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A new mayfly genus of the subfamily Caeninae (Ephemeroptera: Caenidae) from Sumatra and two new *Caenis* species from Papua New Guinea

Peter Malzacher & Arnold H. Staniczek

Abstract

The new Caenidae genus *Liebenauis* (Type species *L. tenuipes*) is described from larval material collected in Sumatra and attributed to the subfamily Caeninae. It is closely related to the tribe *Caenini* and defined by long and very thin legs and modified, finger- or pine needle-shaped chloride cells on the ventral side of the operculate gill. Such types of chloride cells are not known in any other Caeninae. Two new species of *Caenis* from Papua New Guinea are also described.

Keywords: *Liebenauis*, new genus, *Caenis*, new species, Sumatra, Papua New Guinea.

Zusammenfassung

Die neue Caeniden-Gattung *Liebenauis* wird anhand von Larvalmaterial aus Sumatra beschrieben (Typus-Art *L. tenuipes*) und der Unterfamilie Caeninae zugeordnet. Sie ist der Gattung *Caenis* nahe verwandt und zeichnet sich durch lange und sehr dünne Beine sowie abgewandelte, finger- oder piniennadelförmige Chloridzellen an der Unterseite der Deckkiemen aus. Solche Chloridzellen sind bei anderen Caeninae nicht bekannt. Zwei neue *Caenis*-Arten von Papua-Neuguinea werden ebenfalls beschrieben.

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1 Introduction

For a long time only one species of Caenidae was known from the Sunda Archipelago: *Caenis nigropunctata* was described in 1905 by Klapálek. Numerous records of this species were reported by Ulmer (1924, 1939) from Sumatra and Java. This was the only species found in this area, until Sun & McCafferty (2008) described *Oriobrachys mahakam,* a new species of Brachycercinae, from Mahakam, Borneo. A number of new Caenidae from a small area in Eastern Kalimantan (Borneo) were described by Malzacher (2013): *Caenis abdita*, *C. bidigitata*, *C. fregatula*, *C. sebastiani* and *C. unidigitata*, *Clypeocaenis soldani,* and two species of the genus *Kalimaenis*, *K. sibylliana* and *K. staniczeki,* as well as *Caenoculis* (sub. *Tigrocercus*) *nastassjae*. Malzacher (2015) revised the Oriental *Caenis* species and split the specimens determined by Ulmer as *Caenis nigropunctata* into three new species *C. nigropunctatula*, *C. ranauensis,* and *C. ulmeriana*, all from Sumatra, *C. nigropunctatula* also from Java.

Tasmanocoenis novaeguineae was described by van Bruggen (1957) from New Guinea and attributed to Caenidae. This is the only known species of *Tasmanocoenis* from New Guinea, but its placement within this genus is doubtful and will be discussed below.

With the following descriptions of a new genus and species *Liebenauis tenuipes* n. gen., n. sp., and two new species of *Caenis*, *C. ungulata* n. sp. and *C. marawakensis n. sp.*, there are now five genera and 16 valid species of the family Caenidae recorded from the Sunda Archipelago and New Guinea.

Acknowledgements

Our special thanks go to Michel Sartori and Jean-Luc Gattolliat (Musée cantonal de Zoologie, Lausanne) for providing us with the material for investigation, to Susanne Leidenroth, Karin Wolf-Schwenninger, and Milan Pallmann (Staatliches Museum für Naturkunde, Stuttgart) for taking SEMs and macro photographs, and to Michel Sartori (Lausanne) and Phil Suter (Wodonga),who kindly read the manuscript and provided valuable suggestions.

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2 Material and methods

The investigated material is preserved in 75% ethanol. *S*pecimens were collected by Michael Balke (Zoologische Staatssammlung München, Germany) and colleagues during several field trips in Indonesia and Papua New Guinea between 2006 and 2011. The holotypes of Indonesian material are deposited in LIPI (Indonesian Institute of Sciences, Bogor), the remaining material is stored in MZL (Musée cantonal de Zoologie, Lausanne).

Specimens used for SEM were dehydrated through a stepwise immersion in ethanol and then dried by critical point drying (Leica EM CPD300). The mounted material was coated with a 5 nm Au/Pd layer (Leica EM ACE200) and subsequently examined and photographed with a Zeiss EVO LS 15 scanning electron microscope. Digital photographs were enhanced using PhotoFiltre6.5.2 (http://www.photofiltre-studio.com) and Adobe Photoshop 5.

3 Systematic account

Liebenauis **n. gen.**

Etymology

The genus is dedicated to the late German ephemeropterist Ingrid Müller-Liebenau, as a token of gratitude for her cooperativeness and friendly help during Peter Malzacher's "apprentice years" and later on.

Differential Diagnosis

Liebenauis can be characterised and distinguished from all other genera of Caenidae by the following combination of characters: Larva. Habitus, long and slender, with very long and thin legs (Fig. 1), femora about 5 times as long as wide (Figs. 3c, d), claws thin and elongated (3e, f). – Head without ocellar tubercles. – Outline of head without bulges in lateral view. – Antennae very thin (Fig. 2). – Maxillary and labial palps three-segmented. – All legs subequal in length (Figs 1, 2, 3c, d).– Foretibia and foretarsus without filtering setae. –Forefemur without transverse row of bristles. – Mid and hind tibia ventrally without long bristles. – Claws long and slender, hind claws homodont. – Operculate gill with protruding postero-lateral corner, lateral margin nearly straight (Figs 1, 4). Ventral side with a short row of small, round microtrichia beginning a third of gill's length away from anterior-lateral corner (Fig. 4). A central field of modified, finger-like or pine needle-like chloride cells present (Figs 4, 6, 7). – Gill I about as long as gill II. – Most filaments on gill III possess 3 or 4 branches. – Hind margin of sternum IX without a bi-pointed process.

Liebenauis tenuipes **n. sp.**
(Figs 1-7)

Material examined

Holotype, ♂ larva (on microslide): UN11, Indonesia, Sumatra, Barat, Harau Canyon, 0°4′986S, 100°38′244E, 520 m, 27.09.2009, Balke & Amran leg. [LIPI] – Paratype, 1 larva, same dates as holotype [MZL].



Fig. 1. *Liebenauis tenuipes*, n. gen., n. sp., larva, habitus.



Fig. 2. *Liebenauis tenuipes*, n. gen., n. sp., larva, head and thorax.

Etymology

The species epithet refers to the very long and thin legs, from Latin *tenuis*, thin.

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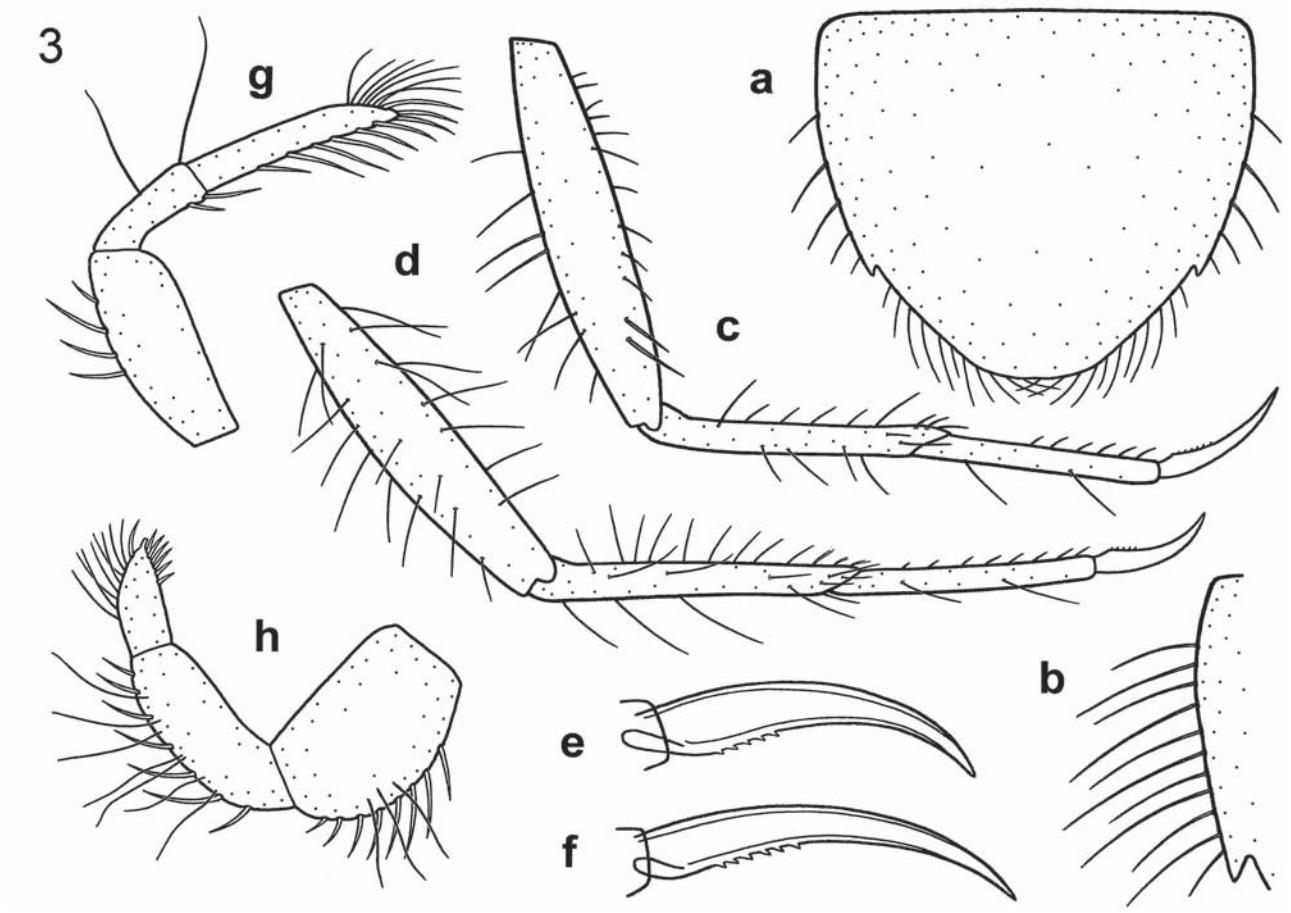


Fig. 3. *Liebenauis tenuipes* n. gen., n. sp., larva. – **a.** Sternum IX.– **b.** Marginal setation of segment VII.– **c.** Foreleg.– **d**. Hind leg.– **e.** Hind claw.– **f.** Foreclaw. – **g.**Maxillary palp.– **h.** Labial palp.

Larva

Measurements and colouration

♀ subadult larva (fully grown, but not yet last instar), body length 4.0-4.5mm, cerci broken off.

Colouration of cuticle: Head yellowish. Pro- and mesonotum brownish with pale or whitish lateral marks, mesonotum with a brown triangular field between wing buds. Abdominal terga VII-IX light brownish. Legs white or yellowish-white.

Epidermal pigmentation: Pattern on dorsal side as in Figs 1 and 2.

Morphology

Cuticle smooth or very finely granulated on parts of head, pro- and mesonotum.

Habitus very slender, with long and thin legs (Fig. 1).

Head: Antennae long and very thin, hair-like (Fig. 2). Genae not bulged. Mandibles dorsolateral with few short bristles. Third segment of maxillary palp 1.7-1.8 times as long as second segment (Fig.3g). Second segment of labial palp 1.7 times as long as third one (along the centre-line) (Fig. 3h). Strong bristles on lateral sides of postmentum, first segment of maxillary palp and first two segments of labial palp (Fig. 3g, h). Similarly long and strong bristles also on lateral margin of paraglossae and on ventral surface, the latter directed medially.

Thorax: Sides of pronotum more or less parallel, straight or slightly convex (Figs 1, 2). Legs long and very slender; femora about 5 times as long as wide; tibiae 10 times as long as wide, all leg margins with long bristles (Figs 2, 3c, d). Forefemur dorsally with two stronger bristles arranged longitudinally, no transverse row (Fig. 3c). Coxal processes inconspicuous, sickle-shaped. Foretarsus ventrally with a row of about 6 long, pointed, simple bristles. Mid and hind tarsus with a similar row of about 10 bristles. Claws very long and slender with 4-7 moderate denticles (Fig. 3e, f).

Abdomen: Abdominal segments with short or very short posterolateral processes, lateral margins provided with long or very long thin bristles (Fig. 3a, b). Posteriomedian process of tergum II short, bluntly pointed. Hind margin of tergum VII and VIII with very

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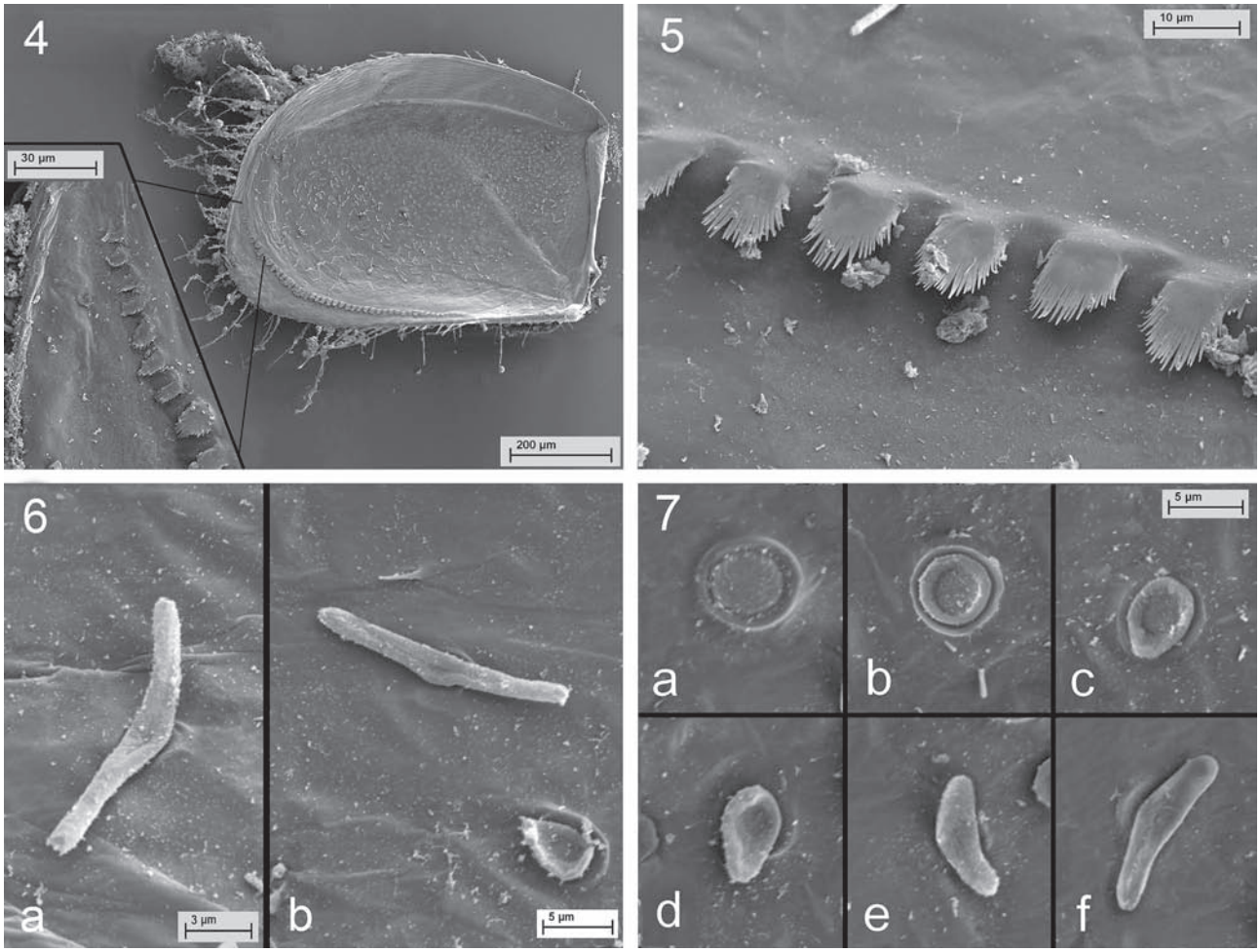


Fig. 4. *Liebenauis tenuipes* n. gen., n. sp., larva. –Operculate gill, ventral side. Inlay shows posterior end of microtrichia row.
Fig. 5. *Liebenauis tenuipes* n. gen., n. sp., larva. –Operculate gill, details of microtrichia row.
Fig. 6. *Liebenauis tenuipes* n. gen., n. sp., larva.–Ventral side of operculate gill, two examples (a, b) of completely developed finger-shaped chloride cells.
Fig. 7. *Liebenauis tenuipes* n. gen., n. sp., larva. –Ventral side of operculate gill, different developmental stages from typical flat (a) to finger-shaped chloride cells (f).

long bristles, erect and posteriorly bowed in lateral view; number reduced on tergum VIII; tergum IX and X with small, blunt denticles. Hind part of sternum IX moderately protruding posteriorly, broadly rounded, with thin bristles apically strongly bent mediad (Fig. 3a); shagreen on dorsal side absent. Operculate gill moderately domed, with protruding postero-lateral corner, lateral margin nearly straight, hind margin provided with long bristles, shorter ones on inner margin (Fig. 4); Y-shaped ridge weakly developed, posterior branch more or less reduced, inner branch with few short bristles on base, few long bristles scattered on sublateral and posterior surface. Ventral side with short row of small, round microtrichia (Fig. 5) beginning a third of its length away from anterior-lateral corner running to the inner end of the postero-lateral protrusion (Fig. 4). Row does not reach hind margin of gill (Fig. 4, small frame); distance between end of row to hind margin about 1/25 of gill length. A large area medially to microtrichia row provided with numerous, finger-shaped cuticular outgrowths (Fig. 6a-b) that represent modified chloride cells. Chloride cells generally consist of an outer bulged ring and a central plate. Fig. 7 shows transitional stages from such typical chloride cells (a) to finger-shaped chloride cells (f) with intermediate stages that show a gradual recession of outer ring (b-e). The inner plate develops another marginal bulge (b) protruding more and more in two opposite directions (c-e), finally forming finger- or pine needle-shaped outgrowths (Figs 6a-b, 7f).Gill I very long (see Fig. 1), about as long as gill II. 25 filaments on gill III each possess 3 or 4 branches.

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Caenis Stephens 1835
Caenis ungulata **n. sp.**
(Figs 8-12)

Material examined

Holotype, ♂ larva (microslide), PNG 102, Papua New Guinea, Marobe, Wagau, Herzog Mts., 06°51′067 S, 146°48′068 E, 19.11.2006, Balke & Kinibel leg. – Other material (*C. ungulata* c.f., dark form): PNG 168, Papua New Guinea, Central prov., Kokoda Trek., 09°19′236 S, 147°31′791 E, 01.2008, 320m, 3 ♀ larvae, Posman leg. [all MZL]

Etymology

The species epithet refers to the long and thin claws, Latin *ungulae*.

Larva

Measurements and colouration

♀ larva, subadult (fully grown, but not yet last instar), body length 3.8mm, cerci broken off.

Colouration of cuticle: Head yellowish. Pro- and mesonotum yellowish brown. Abdomen and legs white or yellowish-white.

Epidermal pigmentation. Pattern on dorsal side as in Fig. 8.

Morphology

Cuticle smooth or very finely denticulated (parts of mesonotum, operculate gill and abdominal terga).

Head: Genae slightly bulged. Mandibles dorsolaterally with a field of bristles of moderate length.Third segment of maxillary palp 1.5 times as long as second segment. Second segment of labial palp nearly two times as long as third one (along the centre-line). Setation of mouthparts similar to that of *Liebenauis tenuipes*; bristles on inner side of maxillary palp segment III narrower.

Thorax: Sides of pronotum subparallel, more or less convex (Figs 8, 9). Femora about 3-3.5 times as long as





Fig. 8. *Caenis ungulata,*n. sp.,larva, habitus.
Fig. 9. *Caenis cf ungulata*, n. sp.,larva, dark morph, habitus.

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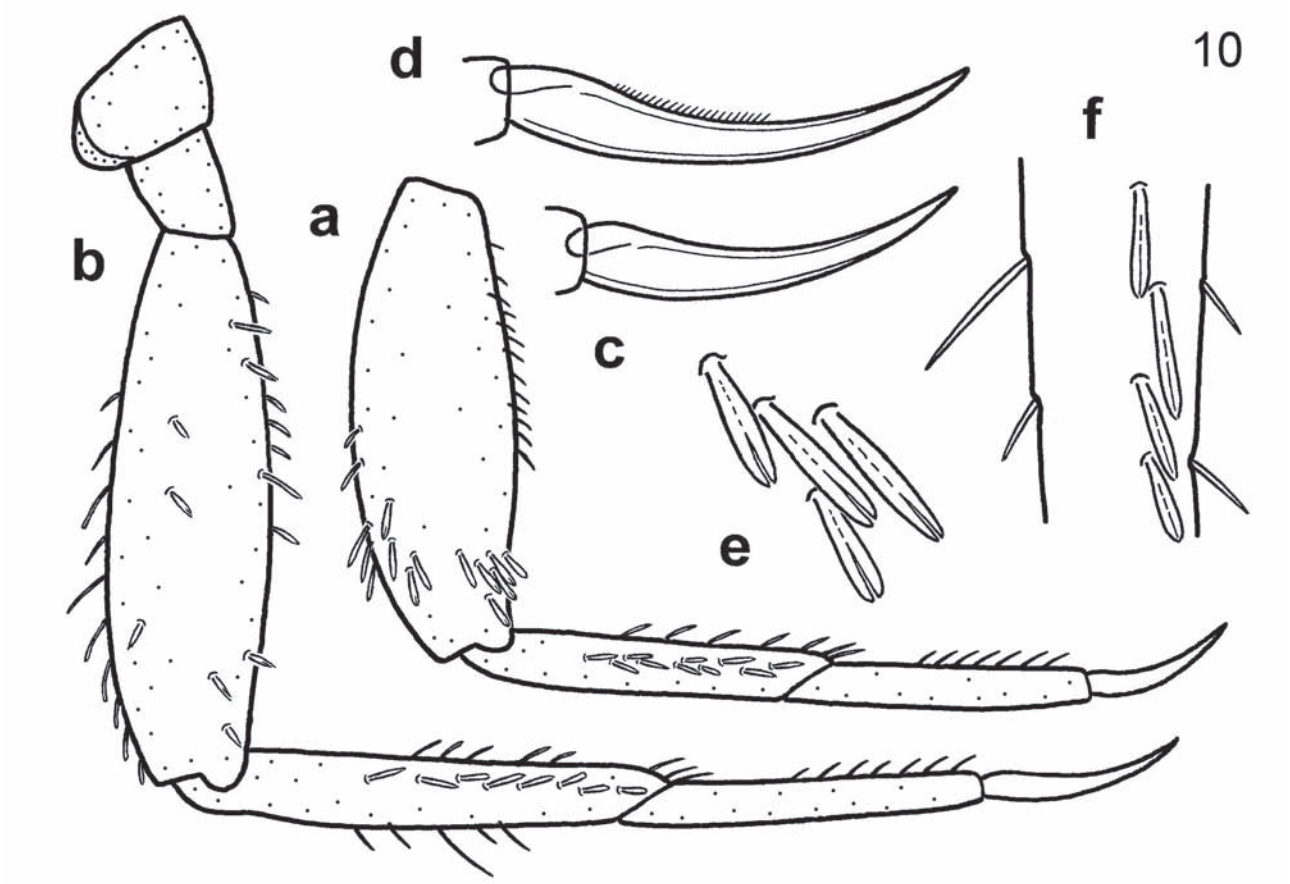
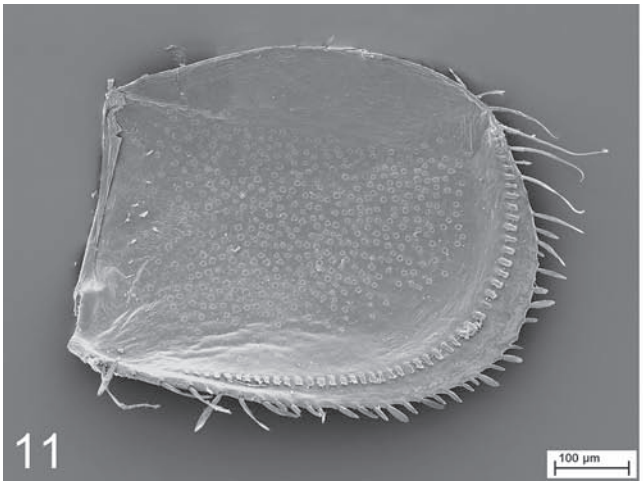


Fig. 10. *Caenis ungulata* n. sp., larva.– **a.**Foreleg.– **b.** Hind leg.– **c.** Fore claw.– **d.** Hind claw. – **e.** bristles from the transverse row on forefemur. – **f.** bristles from the longitudinal row on mid tibia.



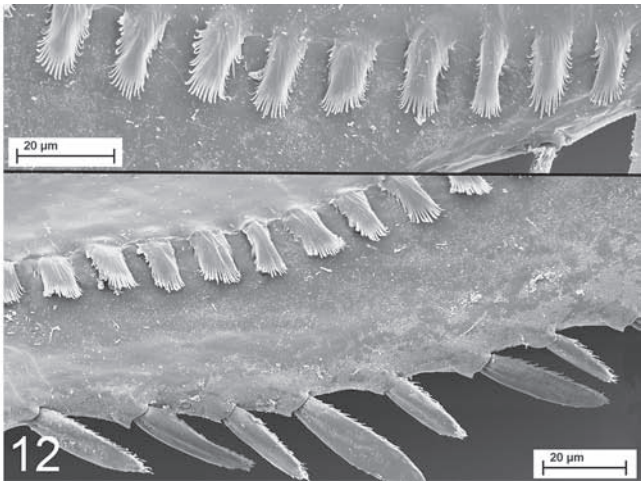


Fig. 11. *Caenis ungulata* n. sp., larva. – Operculate gill, ventral view.
Fig. 12. *Caenis ungulata* n. sp., larva. – Operculate gill. Microtrichia from posterior end of the row (above) and from median region (below).

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wide; tibiae about 7 times as long as wide. All leg margins with short or moderate more or less spatulate bristles. Few bristles also on dorsal side of femora (Fig. 10a, b), on tibiae more or less irregular rows of 8-10 spatulate bristles (Fig. 10f). Forefemur dorsally with a transverse irregular row or band of strong, spatulate bristles (Fig. 10a, e). Coxal processes broadly sickle-shaped. Foretarsus ventrally with a row of about 10 long, pointed, simple bristles. Hind tarsus with a row of about 10 pinnate bristles and a shorter row with 5 pinnate bristles. Claws very long and slender, fore and mid claws without denticles (Fig. 10c), hind claw with a dense row of very thin microdenticles (Fig. 10d).

Abdomen: Abdominal segments with short posterolateral processes, laterally provided with thin, blunt bristles, very short ones on posterior and moderate ones on anterior segments. Hind margin of tergum II with a short, broad triangle (the triangle is erected dorsally and thus not visible in Fig. 8). Hind margin of tergum VII with strong, spatulate bristles of moderate length, tergum VIII-X with

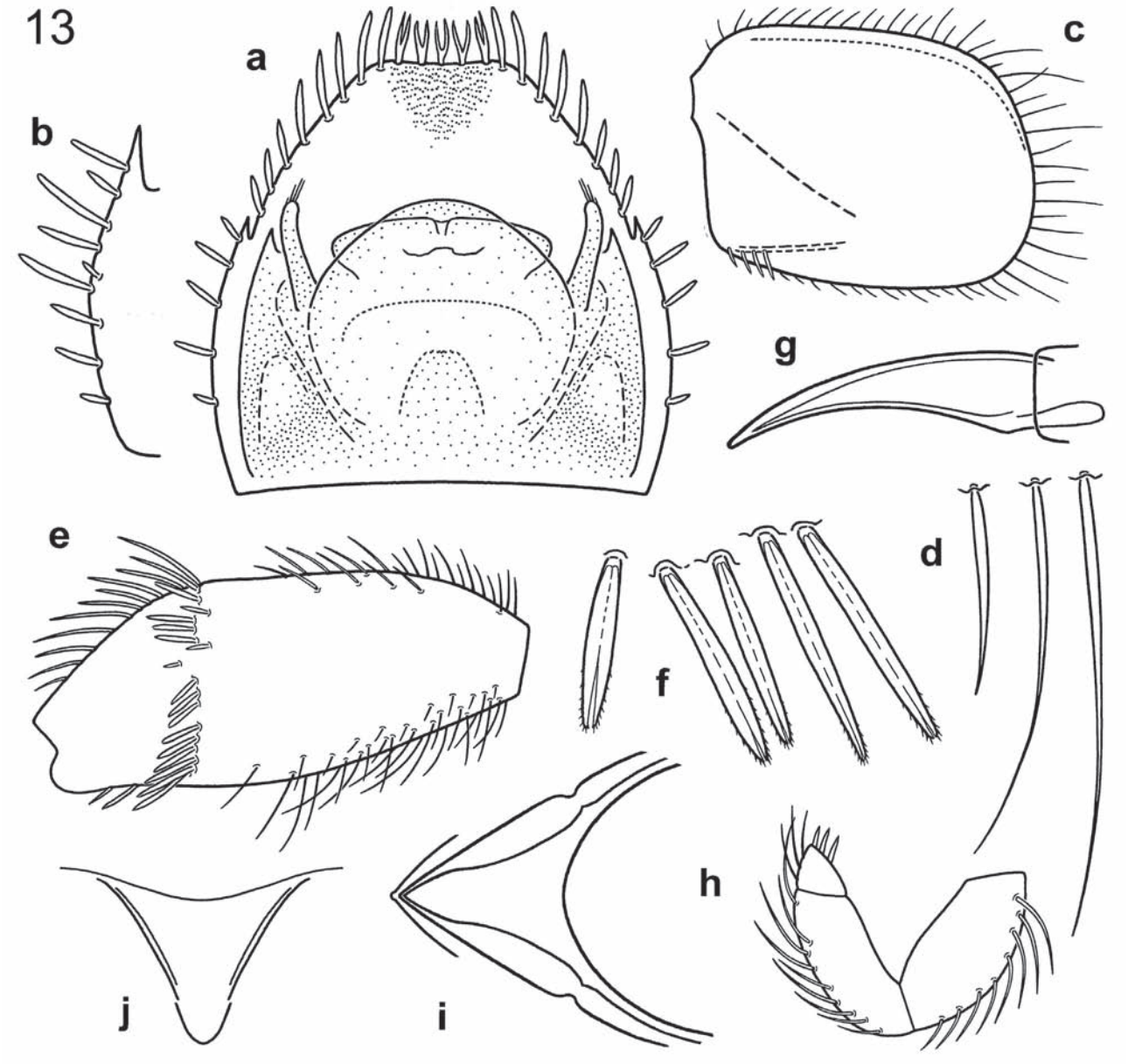


Fig. 13. *Caenis marawakensis* **n. sp.**, larva. – **a.** sternite IX, ♂, with subimaginal genitalia. – **b.** Marginal setation of segment VII.– **c.** Operculate gill.– **d.** Bristles from hind margin of operculate gill. – **e.** Forefemur.– **f.** Bristles from transverse row on forefemur. – **g.** Hind claw. – **h.** Labial palp. – **i.** Subimaginal scutellum. – **j.** Subimaginal prosternal triangle.

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small denticles. Hind part of sternum IX flat and broadly rounded, on the entire length densely provided with strong, spatulate bristles; shagreen on dorsal side consists of irregular transverse rows of very small denticles. Operculate gill with short or moderate spatulate bristles on lateral margin, becoming longer, thin and pointed on hind margin (Fig. 11); inner margin with short and thin bristles; Y-shaped ridge reduced, inner ridge with about 7 spatulate bristles. Ventral side with a row of more or less elongated microtrichia reaching the posterior median corner of the gill (Figs 11, 12). Gill I a little more than half as long as gill II.

In the Owen-Stanley-Range, about 280 km SSE from the locus typicus of *Caenis ungulata*, three ♀ larvae were found that are morphologically nearly identical with the holotype of *Caenis ungulata*, except of showing a much darker colouration (compare Figs 8 and 9). It is impossible to decide with the limited available material, if the dark specimens represent a separate species or only a different colour morph of *Caenis ungulata*.

Differential diagnosis

Caenis ungulata can be distinguished from all other *Caenis* larvae by the following combination of characters: Second segment of labial palp nearly twice as long as the third. Anterolateral margin of mesonotum without tongue-shaped process. Forefemur dorsally with a transverse irregular row or band of strong, spatulate bristles. Coxal processes broadly sickle-shaped. Tibiae with longitudinal rows of spatulate bristles. Claws very long and slender, without denticles, hind claw with a dense row of very fine microdenticles (Fig. 10c and d). Hind margin of tergum VII with moderate bristles, tergum VIII-X with small denticles. Operculate gill with short or moderate spatulate bristles on lateral margin, becoming longer, thin and pointed on hind margin (Fig. 11). Posterior branch of Y-shaped ridge reduced. Row of microtrichia on ventral side running close to lateral and hind margin, reaching the posterior median corner of the gill (Fig. 11).

Caenis marawakensis **n. sp.**
(Fig. 13)

Material examined

Holotype. ♂ larva (on microslide): PNG 90, Papua New Guinea, Gulf prov., Marawaka, Mala, 7°5′664S, 145°44′467E, 1400m, 11.11.2006, Balke & Kinibel leg.–other material: PNG 171, Papua New Guinea, Central prov., Kokoda Trek, 9°14′339S, 147°40′538E, 01.2008, 1400m, 2♀ larvae, Posman leg. [MZL]

Etymology

The species epithet refers to the locality Marawaka where the holotype was found.

Male subimago

The holotype is a male last instar larva. The following subimaginal features are therefore visible and can be described: shape of antenna, arrangement of prosternal ridges, shape of scutellum, posterolateral processes on abdomen, and genitalia:

Base of antennal flagellum not dilated. Prosternal ridges forming a triangle with straight or slightly concave lateral sides, the broadly rounded tip slightly stepped anteriorly (Fig.13j). Tarsomeres 2-4 of foretarsus apically not broadened. Scutellum narrow with pointed posterior tip (Fig. 13i). Abdominal segments with moderate posterolateral processes. Sternite IX and subimaginal genitalia as in Fig. 13a. Penis flatly oval with rounded-triangular lobes. Forceps of moderate length, with an apical tuft of spines, shaft about 3.3 times as long as tuft of spines.

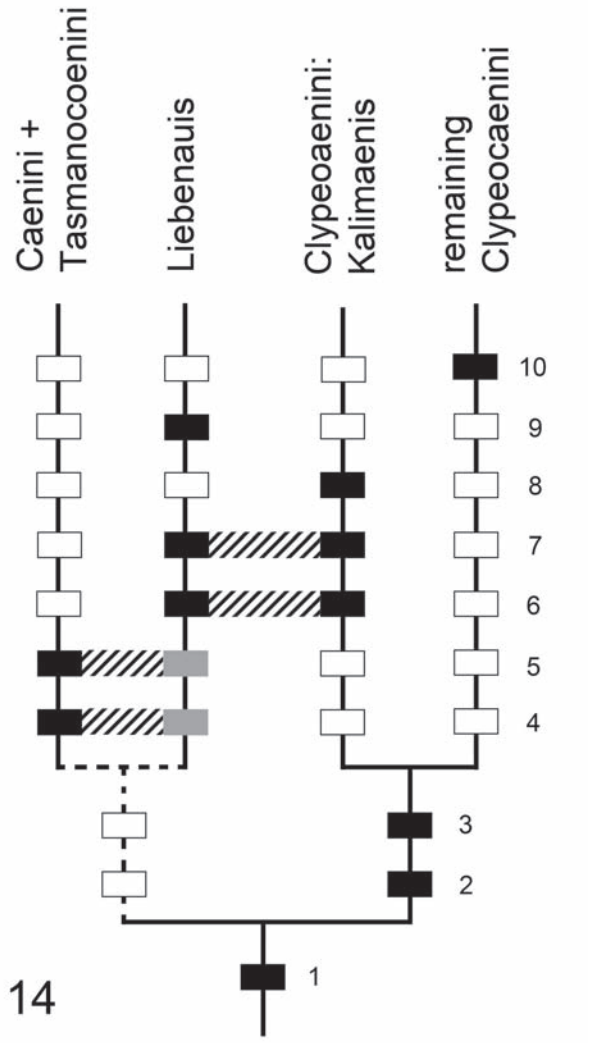


Fig. 14. Phylogenetic argumentation scheme illustrating possible position of *Liebenauis* within Caeninae. White square : plesiomorphic character state ; grey square : intermediate character state ; black square : apomorphic character state, shaded areas indicate potentially convergent characters.

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Larva

Measurements and colouration

Male last instar larva, body length 2.8mm, length of cerci 1.5 mm.

Colouration of cuticle brown to yellowish.

Morphology

Head: Genae slightly bulged out. The whole lateral margin of mandibles and adjoining surface densely covered with long and strong pointed bristles. Similar spines also on pedicles and ventrally of eyes on clypeus. Third segment of maxillary palp 1.2 times as long as second segment. Third segment of labial palp very short, second segment about 3 times as long as the third (along the centre-line); proportions and setation of labial palp as in Fig. 13h.

Thorax: Sides of pronotum slightly convex and diverging anteriorly, anterior corners each with about 7 strong bristles similar to those on head. Coxal processes inconspicuous. Forefemur on dorsal side with a dense transverse row of strong, blunt or spatulate bristles apically slightly frayed (Fig. 13e, f); similar, somewhat longer bristles on hind margin apically from transverse row. All femora broadened. Mid and hind femora marginally with long and strong bristles, few bristles also on dorsal side. Fore and mid tibia with a short longitudinal row of about 5 short pointed bristles, lacking on hind tibia. Fore- and mid tarsus ventrally with a row of 5-6 small and simple bristles. Hind tarsus with a row of 6-7 clearly longer, more or less frayed bristles. Claws relatively small and short, without denticles (Fig. 13g). Except of claws, proportions of legs correspond to those of *Caenis ungulata* (like Fig. 10a, b).

Abdomen: Abdominal segments with posterolateral processes of moderate length; margins with moderate blunt bristles, longer on anterior segments (Fig. 13a, b). Posteriomedian process of tergum II forming an equilateral triangle with pointed tip, hind margin laterally bowed and keeled. Hind margin of tergum VII and VIII with long, strong bristles, tergum IX and X with denticles. Hind margin of sternum IX medially cut or slightly concave, with strong bristles, the median ones deeply bifurcate (Fig. 13a). Dorsal side of sternite IX with a large shagreen field consisting of transverse rows of denticles (Fig. 13a). Operculate gill (Fig. 13c) with moderate, relatively broad bristles on lateral margin, bristles on hind margin longer, basally broadened, apical part hair-like (Fig. 13c, d). Posterior part of Y-shaped ridge reduced, inner ridge with few short and strong basal bristles. Ventral row of short microtrichia running very closely to lateral margin, ending in the middle of hind margin (Fig. 13c). Gill II nearly 2.5 times length of gill I.

Differential diagnosis

Caenis marawakensis n. sp. can be distinguished from all other *Caenis* species by the following combination of characters: Males: Base of antennal flagellum not dilated. Prosternal triangle with slightly stepped, rounded tip (Fig. 13j). Tarsomeres 2-4 of foretarsus apically not broadened. Scutellum narrow with pointed tip (Fig. 13i). Penis oval with rounded-triangular lobes. Forceps of moderate length, with an apical tuft of spines (Fig. 13a). Larva: Anterior margin of head with numerous long and strong pointed bristles. Third segment of labial palp very short, second segment about 3 times as long as the third (Fig. 13h). Anterolateral margin of mesonotum without a tongue-shaped process. Forefemur dorsally with a dense transverse row of strong, blunt or spatulate bristles apically slightly frayed (Fig. 13e, f). Coxal processes inconspicuous. Claws relatively small, without denticles. Hind

Table 1.Characters used in the phylogenetic argumentation scheme (Fig. 14).

		Apomorphic character state	Plesiomorphic character state
1	Forecoxae medially	approximated	widely separated
2	Outer margin of gill III	with not more than 8 filaments consisting of 3 or more branches each	with 15 to 25 filaments consisting of 3 or more branches each
3	Outline of head, lateral view	with bulges, clypeus ± protruding	evenly bowed
4	Gill II, ventral row of microtrichia	reaching hind margin of gill	not reaching hind margin of gill
5	Gill II	with regular row of complex, scale-shaped microtrichia	bands or irregular rows of spines, clusters of spines, or simple scales
6	Legs	long and slender, femora narrowed	shorter, femora broad
7	Claws	long and slender	shorter
8	Maxillary palp	elongated, segment 1 conical, segments 2+3 coiled	Shorter, segments 2+3 not coiled
9	Ventral side of operculate gill	with modified chloride cells	without modified chloride cells
10	Mesonotum	broadened, outline of body more or less evenly curved	not broadened, outline ± irregular

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margin of tergum VII and VIII with long, strong bristles, tergum IX and X with denticles. Sternum IX medially cut or slightly concave, with strong bristles, the median ones deeply bifurcate (Fig. 13a). Posterior part of Y-shaped ridge reduced. Ventral row of microtrichia running very close to lateral margin ending in the middle of the hind margin (Fig. 13c).

4 Discussion

4.1 Phylogeny

The exact phylogenetic position of *Liebenauis tenuipes* is not easy to assess (see also Fig.14, Table 1, characters 1-10): While it can be undoubtedly placed within Caeninae due to its approximated forecoxae (1), its phylogenetic position within Caeninae is not obvious.

Liebenauis does not share any synapomorphy of Clypeocaenini, namely gill III possessing at most 8 filaments with 3 or more branches each (2) and bulged outline of head in lateral view (3) are not present in *Liebenauis tenuipes*. Two characters common with the Clypeocaenini genus *Kalimaenis*, namely the long and slender legs (6) and elongated claws (7) probably are parallel developments.

On the other hand, the two main autapomorphic characters of Caenini + Tasmanocoenini (4, 5) are not typically developed in *Liebenauis tenuipes.* While in Caenini + Tasmanocoenini the ventral row of microtrichia in gill II is reaching the hind margin of the gill cover, it is only closely approximated to the hind margin in *L. tenuipes*, thus constituting an intermediate state compared to the condition in Clypeocaenini (4). Also, in Caenini + Tasmanocoenini the ventral mictrotrichia are organised in a regular row of complex, scale-shaped microtrichia, while in Clypeocaenini bands or irregular rows of spines, clusters of spines, or simple scales are present (5). Although in *L. tenuipes* the microtrichia of the middle sector of the row are relatively complex, they become clearly smaller and irregularly shaped towards the posterior end of the row not reaching the hind margin of the gill. The anterior part of the row is shortened so that the basal third of the gill is without microtrichia. Hence the degree of complexity of microtrichia in *L. tenuipes* can be interpreted as intermediary stage between the plesiomorphic condition in Clypeocaenini and the apomorphic condition in Caenini + Tasmanocoenini (5). So the character distribution within Caeninae would account for a sister group relationship between *L. tenuipes* and Caenini + Tasmanocoenini, provided the long legs with long claws represent a parallel development in *Kalimaenis* (and also in *Caenis ungulata,* see below). *Kalimaenis* moreover shows apomorphic hind claws with groups of fused microdenticles. Also apomorphic are elongated maxillary palps with conical segment 1 and coiled segments 2 and 3 (8). The remaining Clypeocaenini share a synapomorphic mesonotum (see also Fig. 14), which is broadened, and a more or less evenly curved outline of body (10). A unique apomorphy of *Liebenauis* is the presence of modified chloride cells of pine needle shape in the central part of the operculate gill, medially to the row of microtrichia (9). Such modified chloride cells have not been found in other Caenidae. In *Caenoculis* there may be similar structures, but these occur in the peripheral parts of the operculate gill, well lateral of the row of microtrichia, where chloride cells are not present. Hence these structures in *Caenoculis* cannot be modified chloride cells, but rather are mere cuticular modifications.

Caenis ungulata shares the apomorphic characters of the tribes Caenini/Tasmanocoenini, i.e. operculate gill with a regular row of complex, scale-shaped microtrichia (4) that reaches the hind margin of the gill (3). As its habitus and other characters are *Caenis*-like, the species is here assigned to the genus *Caenis*, although it is characterized by its long and thin claws that have not been found in any other species of *Caenis*.

4.2 Biogeography

Liebenauis tenuipes is for now only reported from Sumatra, thus its distribution at present is restricted west to the Wallace Line, which also accounts for all hitherto described species of *Caenis* from the Sunda Archipelago. However, both new species, *C. ungulata* and *C. marawakensis*, are the first known species of *Caenis* that are reported from New Guinea, thus marking the first records of *Caenis* from the Sunda Archipelago east of the Wallace Line. Moreover, there are several species of *Caenis* also reported from different Pacific islands east of the Wallace Line (Flowers 1990; Evenhuis 2006, Malzacher & Staniczek 2007, Ulmer 1924), so its previous absence from the eastern Sunda Archipelago is due to insufficient collecting rather than reflecting any biogeographic borders. *Tasmanocoenis novaeguineae* van Bruggen, 1957 was hitherto the only known species of Caenidae from New Guinea. The genus *Tasmanocoenis* is otherwise only known from Australia, which would perfectly fit with its biogeographical restriction east to the Wallace Line. However, the figure of the genitalia in the original description (van Bruggen 1957) rather resembles genitalia that are characteristic for *Caenis*. This would make *T. novaeguineae* yet another species of *Caenis* reported east of the Wallace Line. However, as the material was not available to us, we refrain here from designating a new combination.

All available distributional records thus point to a broad distribution of *Caenis* throughout the Oriental and Australian Region with the exception of Australia itself, where it is replaced by *Tasmanocoenis*.

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