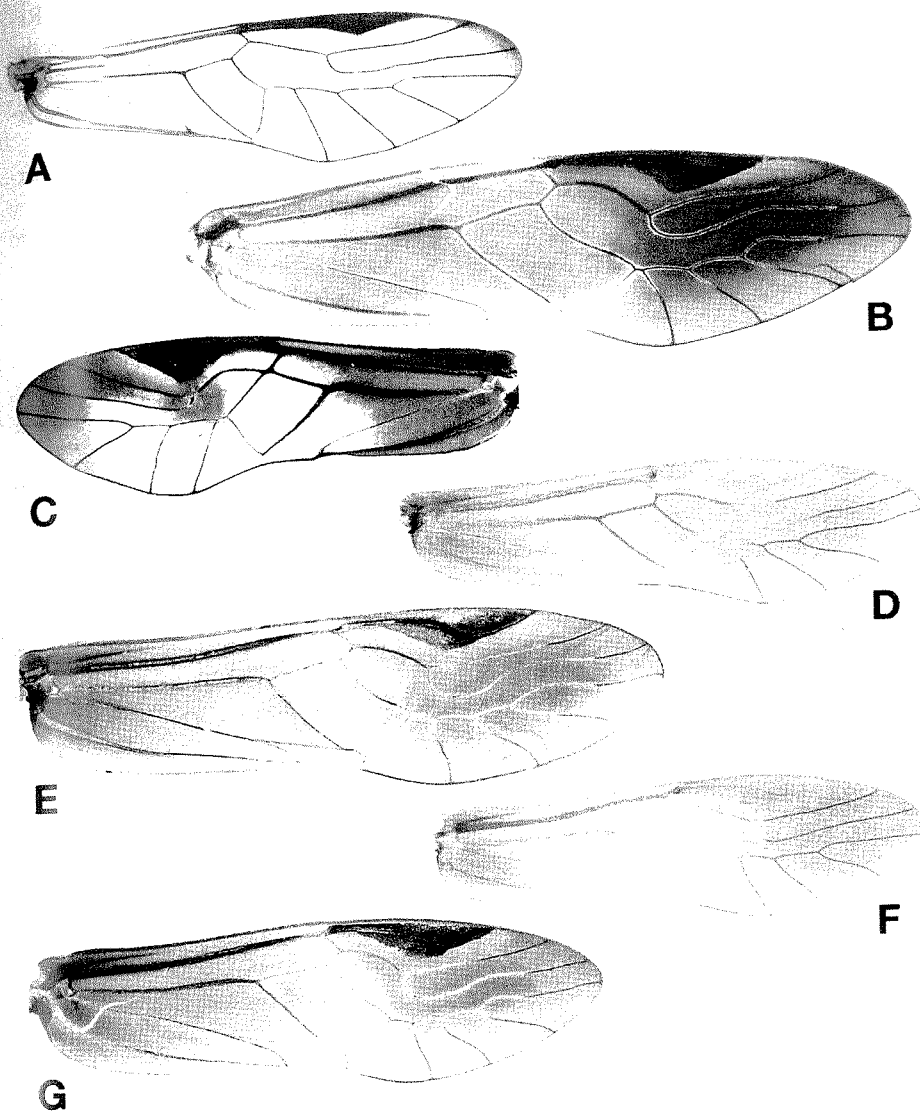


FIG. 2

Fore wings of *Sigmatoneura* spp. A: *S. kakisayap* sp. n., male holotype; B: *S. kakisayap* sp. n., female paratype; C: *S. semicolorata*, male holotype; D: *S. lehahsayap* sp. n., male holotype; E: *S. lehahsayap* sp. n., female paratype; F: *S. longicornis*, male from Brunei; G: *S. longicornis*, female from Singapore.

segments of maxillary palpus white. IO/D=2.9. Thorax: laterally with broad longitudinal white band. Mesoscutellum yellowish white. Fore wing (Fig. 2B) blackish brown, with white region along first section of CuA1 and along posterior wing margin between veins CuA2 and An1; veins and pterostigma black, except the following

yellowish white veins: basal section of Rs, basal 2/3 of R2+3, basal 3/4 of R4+5, Rs-M cross vein, M, basal parts of M branches, and CuA; R4+5 strongly sinuate in the middle, Rs-M cross vein long, first section of CuA1 directed anterodistally, CuA1+M connection short. Hind wing pale brown, its veins black. Legs (Fig. 1B): hind leg normal, hind tibia white in distal 2/3.

Genitalia. Subgenital plate (Fig. 5A): egg guide pointed apically, with transversal crest basally; body of subgenital plate wide, connected with egg guide by narrow sclerite, anteromedian part broadly membranous. Gonapophyses (Fig. 5B): ventral valve long; dorsal valve widely membranous, without distal process; external valve short and wide, densely covered with long setae along posterior margin.

Length (in mm): body 4.6-5.1; fore wing 7.9-8.4; hind wing 5.2-5.3.

Distribution. Malaysia (peninsula and Sabah), Indonesia (Sumatra).

Etymology. The specific epithet, a noun in apposition, is a combination of two Malayan words, kaki (= leg) and sayap (= wing). The synonymized generic name *Podopteroecus* is a combination of the Greek words for «leg» and «wing».

Remarks. This new species can be distinguished from the other species of the genus *Sigmatoneura* by the long hind tibia with dorso-ventrally symmetrical wing-like expansions in the male (Fig. 3A, cf. 3BC) and by the morphology of the subgenital plate in the female.

Males and females of this species (Fig. 1AB) are significantly different in fore wing coloration and venation, and in hind leg morphology. Therefore male-female conspecificity was also checked by analysing a 957 bp fragment of the 18S rDNA gene sequence (GenBank accession numbers: AY630557 for holotype male and DQ116946 for one female paratype from Gunung Jasar). No substitution has been identified between the gene sequences of the male holotype and the female paratype, which supports conspecificity.

***Sigmatoneura semicolorata* (Banks) comb. n.**

Figs 1C, 2C, 6

*Dinopsocus semicoloratus* Banks, 1920: 307.

*Eremopsocus (Dinopsocus) semicoloratus*: Smithers, 1967: 98.

Specimen examined. Holotype male. PHILIPPINES, Luzon, Makiling, leg. C. F. Baker (MCZ: 10801).

Redescription (coloration in dried condition). MALE (Fig. 1C). Head blackish brown. Appendices blackish brown; first flagellomere thickened. Eye small, IO/D=2.4. Thorax blackish brown. Fore wing (Fig. 2C) hyaline, basal 1/3 and apical part blackish brown, anterior part of apical marking extending proximally to apical part of Rs and CuA1+M connection, veins and pterostigma black; venation normal, Sc reaching C, Rs and M fused for a short distance, first section of CuA1 directed anterodistally, CuA1+M connection short. Hind wing hyaline, basal 1/3 brown, veins black. Legs (Fig. 1C) blackish brown; hind tibia almost normal, very slightly flattened apically. Abdomen blackish brown, with whitish longitudinal band laterally.

Terminalia. Dorsal shelf of clunium absent (Fig. 6AB). Epiproct (Fig. 6B) with narrow membranous region anteromedially, and with slight transversal swelling medially. Paraproct as in Fig. 6AB. Hypandrium (Fig. 6C) with smooth surface posteriorly, lateral region with some weak wrinkles, anterolaterally fused with clunium,

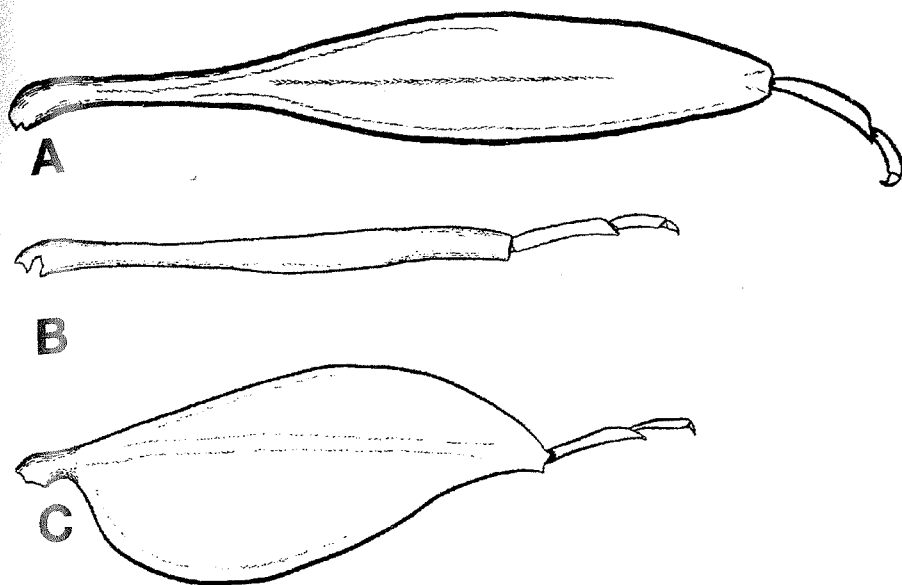


FIG. 3

Male hind tibiae of *Sigmatoneura* spp. A: *S. kakisayap* sp. n., male holotype; B: *S. lehmsayap* sp. n., male holotype; C: *S. longicornis*, male from Brunei.

anteromedially with triangular membranous region, posteriorly with roughly trapezoidal projection. Phallosome (Fig. 6D) relatively long, opened basally; parameres rather well sclerotized; aedeagus gradually narrowing to truncated posterior end, posterior margin slightly concave and with tiny denticles posterolaterally; phallobase tapering anteriorly, without projection.

Length (in mm): body 3.8; fore wing 5.9; hind wing 4.1.

*Distribution.* Philippines (Luzon).

*Remarks.* *S. semicolorata* can be distinguished from the other species of the genus *Sigmatoneura* by the unique male fore wing markings. *S. kakisayap* sp. n., described above, has also hyaline fore wings with some dark brown markings, but it differs from *S. semicolorata* by the absence of a thickened first flagellomere and by the greatly expanded hind tibia. The presence of a thickened first flagellomere in *S. semicolorata* indicates some relationships with the two species described below, but coloration of fore wing in male is remarkably different. The female of *S. semicolorata* is so far unknown.

*Sigmatoneura lehmsayap* Yoshizawa & Lienhard, sp. n. Figs 2DE, 3B, 7, 8A

(?) *Dinopsocus atratus* Banks sensu New, 1978: 45 (see remarks below).  
Not *Dinopsocus atratus* Banks, 1920: 307 (see *S. longicornis*, below).

*Holotype.* Male. INDONESIA (N-Sumatra), «Holzweg 2», 10 km NE Prapat, 1050 m, 98°57' E, 2°44' N, 9. i. 1988, leg. E. W. Diehl (MHNG).



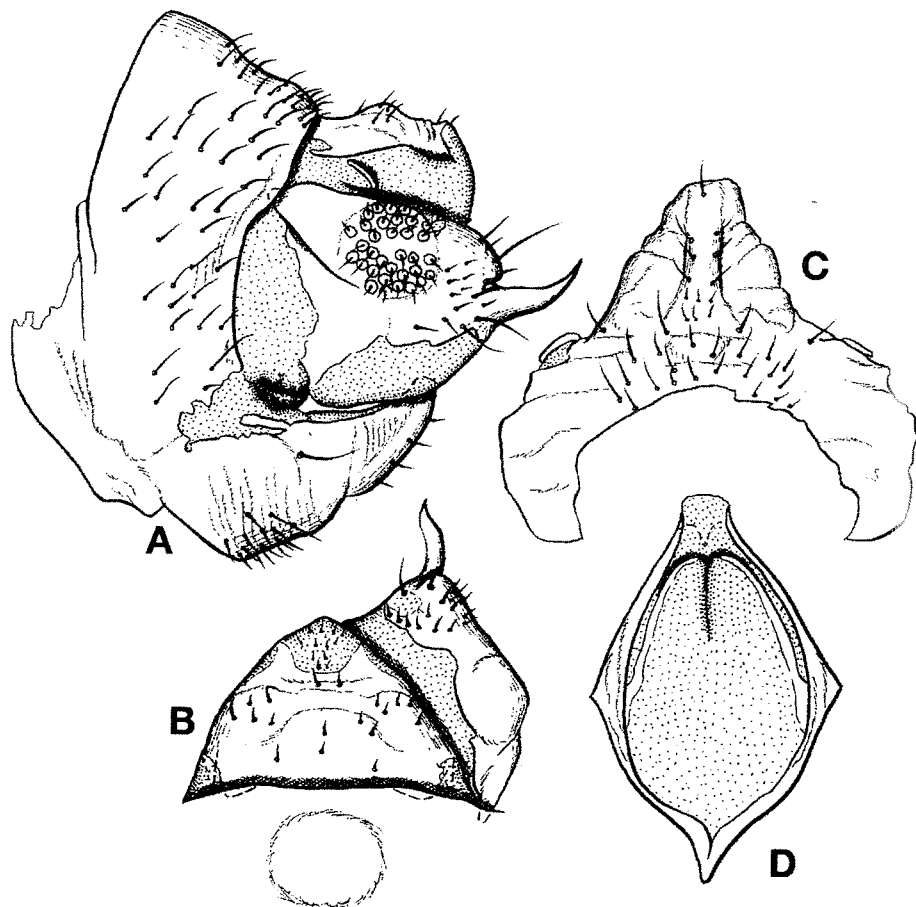


FIG. 4

Male terminalia (holotype) of *Sigmatoneura kakisayap* sp. n. A: terminalia, lateral view; B: epi-proct and left paraproct (trichobothrial field not figured), dorsal view; C: hypandrium, ventral view; D: phallosome, ventral view.

*Paratypes.* INDONESIA (N-Sumatra): 1 female, same locality as for holotype, 27. xi. 1989, leg. E. W. Diehl (MHNG); 1 female, Huta Padang, 99°14' E, 2°45' N, 400 m, 2. ii. 1991, leg. H. Malicky (MHNG).

*Description.* MALE. (Male holotype in bad condition, coloration of body, except for wings, almost indistinguishable: i.e., just uniformly pale brown without any distinct marking). First flagellomere thickened. Eye small, IO/D=2.6. Fore wing (Fig. 2D) pale brown, veins black; venation normal, Sc ending in cell c, Rs-M cross vein short, first section of CuA1 directed anterodistally, CuA1+M connection short. Hind wing pale brown, basal 1/3 darker, veins brown. Hind tibia (Fig. 3B) with very weakly developed asymmetrical expansions along distal half, ventral expansion stronger (confirmed for both hind legs).

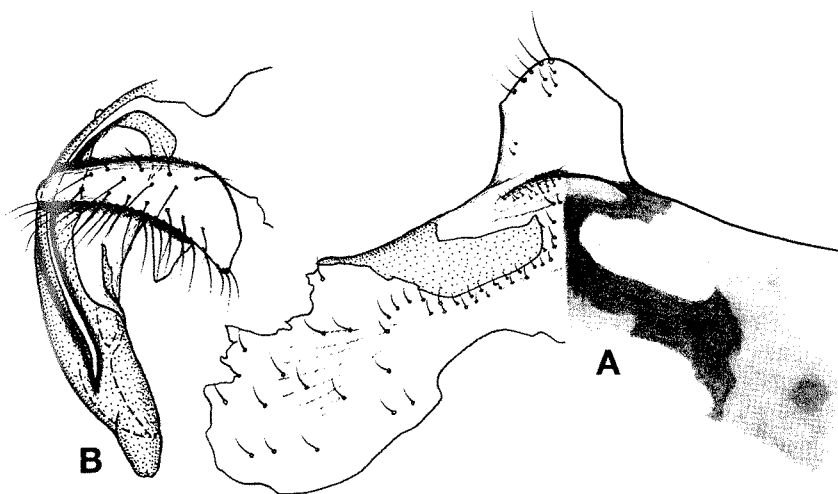


FIG. 5

Female genitalia (paratype) of *Sigmatoneura kakisayap* sp. n. A: subgenital plate, showing structure (left) and color pattern (right); B: gonapophyses.

**Terminalia.** Dorsal shelf of clunium absent (Fig. 7A), dorsal region of clunium with round shallow concavity in the middle. Epiproct (Fig. 7A) with membranous region anteromedially. Paraproct as in Fig. 7A. Hypandrium (Fig. 7B) with smooth surface, only laterally with few wrinkles, anterolaterally fused with clunium, anteromedially with broad membranous region, posteriorly with semicircular projection. Phallosome (Fig. 7C): parameres very weakly sclerotized; aedeagus gradually narrowing to truncated posterior end, posterior margin slightly rounded and with tiny denticules; phallobase gradually tapering anteriorly, with short projection (anteriorly).

Length (in mm): body 4.6; fore wing 6.2; hind wing 4.3.

**FEMALE.** Head brown; gena white. Appendices brown; first and second segments of maxillary palpus paler. First flagellomere thickened. Eye black, IO/D=3.0. Thorax brown, laterally with broad longitudinal white band; meso- and metascutellum paler. Fore wing (Fig. 2E) brown, with white region along first section of CuA1 and along posterior wing margin between veins CuA2 and An1; veins and pterostigma black, except the following yellowish white veins: basal section of Rs, basal 2/3 of R2+3, basal 3/4 of R4+5, Rs-M cross vein, M, basal parts of M branches, and CuA; R4+5 strongly sinuate in the middle, Rs-M cross vein long, first section of CuA1 directed anterodistally, CuA1+M connection short. Hind wing pale brown, with darker portion anteroproximally; veins black. Legs brown; trochanters and base of femora paler; hind leg of normal cylindrical shape.

**Genitalia.** Subgenital plate (Fig. 8A): egg guide with a pair of very shallow trenches anterolaterally, truncated apically, apical margin folded upwards and some apical setae arising from dorsal surface of egg guide; body of subgenital plate wide, connected with egg guide by narrow sclerite, anteromedian part broadly membranous. Gonapophyses as in *S. kakisayap* sp. n. (see description above).

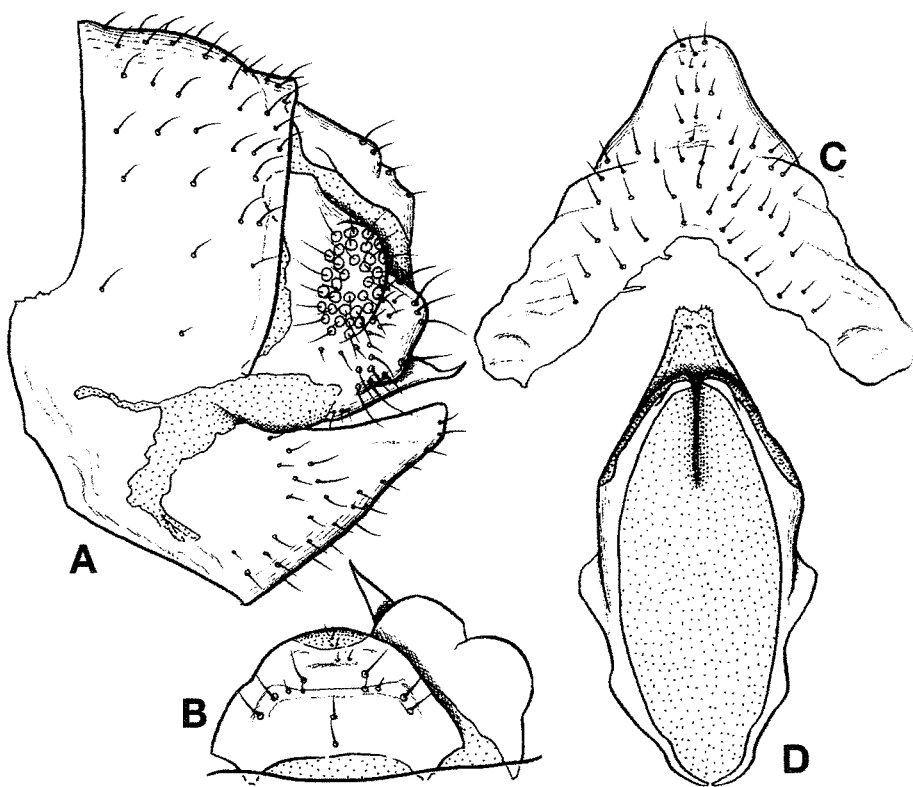


FIG. 6

Male terminalia (holotype) of *Sigmatoneura semicolorata*. A: terminalia, lateral view; B: epi-proct and left paraproct (trichobothrial field not figured), dorsal view; C: hypandrium, ventral view; D: phallosome, ventral view.

Length (in mm): body 4.2-5.0; fore wing 7.2-7.6; hind wing 5.2-5.3.

*Distribution.* Indonesia (Sumatra).

*Etymology.* The specific epithet, a noun in apposition, is a combination of two Indonesian words, lemah (= weak) and sayap (= wing). The synonymized genus *Podopterus* was characterized by the wing-like hind tibia of males, but in this species the hind tibia is only weakly expanded in males.

*Remarks.* *S. lehmsayap* sp. n. is most similar to *S. longicornis*, redescribed below, because of the thickened first flagellomere in both sexes and the widely pigmented fore wing in males. However, these species can be clearly distinguished by the shape of the male hind tibia. In having a less expanded hind tibia, *S. lehmsayap* is similar to most *Sigmatoneura* species, but it differs from them by its thickened first flagellomere.

The female from Kuala Lumpur described by New (1978) as *Dinopsocus atratus* shows an egg guide which is strikingly similar to that of *S. lehmsayap* (cf. Fig. 8A

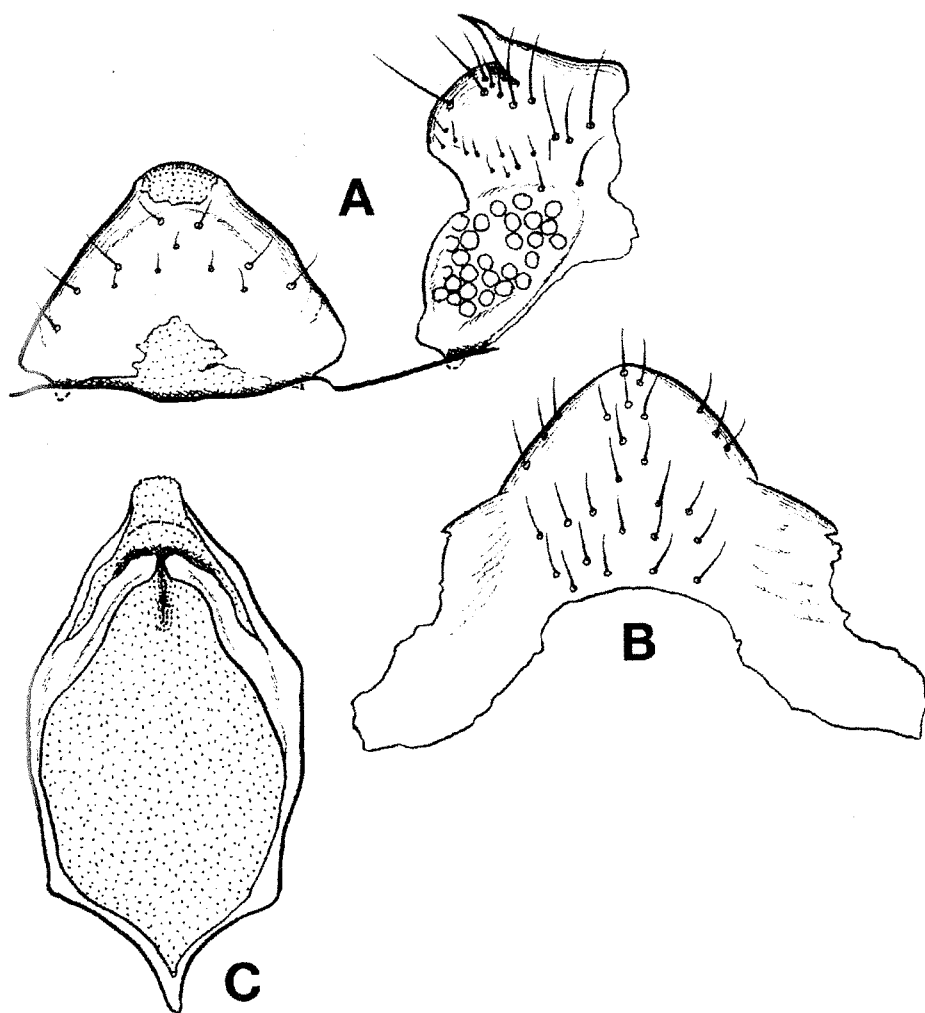


FIG. 7

Male terminalia (holotype) of *Sigmatoneura lemahsayap* sp. n. A: epiproct and left paraproct; B: hypandrium, ventral view; C: phallosome, ventral view.

and New, 1978: fig. 6). Therefore we consider it as very probable that New's specimen does not belong to *S. longicornis* (= *D. atratus*, see below) but to *S. lemahsayap*. The specimen from Kuala Lumpur should be re-examined to check this hypothesis.

*Sigmatoneura longicornis* (Banks) comb. n.

Figs 1DE, 2FG, 3C, 8B, 9

*Podopterus longicornis* Banks, 1920: 308.

*Eremopsocus* (*Podopterus*) *longicornis*: Roesler, 1944: 147; New, 1975: 245 (redescription of male, see remarks below).

*Dinopsocus atratus* Banks, 1920: 307, **syn. n.**

(?) Not *Dinopsocus atratus* Banks sensu New, 1978: 45 (see remarks on *S. lehmsayap*, above).  
*Eremopsocus (Dinopsocus) atratus*: Roesler, 1944: 147.

*Specimens examined.* Lectotype female of *Dinopsocus atratus* (present designation), [MALAYSIA (Sabah):] Borneo, Sandakan, leg. C. F. Baker (MCZ: 10800); paralectotype female of *D. atratus* (present designation), PHILIPPINES [Luzon], Mt. Banahao, leg. C. F. Baker (MCZ: 10800); non-type female of *D. atratus* mentioned in the original description, SINGAPORE, leg. C. F. Baker (MCZ).

BRUNEI: 1 male (reared from nymph) and 4 nymphs, Bru-88/30 (Belait District), Sungai Liang, Arboretum of Forest Service, primary forest (mixed dipterocarp forest), alt. about 50m, 21. xi. 1988, leg. C. Lienhard (MHNG); 1 male, Bru-88/42, same locality and collector, alt. 20-50 m, 25. xi. 1988 (SEHU). MALAYSIA (Sabah): 1 female, Sepilok, 24 km W of Sandakan, v-viii, 1983, leg. S. Nagai (MHNG). SINGAPORE: 1 female, Bukit Timah Nature Reserve, 16. xi. 1981, leg. D. H. Murphy (MHNG); 1 female, same locality, no date, leg. D. H. Murphy (MHNG).

*Diagnosis.* The male of this species is easily distinguishable from any other psocid by the unique structure of its hind tibia, which is distinctly paddle-shaped due to a conspicuous, flattened, wing-like expansion on each side; these expansions are dorso-ventrally asymmetrical, the ventral expansion is broadest at basal 1/3 and the dorsal expansion broadest at distal 1/3 (Fig. 3C). The female of this species is very similar to that of *S. lehmsayap* sp. n., described above, but can be distinguished by the shape of egg guide (Fig. 8B).

Length of male (Bru-88/42, in mm): body 4.5; fore wing 5.8; hind wing 4.1.

*Redescription of male terminalia.* Clunial dorsal shelf absent (Fig. 9AB). Epiproct (Fig. 9B) with membranous region anteromedially. Paraproct as in Fig. 9AB. Hypandrium (Fig. 9C) with smooth surface, only mediolaterally with few wrinkles; anterolaterally fused with clunium; anteromedially with broad membranous region; posteriorly with semicircular projection. Phallosome (Fig. 9D): parameres very weakly sclerotized; aedeagus narrowing to truncated posterior end, posterior margin slightly concave; phallobase gradually tapering anteriorly, with very short projection (anteriorly).

*Description of female.* Very similar to the previous species, *S. lehmsayap* sp. n., but smaller. Apical margin of egg guide of subgenital plate truncated in *S. lehmsayap* but arched in *S. longicornis* (Fig. 8AB).

Length (in mm): body 4.5-4.8; fore wing 6.6-6.7; hind wing 4.6-4.8.

*Distribution.* Singapore (Banks, 1920; New, 1975; present study), Malaysia (Sabah [Banks, 1920 and present study]; peninsula [Banks, 1938]), Brunei (present study), Philippines (Banks, 1920). NOTE: Soehardjan (1958) lists *Dinopsocus atratus* for Sarawak, probably because of an erroneous interpretation of Banks' original statement («Borneo: Sandakan»), and Endang *et al.* (2002) erroneously list it for Indonesia.

*Remarks.* *S. longicornis*, the type species of *Podopterus*, has been described from a male collected in Singapore (sex not mentioned in the original description, but the holotype of *Podopterus longicornis* must be a male because of having a broadly expanded hind tibia). Banks' description and figures (Banks, 1920: pl. 1, fig. 4, fore wing and hind tibia) closely correspond to our specimens from Brunei, and we are convinced that they belong to the same species. *S. longicornis* has briefly been redescribed by New (1975) on the basis of three males from Singapore. The only significant difference between New's description and our observations on the Brunei males

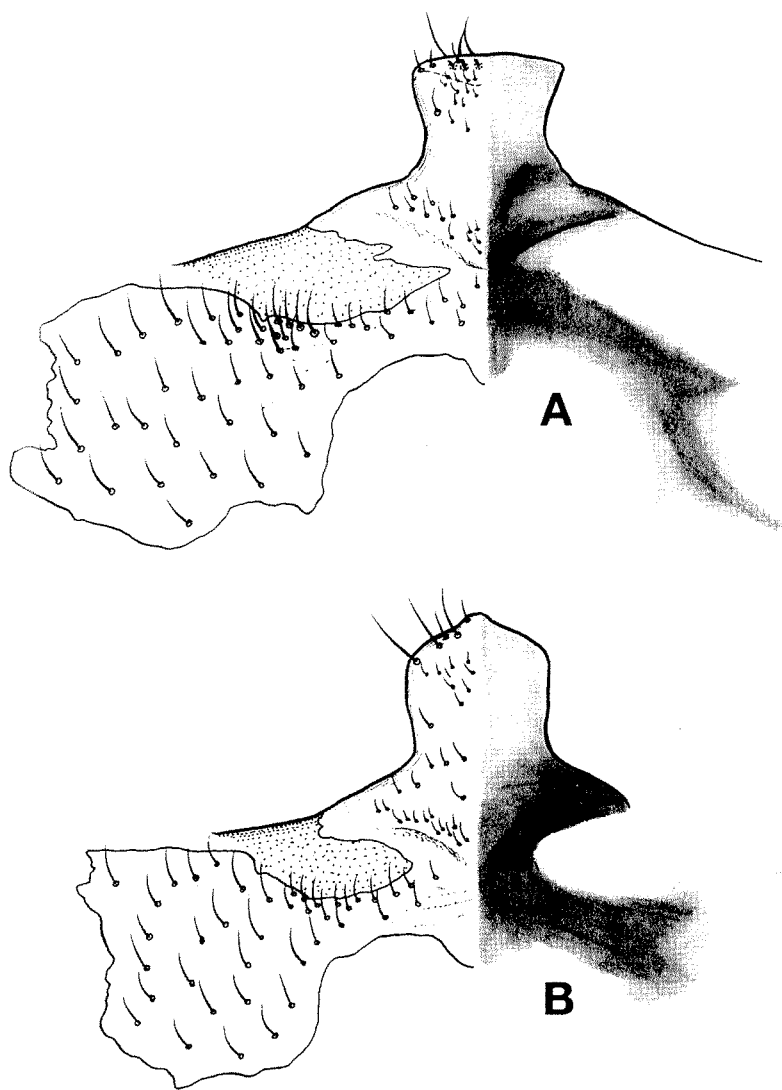


FIG. 8

Female subgenital plates. A: *Sigmatoneura lehmsayap* sp. n. (paratype); B: *Sigmatoneura longicornis* (specimen from Singapore).

concerns the «broad rugose apex» of the phallosome mentioned by New, which contrasts with the slightly concave, smooth apical margin of the phallosome in the Brunei material. The differences concerning the shape of the expanded hind tibia and of the phallobase between our Figs 3C and 9D and New's figures 8 and 11, are probably due to deformations by slide-mounting (phallosome) and to some teratological phenomena or optical distortion (hind leg). In our opinion, it is not very likely that

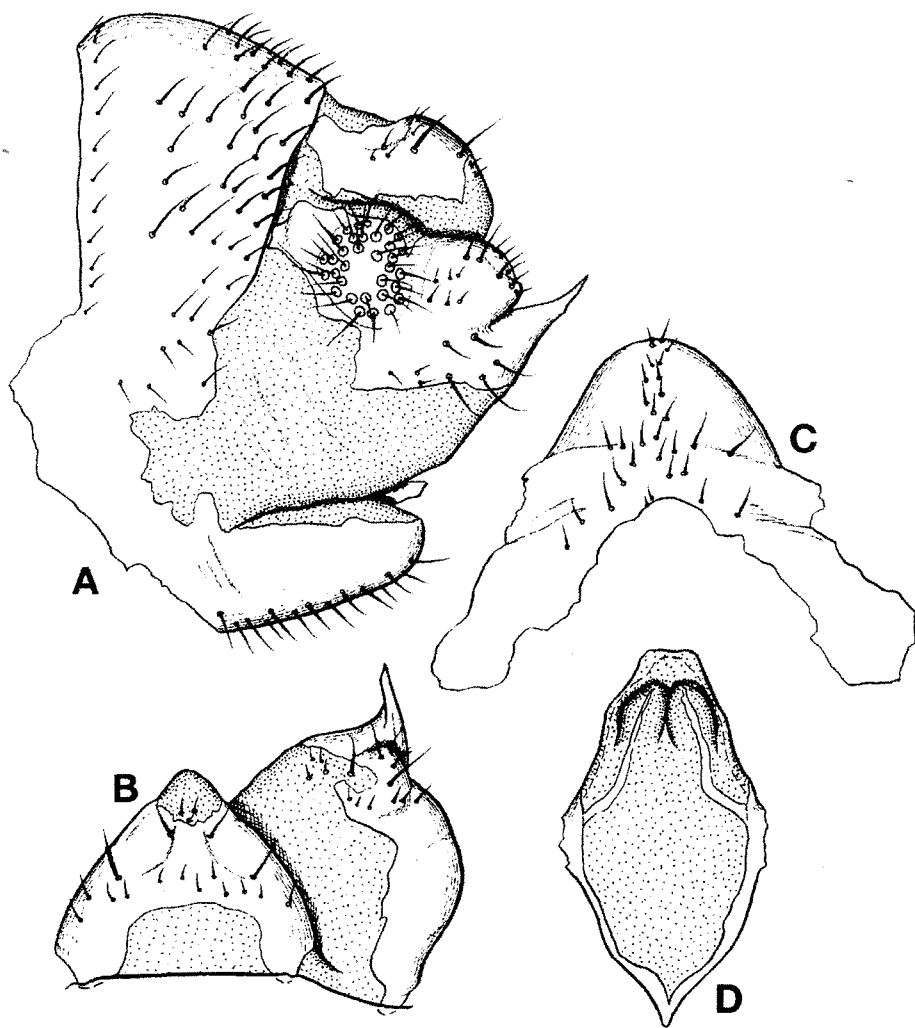


FIG. 9

Male terminalia of *Sigmatoneura longicornis* (specimen from Brunei). A: terminalia, lateral view; B: epiproct and left paraproct (trichobothrial field not figured), dorsal view; C: hypandrium, ventral view; D: phallosome, ventral view.

New's specimens belong to an additional species closely related to *S. longicornis*. However, this possibility can only be excluded with certainty after a re-examination of New's material. Concerning shape of hind tibia, our Brunei males correspond more closely to Banks' than to New's figure. In our opinion this justifies the assumption that these specimens are conspecific with the male holotype of *S. longicornis*.

Male and female specimens of the present material assigned to *S. longicornis* are superficially highly divergent and have not been collected simultaneously. There-

fore the proposed male-female combination remains somewhat tentative. However, three females examined above were collected in Singapore, type locality of *S. longicornis*. Their morphological features do not contradict the present observations concerning sexual dimorphism in the genus *Sigmatoneura* (see Discussion, below). The only other *Sigmatoneura* species with a thickened first flagellomere, from which female genital morphology has been described, is *S. lehahsayap* sp. n., which is distinguished by the shape of its egg guide (Fig. 8AB).

## DISCUSSION

In the present study we examined some psocid species that have been or that can be assigned to the genera *Podopterocus* and/or *Dinopsocus* which are here placed in the synonymy of *Sigmatoneura*. Although a greatly expanded hind tibia has been recognized as the most prominent diagnostic character of *Podopterocus*, our present examination revealed that in some species the hind tibia is sexually dimorphic in shape. Since *Podopterocus* has been diagnosed by such a dimorphic character, the genus has been known only from males. The genus *Dinopsocus* on the other hand has been characterized by the thickened first flagellomere, but this character is also present in males and females of *Podopterocus longicornis*, the type species of *Podopterocus* (Fig. 1DE). Furthermore, the lectotype of *Dinopsocus atratus* (type species of *Dinopsocus*) is considered to be a female of *P. longicornis*. As already suggested by New (1978), it is now evident that females of *Podopterocus* have been assigned to the genus *Dinopsocus* because of this extreme sexual dimorphism. Male-female combination of these highly sexually dimorphic psocids was confirmed genetically only for *Sigmatoneura kakisayap* sp. n., described and discussed above, the female of which is not of «*Dinopsocus* type» (i.e., lacking a thickened first flagellomere). However, the result of the molecular male-female match clearly indicates that the expanded hind tibia is a secondary sexual character only developed in males, while corresponding females have a normal cylindrical hind tibia. Similar sexual dimorphism is also known in some psocids of the family Caeciliusidae. For example, in the *flavidus* group of the genus *Valenzuela* Navas (see Mockford, 1993; Lienhard, 1998) and in the genus *Phymocaecilius* Li (see Li Fasheng, 2002) a more or less conspicuous swelling of the fore tibia (and sometimes middle tibia) has been observed in males, never in females. Based on these observations, we concluded that the species described under *Podopterocus* and *Dinopsocus* are actually congeners. The above mentioned molecular-based match of a «*Podopterocus* type» male with a «*Sigmatoneura* type» female definitively confirmed close relationships between these taxa, as already suggested by New (1978). In the following we discuss the arguments in favor of synonymizing *Podopterocus*, *Dinopsocus* and *Sigmatoneura* instead of assigning subgeneric status to *Podopterocus/Dinopsocus* within the genus *Sigmatoneura* s. l.

Mosaic distribution of the diagnostic characters of *Podopterocus* and *Dinopsocus* is evident. *S. longicornis*, *S. lehahsayap* sp. n. and *S. semicolorata* belong to the «*Dinopsocus* type» in having a thickened first flagellomere in both sexes. In contrast, *S. longicornis* and *S. kakisayap* are clearly of the «*Podopterocus* type» in having a greatly expanded paddle-shaped hind tibia in males. *S. lehahsayap* has a slightly but distinctly expanded hind tibia and therefore is close to «*Podopterocus*



type». Checking our material of *Sigmatoneura* s. str. (i. e., species without thickened first flagellomere and without significant expansion of male hind tibia: e. g., *S. kolbei*), we observed a general tendency for very slight expansion and flattening of the hind tibia in males.

The apomorphic presence of a long Rs-M cross vein in the fore wing was observed in all possible *Podopterus* and/or *Dinopsocus* species (except for *S. semicolorata*). However, an Rs-M cross vein was also observed in some *Sigmatoneura* s. str. species, showing a certain variability from almost fused at one point to as long as in *S. kakisayap*. All known species of the subgenus *Sigmatoneura* (*Longifolia*) Li, 2002 also have a long Rs-M cross vein (Li Fasheng, 2002). Therefore, this character state also cannot be used to diagnose *Podopterus* and/or *Dinopsocus*.

The thickened first flagellomere is shared by three of four species examined above (*S. longicornis*, *S. lehahsayap* and *S. semicolorata*), but a secondary reversal of the character state in *S. kakisayap* is also possible (see also discussion below). New (1978) mentioned that the subcosta of *Dinopsocus* is long and approaching R, whereas that of *Sigmatoneura* is short and approaching the costa, and he tentatively considered this character as diagnostic for these genera. However, in all specimens examined here, the subcosta is short and approaching the costa (Fig. 2). No other apomorphic characters clearly characterizing *Podopterus* and/or *Dinopsocus* could be found. Judging from these observations, we concluded that the differences between *Sigmatoneura* s. str. and *Podopterus*/*Dinopsocus* are continuous or highly homoplastic and that it is impossible to clearly define the latter genera. Thus, synonymizing these genera with *Sigmatoneura* is the most reasonable and practical solution. Monophyly of *Sigmatoneura*, including *Podopterus*, *Dinopsocus* and the subgenus *Longifolia*, is well supported by the following unique autapomorphies: female fore wing blackish brown in ground color, with veins R2+3, R4+5 and first section of CuA1 white, and with vein R4+5 strongly sinuate; sexual dimorphism in fore wing coloration and venation. Molecular data (18S rDNA: Johnson *et al.*, 2004) also show that *Sigmatoneura*, including *Podopterus*/*Dinopsocus* (at least *S. kakisayap*), form a monophyletic group.

Among the species examined above, *S. longicornis*, *S. lehahsayap* and *S. semicolorata* share an apomorphic character state, the thickened first flagellomere, whereas *S. kakisayap* has normal antennae in both sexes. In contrast, *S. longicornis* and *S. kakisayap* share an apomorphic condition, the well expanded hind tibia, whereas in *S. lehahsayap* and *S. semicolorata* the male hind tibia is only slightly expanded. As already mentioned above, there are conflicts in the distribution of apomorphic character states among these species. Well expanded paddle-shaped hind tibia in males might have evolved independently in *S. longicornis* and *S. kakisayap*, because the expansion in *S. kakisayap* is symmetrical, whereas that in *S. longicornis* and *S. lehahsayap* is clearly asymmetrical, although weakly developed in the latter species.

The subgenus *Longifolia* was recognized in the genus *Sigmatoneura* by Li Fasheng (2002). This subgenus shares the characteristic sexual dimorphism in the fore wing coloration and venation with the subgenus *Sigmatoneura*. *Longifolia* is characterized by the elongate egg guide of the female subgenital plate (autapomorphic for the subgenus) and thus monophyly of the subgenus can be confirmed. However, no

apomorphy supporting the monophyly of the subgenus *Sigmatoneura* is known. Although we do not propose here synonymy of *Sigmatoneura* and *Longifolia*, we would like to point out the fact that Li's treatment probably established a paraphyletic taxon (the subgenus *Sigmatoneura*).

*Podopterocus* and *Dinopsocus* have previously been assigned to the tribe Cerastipsocini, whereas *Sigmatoneura* has been classified under the tribe Metylophorini sensu Mockford (1993) (Smithers, 1980; Lienhard & Smithers, 2002). Placement of *Sigmatoneura* into Metylophorini is based on the shape of the gonapophyses, i. e., absence of the distal process of the dorsal valve, which is considered to be an autapomorphy for the tribe. Females of possible *Podopterocus* and *Dinopsocus* examined here also have this character state (Fig. 5B); therefore placement of *Sigmatoneura*, including *Podopterocus* and *Dinopsocus*, into Metylophorini is justified. Li Fasheng (2002) established the subfamily Sigmatoneurinae for the genus *Sigmatoneura*, and assigned the tribes Cerastipsocini and Metylophorini (sensu Mockford, 1993) to a different subfamily (Cerastipsocinae). As mentioned above, the genus *Sigmatoneura* shares an apomorphic character with the other genera of Metylophorini, and Li's subdivision of the family Psocidae has to be rejected.

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