

New mayfly species of *Caenis* and *Kalimaenis* from Thailand and descriptions of two new genera of the subfamily Caeninae (Ephemeroptera: Caenidae)

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New mayfly species of *Caenis* and *Kalimaenis* from Thailand and descriptions of two new genera of the subfamily Caeninae (Ephemeroptera: Caenidae)

PETER MALZACHER & NARUMON SANGPRADUB

Abstract

Six new species of *Caenis* from Thailand are described herein: *Caenis ludovici* **n. sp.**, *Caenis nasuta* **n. sp.**, *Caenis longiforcipata* **n. sp.**, *Caenis karenae* **n. sp.**, *Caenis obtusostilata* **n. sp.** and *Caenis acutostilata* **n. sp.**, as well as the larvae of *Caenis picea* Kimmins, 1947 and *Caenis ulmeriana* Malzacher, 2013, which were so far only known as males. Furthermore, a new species of the genus *Kalimaenis*, *Kalimaenis procera* **n. sp.**, is described. Also described from the same area are two new genera of the subfamily Caeninae: *Elatosara* **n. gen.** (Type species *Elatosara phanomensis* **n. sp.**) most probably belongs to the tribe Clypeocaenini; *Thainis* **n. gen.** (Type species *Thainis kalimaenoides* **n. sp.**), is classified within the tribe Caenini. The phylogeny of the new genera is discussed. A larval key to the Caeninae from Thailand is provided and the key to the male *Caenis* of the Oriental region (MALZACHER 2015) is replenished.

Keywords: New species, *Caenis*, *Kalimaenis*, new genera, *Elatosara*, *Thainis*, phylogeny, Thailand.

Zusammenfassung

Sechs neue Arten der Gattung *Caenis* aus Thailand werden beschrieben: *Caenis ludovici* **n. sp.**, *Caenis nasuta* **n. sp.**, *Caenis longiforcipata* **n. sp.**, *Caenis karenae* **n. sp.**, *Caenis obtusostilata* **n. sp.** und *Caenis acutostilata* **n. sp.**, wie auch die Larven von *Caenis picea* Kimmins, 1947 und *Caenis ulmeriana* Malzacher, 2013, Arten, von denen bisher nur die Männchen bekannt waren. Weiterhin wird eine neue Art der Gattung *Kalimaenis*, *Kalimaenis procera* **n. sp.** beschrieben. Ebenfalls aus demselben Gebiet beschrieben werden zwei neue Gattungen der Unterfamilie Caeninae: *Elatosara* **n. gen.** (Typus-Art *Elatosara phanomensis* **n. sp.**), eine Gattung, die sehr wahrscheinlich dem Tribus Clypeocaenini zuzuordnen ist, und *Thainis* **n. gen.** (Typus-Art *Thainis kalimaenoides* **n. sp.**), eine Gattung des Tribus Caenini. Die Phylogenie der neuen Gattungen wird diskutiert, ein Schlüssel für alle Larven der Caeninae Thailands erstellt und der Schlüssel für die Männchen von *Caenis* der Orientalis (MALZACHER 2015) ergänzt.

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1 Introduction

MALZACHER (2015) revised the species of *Caenis* of the Oriental region. Besides several ‘species inquirenda’,

insufficiently described by different authors during the 20th century, he listed 14 species that can be described based on modern diagnostic criteria. Five of them are also recorded from Thailand: *Caenis nigropunctatula*

Malzacher, 2013, *Caenis ulmeriana* Malzacher, 2013, *Caenis guttata* Malzacher, 2013, *Caenis gephyria* Malzacher, 2013, and *Caenis picea* Kimmins, 1947. Six new species are described herein and larval specimens can be assigned to two species previously known as males only, *Caenis picea* Kimmins, 1947 and *Caenis ulmeriana* Malzacher, 2013.

Caenis is the only genus of the subfamily Caeninae so far known from Thailand. Another genus, *Clypeocaenis*, is known from Iran, India, Vietnam (SOLDÁN, 1978, 1983), and Borneo (MALZACHER 2013), and thus can also be expected from Thailand. A new species of *Kalimaenis*, another genus described from Borneo (MALZACHER 2013), is described herein from a few larvae. Finally, the larvae of two new genera of Caeninae are described.

Within Brachycercinae, two species of two genera of the new tribe Caenoculini could be recorded from Thailand recently: *Caenoculis* cf. *bishopi* Soldán and *Tigrocercus dangi* (Soldán, sub. *Caenoculis*) (MALZACHER & SANGPRADUB 2017).

Acknowledgements

Our special thanks go to the administrations of Nam Nao National Park, Kaeng Krachan National Park, Phu Khiao Wildlife Sanctuary, Phu Phan National Park, Thap Lan National Park, Phu Kradueng National Park, and the Mekong River Commission for collecting and research permissions, to SUSANNE LEIDENROTH, KARIN WOLF-SCHWENNINGER and MILAN PALLMANN (SMNS) for taking SEMs and macro photographs, to ARNOLD STANICZEK (SMNS) and MICHEL SARTORI (Musée de Zoologie, Lausanne) who kindly read the manuscript and provided valuable suggestions.

2 Material and methods

The investigated material is preserved in 75% ethanol. Specimens were collected by one of us (NS) within the framework of ecological investigations in tributaries of the Mekong River, northeast Thailand. The holotypes are stored in the State Museum of Natural History, Stuttgart, Germany, some paratypes also in the Applied Taxonomic Research Center, Khon Kaen University, Thailand.

The abbreviations used on labels of the coll. Sangpradub refer to provinces, rivers or National Parks of Thailand: CHI = Chi River, CYP = Prov. Chaiyaphum, KKJ = Kaeng Krachan National Park, LAO = Laos, MUN = Mun River, MRC = Mekong River, NKK = Prov. Nakhon Ratchasima, PCB = Prov. Petchabun, POG = Phong River, SKK = Prov. Sakon Nakhon, SKP = Prov. Nakhon Phanom, THW = Tad Hong Waterfall.

Specimens used for SEM were dehydrated through a step-wise immersion in ethanol and then dried by critical point drying. The mounted material was coated with a 20 nm Au layer, examined and photographed with a Zeiss EVO LS 15 scanning electron microscope. Macro photographs were taken with a Leica DMC 5400 digital camera on a Leica Z16APO Macroscopic, processed with Leica Application Suite™ Version 3.1.0 and Helicon Pro 6.7.1 to obtain combined photographs with extended depth of field. Digital photographs were enhanced by using PhotoFiltre6.5.2 (<http://www.photofiltre-studio.com>).

3 Systematic account

3.1 Genus *Caenis* Stephens, 1835

Caenis ludovici Malzacher, n. sp.
(Fig. 1)

Material examined

Holotype, ♂ larva (on microslide): SKP 1.2, Thailand, Nakhon Phanom Prov., Tat Kham Waterfall, 17°57'03.65"N, 104°09'13.30"E, 190m, 20.03.2012, N. Sangpradub leg., SMNS_EPH_007784_M. – Paratype, 1 ♂ larva, same data as holotype.

Etymology

The species is dedicated to my third grandchild Ludovico.

Male subimago

The holotype is a last instar male larva. The following subimaginal features are therefore visible and can be described:

Base of antennal flagellum dilated, dilated part half as wide and about three fourth as long as pedicel. Prosternal ridges forming a narrow trapezoid with straight or slightly concave lateral sides. Segments 2 and 3 of fore tarsus each with a long apico-median projection, segment 4 with two projections, a lateral and a median one (Fig. 1c). Scutellum very broad. Abdominal segments with very short posterolateral processes. Sternite IX and subimaginal genitalia as in Fig. 1a. Penis narrow, postero-laterally broadly rounded, ventrally with 4–5 parallel folds forming a V. Forceps straight and very broad, with a strong, stepped apical spine (Fig. 1b).

Larva

Measurements and colouration

Male larva of last instar, body length 3.8 mm, length of cerci 2.5 mm.

Colouration of cuticle light yellowish-brown to yellowish. Epidermal pigmentation: Traces of pigments on vertex, pronotum and abdominal terga. Pronotum with two paramedian spots. Operculate gills brownish.

Morphology

Cuticle: surface scattered with long or very long, thin hair-like bristles, particularly on marginal parts of body, on wing buds and on operculate gills; most of these bristles are erected, body therefore seems to have a halo of hairs.

Head: Genae not bulging out. Mandibles dorsolaterally with numerous moderate bristles. Labial palp besides the marginal strong spines laterally with numerous long hair-like bristles. Similar bristles scattered on prementum. Ratios of maxillary and labial palps and their segments see Table 1.

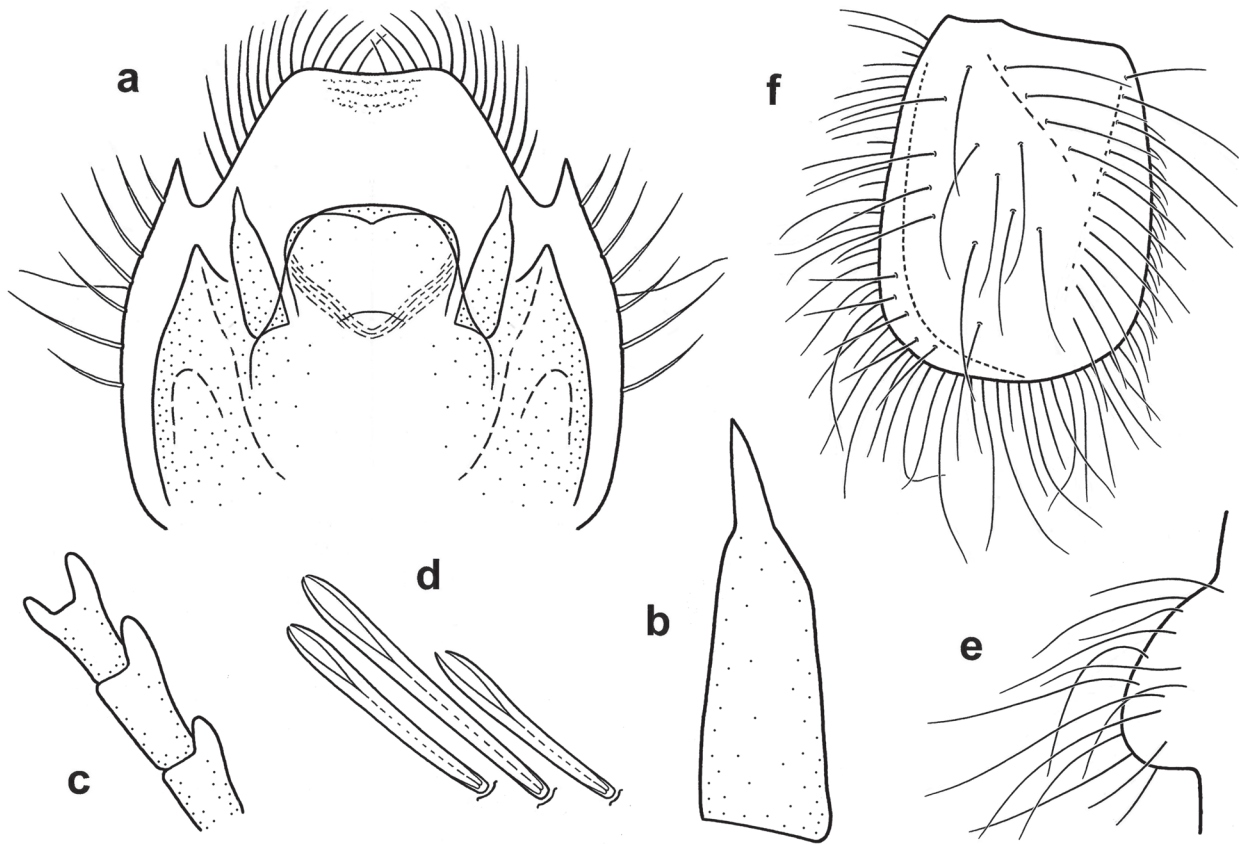


Figure 1. *Caenis ludovici* n. sp., larva. – **a.** Sternite IX, ♂ with subimaginal genitalia. **b.** Forceps. – **c.** Segments 2–4 of male subimaginal foreleg. – **d.** Bristles from the transverse row on forefemur. – **e.** Nose-shaped process from antero-lateral margin of mesonotum. – **f.** Operculate gill.

Thorax: Sides of pronotum convex and slightly diverging anteriorly, with about 12 long bristles, between them short, more or less spatulate ones. Sides of mesonotum with an anterior-lateral nose-shaped projection provided with long bristles (Fig. 1e). Coxal processes inconspicuous. Forefemur on dorsal side with a dense transverse row of about 10 (7 + 3) long, spatulate bristles (Fig. 1d); similar, but longer bristles on margin apically from the transverse row, together with few very long pointed bristles. Mid and hind femora marginally and basally on dorsal side with very long, hair-like bristles, apically with spatulate ones, a little narrower than those from the transverse row, a little stronger, long bristles on tibiae. Foretarsus ventrally with 3–4 very short and inconspicuous simple bristles. Mid and hind tarsus with a row of 5–6, somewhat longer bristles. Hind tarsus additionally with an apical pinnate bristle. Claws slender, slightly bowed, with few, small denticles.

Abdomen: Abdominal segments with posterolateral processes of moderate length; margins with long bristles, basally more or less broadened (Fig. 1a). Bristles of all segments (III–IX) of similar shape and length, about 12 on

segment VII, about 7 on segment IX. Posteriomedian process of tergum II very short, broadly triangular. Hind margin of tergum VII–IX with very long, hair-like bristles, tergum X with small denticles. Hind margin of sternum IX medially cut or slightly concave, with long bristles, the median ones a little shorter and bent medially (Fig. 1a). Shagreen on dorsal side of sternite IX consisting of about 3 long irregular rows of denticles parallel to hind margin (Fig. 1a). Operculate gill with long or very long bristles on lateral and hind margin, bristles on inner margin shorter; dorsal surface with very long, erect bristles, the longest more than half as long as width of gill (Fig. 1f). Y-shaped ridges inconspicuous, posteriorly reduced, marked by rows of long bristles. Ventral row of microtrichia running relatively close to lateral margin ending in the middle of hind margin (Fig. 1f). Gill I more than half as long as gill II, with segment I a little elongated.

Differential Diagnosis

Caenis ludovici can be distinguished from all other *Caenis* species by the following combination of characters:

Male: Base of antennal flagellum dilated. Segments 2 and 3 of foretarsus each with a long apico-median projection. Penis narrow, postero-laterally broadly rounded, ventrally with 4–5 parallel folds forming a V (Fig. 1a). Forcipes straight and very broad, with a strong, stepped apical spine (Fig. 1b). Larva: Cuticle, particularly marginal parts of body, wing buds, and operculate gills scattered with long, erected hair-like bristles. Sides of pronotum with about 12 long bristles, between them with short, more or less spatulate ones. Sides of mesonotum with an anterior-lateral nose-shaped projection provided with long bristles (Fig. 1e). All claws basally with few small denticles. Hind margin of tergum VII–IX with very long hair-like bristles, tergum X with small denticles. Hind margin of sternum IX medially cut or slightly concave, with long bristles.

Caenis nasuta Malzacher, **n. sp.**
(Fig. 2)

Material examined

Holotype, ♂ larva (microslide), CYP 3.2, Thailand, Chaiyaphum Prov., Huai Tat Fa, Phu Khiao Wildlife Sanctuary, 07.05.1996, **SMNS_EPH_007785_M**.

Paratypes: CYP 3.4, Thailand, Chaiyaphum Prov., Tat Fa Noi, Phu Khiao Wildlife Sanctuary, 07.02.1996, 1♀ larva. – CYP 3.5, Thailand, Chaiyaphum Prov., Huai Mai Sod Noi, Phu Khiao Wildlife Sanctuary, 15.11.1998, 3♂ larvae, 1♀ larva. – CYP 3.6, Thailand, Chaiyaphum Prov., Huai Mai Sod Yai, Phu Khiao Wildlife Sanctuary, 15.11.1998, 1♂ larva, 2♀ larvae.

Other material: PCB 5.3, Thailand, Petchabun Prov., Yakraue, Nam Nao National Park, 16° 44' 21.60"N, 101° 34' 28.84"E, 24.04.2002, 3♀ larvae. – PCB 5.6, Thailand, Petchabun Prov., Yakraue, Nam Nao National Park, 16° 44' 21.60"N, 101° 34' 28.84"E, 17.08.2014, 1♀ larva. – PCB 5.9, Thailand, Petchabun Prov., Yakraue, Nam Nao National Park, 16° 44' 21.60"N, 101° 34' 28.84"E, 24.04.2002, 3♂ larvae. – CYP 1.6, Thailand, Chaiyaphum Prov., Huai Tat Fah Noi, 16° 27' 24.50"N, 101° 47' 41.10"E, 28.03.2000, 1♀ larva. – SKK 1.1, Thailand, Sakon Nakhon Prov., Huai Ven Prai, 20.04.1998, 2♀ larvae. – LOI 3.1, Thailand, Loei Prov., Huai Wang Yow, 16° 58' 94.20"N, 101° 46' 60.50"E, 09.11.2002, 2♀ larvae. – SKP 1.2, Thailand, Nakhon Phanom Prov., Tat Kham Waterfall, 17° 57' 03.65"N, 104° 09' 13.30"E, 20.03.2012, 1♀ larva. – THW 1.1, Thailand, Loei Prov., Tad Hong Waterfall, Phu Kradueng National Park, 16° 48' 11.60"N, 101° 34' 52.90"E, 09.12.2010, 3♀ larvae. – POG 2.6, Thailand, Loei Prov., Phong River, 16° 50' 50.20"N, 101° 56' 13.80"E, 23.02.2011, 1♂ larva. – all N. Sangpradub leg.

Etymology

The species epithet refers to the nose-shaped lateral projections on mesonotum, from Latin *nasus*, nose.

Male subimago

The holotype and some other specimens are male last instar larvae. The following subimaginal features are therefore visible:

Base of antennal flagellum dilated, dilated part 0.4 times as wide and about as long as pedicel. Prosternal ridges

forming a very narrow trapezoid with concave lateral sides. Segments 2 and 3 of foretarsus each with a moderate apico-median projection, segment 4 with two projections, a lateral and a median one. Abdominal segments each with short triangular posterolateral process. Sternite IX and subimaginal genitalia as in Fig. 2a. Penis of moderate width, postero-laterally rounded, no ventral fold visible. Forcipes straight and of moderate length, apically with a tuft of thin sclerotized spines (Fig. 2d).

Larva

Measurements and colouration

Male larva of last instar, body length 3.0–3.2 mm, length of cerci 1.7 mm. Female larva of last instar, body length 3.8 mm, length of cerci 3.0 mm.

Colouration of cuticle yellowish-brown. Epidermal pigmentation: Transverse stripe of brownish pigments between antennal bases, each a pair of paramedian spots on pro- and mesonotum together with diffuse marks. Abdominal terga I–II with brownish transverse bands, Terga VII–IX with broad median marks divided from paratergal dashes by pale spots. Operculate gills shaded brownish.

Morphology

Cuticle: with very small granules (head, pronotum) or denticles (mesonotum, operculate gill, median field of the latter with net meshes).

Head: Genae slightly bulged. Mandibles with a dorsolateral band of very thin bristles. Outer margin of segments 1 and 2 of labial palp with numerous strong bristles. Ratios of maxillary and labial palps and their parts see table 1.

Thorax: Sides of pronotum straight or slightly convex, anteriorly diverging, with small denticles, without setation. Sides of mesonotum with an anterior-lateral nose-shaped projection densely provided with short spatulate bristles (Fig. 2g). Coxal processes tongue-shaped, broadly rounded triangular, process of hind coxa longer than that of mid coxa (Fig. 2f). Forefemur on dorsal side with transverse row of conspicuous, broadly spatulate bristles (Figs 2e); somewhat longer bristles on hind margin apically from the transverse row. Mid and hind femora and tibiae marginally with moderate, blunt, or slightly spatulate bristles. On dorsal side scattered bristles shaped like bristles of transverse row. Foretarsus ventrally with 4–6 short, simple or slightly pinnate bristles. Mid tarsus with a row of about 7 bristles, apically pinnate, basally simple, and hind tarsus with an outer row of about 6–7 pinnate bristles and an inner row of about 6 simple and one apical pinnate bristle. Foreclaws slender, with 2–3 very small basal denticles, mid claw with about 5 small basal denticles, hind claw with a dense row of microdenticles or pins only, or additionally with one or two small basal denticles.

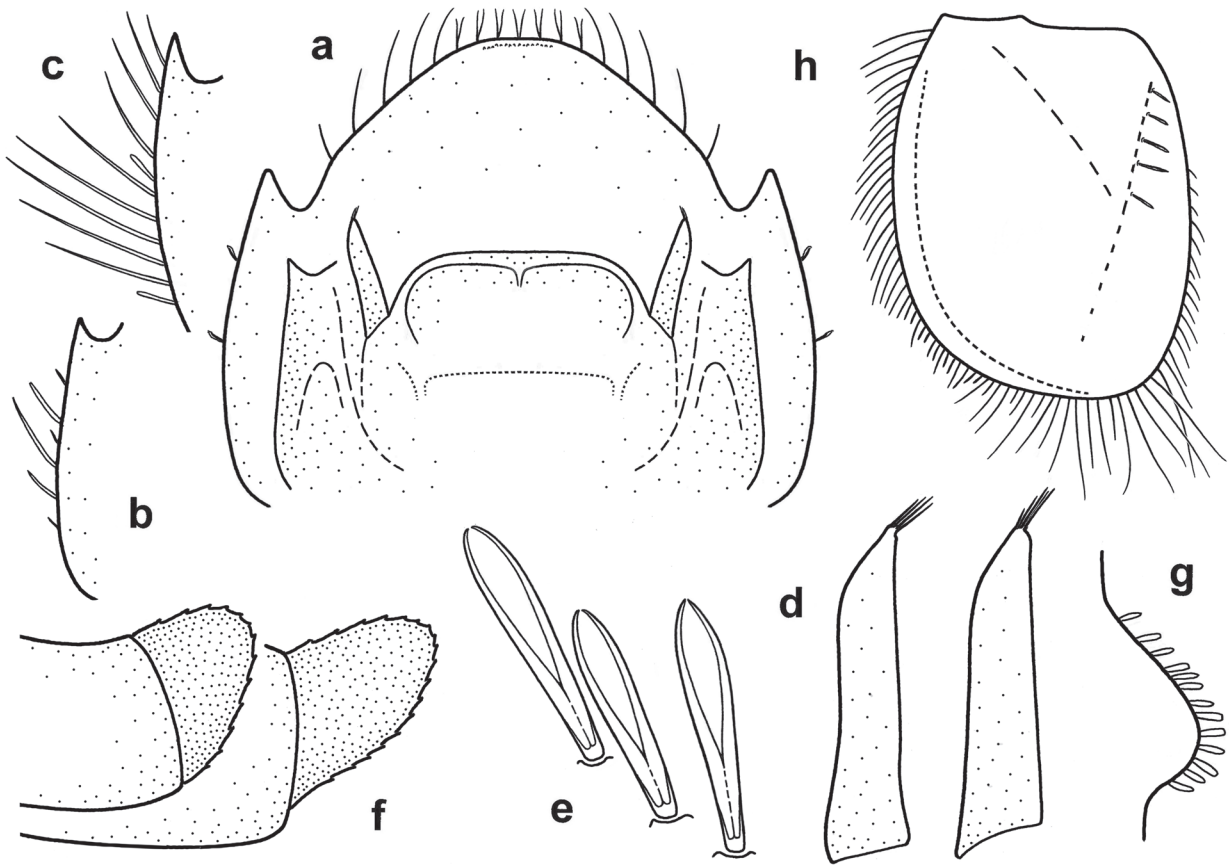


Figure 2. *Caenis nasuta* n. sp., larva. – **a.** Sternite IX, ♂, with subimaginal genitalia. – **b.** Marginal setation of segment VIII. – **c.** Marginal setation of segment VII. – **d.** Forcipes, different shapes. – **e.** Bristles from the transverse row on forefemur. – **f.** Coxal processes from mid leg (left) and hind leg (right). – **g.** Nose-shaped process from antero-lateral margin of mesonotum. – **h.** Operculate gill.

Abdomen: Abdominal segments with posterolateral processes of moderate length, on segment VIII and IX shorter; margins with 6–12 thin, densely arranged bristles, most of them long and pointed (Fig. 2c), segment VIII with about 3 bristles of moderate length and few very short ones (Fig. 2b), segment IX with only one or two short bristles or without (Fig. 2a). Dorsolateral group of bristles on tergum VII composed of 30–40 pinnate bristles, the lateral ones long and strongly pinnate. Tergum II with cone-shaped, erect posteriomedian process, hind margin laterally with rounded denticles. Hind margin of tergum VII with about 20–25 long bristles, tergum VIII with about 8–12 slightly shorter bristles, tergum IX and X with small rounded denticles. Hind margin of sternum IX rounded, with moderate, thin bristles, the median ones deeply bifurcated (Fig. 2a). Shagreen on dorsal side of sternite IX consisting of only 1 rows of very small denticles immediately on hind margin (Fig. 2a). Operculate gill (Fig. 2h) with moderate bristles on lateral margin and long ones on hind margin, about 12 short or very short spatulate bristles on

posterior-lateral corner, bristles on inner margin moderate or short; dorsal surface without bristles. Y-shaped ridges flat, inner ridge anteriorly with 5 spatulate bristles of moderate length, posterior part reduced. Ventral row of microtrichia running close to lateral and posterior margin ending at the inner corner (Fig. 2h). Gill II about 2 times length of gill I.

Differential diagnosis

Caenis nasuta can be distinguished from all other *Caenis* species by the following combination of characters: Male: Base of antennal flagellum dilated. Prosternal ridges forming a very narrow trapezoid with concave lateral sides. Segments 2 and 3 of foretarsus each with a moderate, apico-median projection. Penis lobes broadly rounded (Fig. 2a). Forcipes straight and of moderate length, apically with a tuft of thin spines (Fig. 2d). Larva: Sides of mesonotum with an anterior-lateral, nose-shaped projection densely provided with short, spatulate bristles (Fig. 2g). Coxal processes tongue-shaped, with

denticulated margins (Fig. 2f). Ventral row of microtrichia on operculate gill running close to lateral and posterior margin ending at the inner corner (Fig. 2h). Gill II about 2 times length of gill I.

Caenis longiforcipata Malzacher, **n. sp.**

(Fig. 3)

Material examined

Holotype. ♂ larva (on microslide): CYP 3.4, Thailand, Chaiyaphum Prov., Tat Fa Noi, Phu Khiao Wildlife Sanctuary, 07.02.1996, **SMNS_EPH_007786_M**.

Paratype: CYP 3.10, Thailand, Chaiyaphum Prov., Nong Kog Koy stream, N 16° 06' 46.00", E 102° 00' 01.31", 31.08.2003, 1♂ larva.

Other material: PCB 3.3, Thailand, Petchabun Prov., Nam Nao National Park, 16°38'24.02"N, 101°34'52.90"E, 740 m, 09.04.2013, 1♂ larva. – SKP 1.3, Nakhon Phanom Prov., Tat Pho Waterfall, 17° 57' 46.58"N, 104° 08' 24.39"E, 23.09.2012, 1♀ larva. – SKK 1.4, Thailand, Sakon Nakhon Prov., Keng Mod Dang, Phu Phan National Park, 12.02.1998, 1♀ larva. PNG 90, Papua New Guinea, Gulf prov., Marawaka, Mala, 7°5'664S, 145°44'467E, 1400 m, 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, 1400 m, 2♀ larvae, POSMAN leg. [MZL]

Etymology

The species epithet refers to the very long forcipes.

Male subimago

The holotype is a male last instar larva. The following subimaginal features are therefore visible:

Base of antennal flagellum not dilated. Prosternal ridges anteriorly more or less parallel, forming a rectangle or trapezoid (Fig. 3c). Segments 2–4 of foretarsus apically each with two projections, a lateral and a median one. Abdominal segments with short posterolateral processes. Sternite IX and subimaginal genitalia as in Fig. 3a. Penis broad, anvil-shaped, no ventral fold visible. Forcipes very long, with parallel sides, apical third slightly bend medially, with a tuft of short sclerotized spines (Fig. 3b).

Larva

Measurements and colouration

Male last instar larva: body length 3.3–3.5 mm, length of cerci 2.3 mm. Female last instar larva: body length 5.0 mm, length of cerci 3.0 mm.

Colouration of cuticle yellowish to brown. Epidermal pigmentation: All specimens are last instar larvae with imaginal pigmentation visible below larval cuticle.

Morphology

Cuticle: inconspicuous, mesonotal nose and dorsal surface of femora and tibiae with small denticles.

Head: Genae scarcely bulged. Mandibles with a dorso-lateral band of long, bowed bristles. Ratios of maxillary and labial palps and their parts see Table 1.

Thorax: Sides of pronotum straight or slightly convex, anteriorly diverging, with small denticles, without setation. Sides of mesonotum with an anterior-lateral nose-shaped projection without setation. Coxal processes inconspicuous. Forefemur on dorsal side with a transverse row of conspicuous, broadly spatulate bristles; slightly longer bristles on hind margin apically from the transverse row. Mid femora with long marginal bristles only apically on hind margin (Fig. 2i); hind femora with long, blunt or spatulate bristles on fore- and hind margin (Fig. 2j). Dorsal side of mid and hind femora with numerous bristles like those from transverse row, a little longer and narrower (Figs 2i and j). Foretarsus ventrally with 4 simple bristles. Mid tarsus with a row of about 6–7 bristles, the apical ones pinnate, the basal ones simple, and hind tarsus with an outer row of about 6 pinnate bristles and an inner row of about 6 simple bristles; both rows close together. Fore claw thin and slender, with about three small basal denticles (Fig. 3f); mid claw broader and bowed with about 5 small, basal denticles (Fig. 3g); hind claw with tip strongly bent and a dense row of microdenticles or pins, the apical ones clearly longer than the basal ones, without basal denticles (Fig. 3h).

Abdomen: Abdominal segments with posterolateral processes of moderate length, on segment VIII and IX shorter. Marginal setation sparser as in *C. nasuta*. Segments VI and VII with 6–7 moderate or long bristles with short or elongated, thin tips; segment VIII with about 4 short or moderate, blunt or shortly pointed bristles; segment IX with 1–3 short, blunt bristles (Fig. 3a). Tergum II with a flat, triangular, erect posteriomedian process. Dorsolateral group of bristles on tergum VII composed of 15–20 relatively short, pinnate bristles, the longest half as long as the longest in *C. nasuta*. Hind margin of tergum VII with about 20 bristles, most of them long and pointed or apically hair-shaped, few of moderate length with a short tip and one or two apical ones short and spatulate. The row of about 6 moderate bristles on hind margin of tergum VIII with a median gap. Hind margin of tergum IX and X with small rounded denticles. Hind margin of sternum IX broadly rounded, with few thin bristles, the median ones bifurcated (Fig. 3a). Shagreen on dorsal side of sternite IX nearly invisible, sometimes few, very small denticles on hind margin. Operculate gill (Fig. 3d) with bristles of moderate length on lateral margin and long ones on hind margin, few short or moderately long, spatulate bristles on posterior-lateral corner, bristles on inner margin moderately long or short; bristles sparser than in *C. nasuta*. Y-shaped ridges strongly reduced, the inner ridge only represented by few bristles: anteriorly 4 short to moderate, spatulate bristles, posteriorly three long and

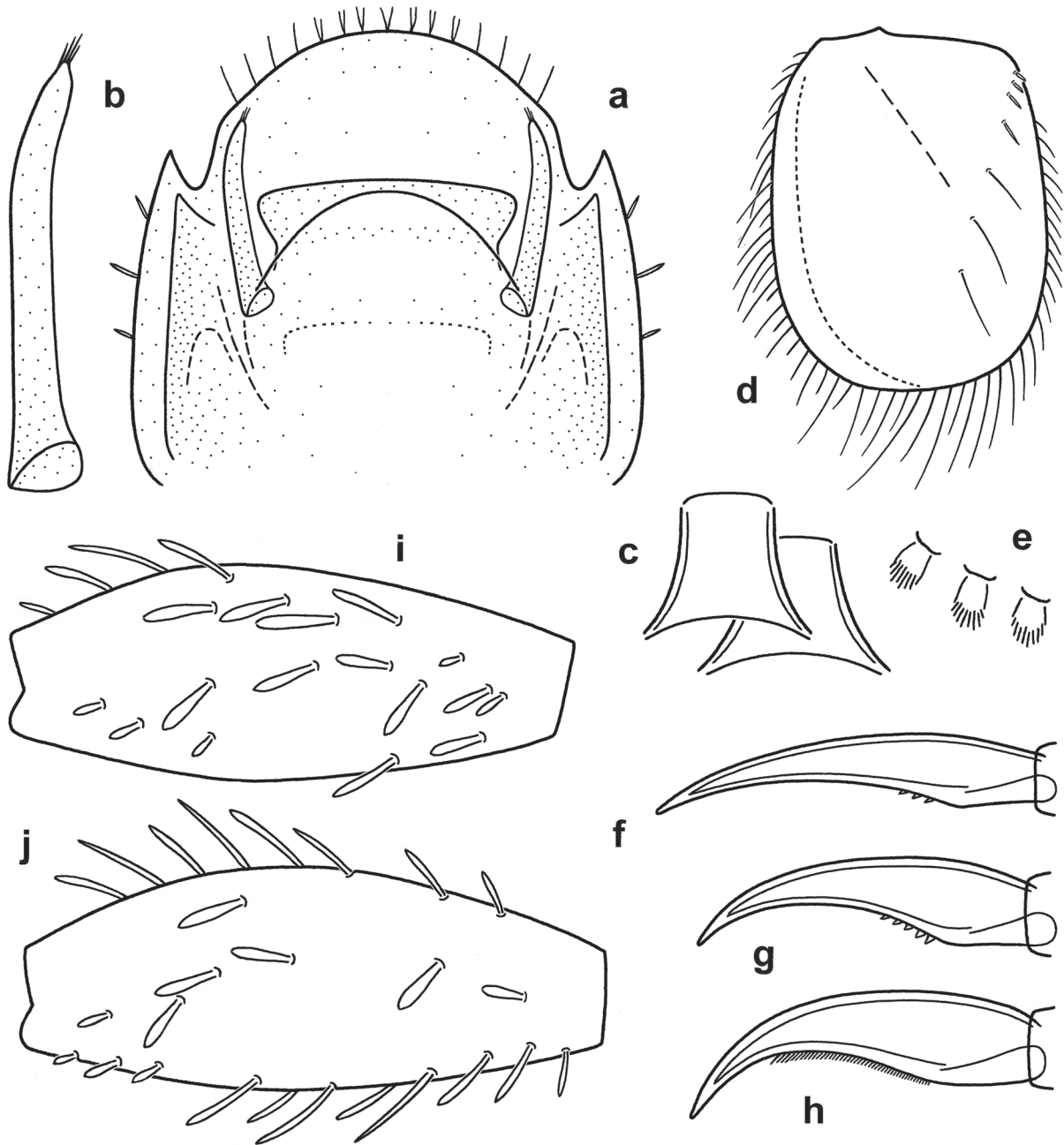


Figure 3. *Caenis longiforcipata* n. sp., larva. – **a.** Sternite IX, ♂, with subimaginal genitalia. – **b.** Forceps. – **c.** Prosternal ridges, different shapes. – **d.** Operculate gill. – **e.** Microtrichia from row on ventral side of operculate gill. – **f.** Foreclaw. – **g.** Mid claw. – **h.** Hind claw. – **i.** Mid femur, dorsal view. – **j.** Hind femur, dorsal view.

thin ones (Fig. 3d). Ventral row of microtrichia a little more distant to the lateral margin as in *C. nasuta*, ending in the middle of hind margin (Fig. 3d). Microtrichia short, more or less rounded (Fig. 3e). Gill II about 1.4 times length of gill I.

Egg

Broadly oval. Chorion with very fine pores. Two coiled-rope epithemata of a modified perpusilla subtype (see MALZACHER 2011, fig. 13, pp. 65 and 73); about

6–8 threads forming loops and ending in the same number of tiny elongated knobs. Micropyle of moderate length, without widened mouth and visible sperm-guide.

Differential diagnosis

Caenis longiforcipata can be distinguished from all other *Caenis* species by the following combination of characters: Male: Base of antennal flagellum not dilated. Prosternal ridges anteriorly more or less parallel, forming a rectangle or broad trapezoid (Fig. 3c). Segments 2–4 of foretarsus apically each with two projections, a lateral and a median one. Penis broad, anvil-shaped. Forcipes very long, with parallel sides, with a tuft of short sclerotized spines (Fig. 3b). Larva: Sides of mesonotum with an anterior-lateral nose-shaped projection without setation. Fore- and mid claws with few basal denticles, hind claw only with a long, dense row of microdenticles or pins (Fig. 3h). Shagreen on dorsal side of sternite IX nearly invisible, sometimes few very small denticles on hind margin. Y-shaped ridges of operculate gill strongly reduced, the inner one only represented by few bristles: anteriorly 4 short to moderate spatulate bristles, posteriorly three long and thin ones (Fig. 3d). Egg: Two coiled-rope epithemata of a modified *perpusilla* subtype.

Caenis ulmeriana group

Remarks: There are numerous similar larvae with variable characters. However, males of last instar show some differences in subimaginal genital structures. There are two differing types and a couple of intermediate stages. The genitalia of one type are very similar to the genitalia of *Caenis ulmeriana*, a species that is widely distributed in the eastern Oriental realm. Here we will describe this larval type as larva of *Caenis ulmeriana*, although it cannot be excluded that there are different species with very similar larvae.

Caenis ulmeriana Malzacher, 2015 (Figs 4–8)

MALZACHER (2015: 33)

Material examined

PCB 7.1, Thailand, Petchabun Prov., Huai Mod, Nam Nao National Park, 16° 40' 05.70"N, 101° 44' 11.8"E, 20.07.2002, 4♂ larvae, 1♀ larva. – CYP 1.6, Thailand, Chaiphaphum Prov., Huai Tat Fah Noi, 16° 27' 24.50"N, 101° 47' 41.10"E, 23.03.2000, 1♂ larva. – NKK 1.3, Thailand, Nakhon Ratchasima Prov., Wang Tao Waterfall, Thap Lan National Park, 14° 20' 12.13"N, 102° 14' 33.69"E, 27.04.2014, 2♂ larvae. – THW 1.1, Thailand, Loei Prov., Tad Hong Waterfall, Phu Kradueng National Park, 16° 48' 11.60"N, 101° 34' 52.90"E, 09.12.2010, 2♂ larvae, 3♀ larvae. – POG 1.8, Thailand, Maha Sarakham Prov., Ban Kui Pang, Phong River, 16° 23' 31.70"N, 102° 57' 19.20"E, 24.12.2004, 2♂ larvae, 1♀ larva. – POG 2.2, Thailand, Khon Kaen Prov., Huai Bong,

Phong River, 16° 57' 32.40"N, 101° 49' 04.00"E, 21.08.2002, 2♂ larvae, 6♀ larvae. – POG 2.4, Thailand, Loei Prov., Huai Phong Go, Phong River, N 16° 52' 00.49", E 101° 52' 11.10", 23.02.2011, 5♂ larvae, 4♀ larvae. – POG 2.8, Thailand, Khon Kaen Prov., Ban Huaisai, Phong River, N 16° 46' 20.30", E 102° 38' 03.50", 23.02.2011, 1♂ larva, 1♀ larva. – POG 2.10, Thailand, Khon Kaen Prov., Ban Kut Kwang, Phong River, N 16° 42' 16.70", E 102° 49' 29.40", 24.02.2011, 1♂ larva, 2♀ larvae. – POG 3.2, Thailand, Khon Kaen Prov., Huai Sun, Phong River, N 16° 31' 06.63", E 102° 53' 55.14", 12.07.2013, 1♂ larva, 1♀ larva. – all N. Sangpradub leg.

Male subimago

Some specimens are male last instar larva. The following subimaginal features are therefore visible:

Base of antennal flagellum not dilated. Prosternal ridges forming an elongated, cone-shaped structure. Segments 2–4 of fore tarsus apically each with two projections, a lateral and a median one; projections on segments 2 and 3 rather long, on segment 4 short. Abdominal segments with short to moderate posterolateral processes. Sternite IX and subimaginal genitalia as in Fig. 4a. Penis broadly rounded, ventral fold medio-posteriorly protruding, forming a semicircular or semi-elliptical process. Forcipes moderate, straight, sides apically slightly converging, with a tuft of sclerotized spines, the longest clearly wider as the others (Fig. 4c). The above-mentioned differing type shows a penis without semicircular ventral fold (Fig. 4b) and forcipes with elongated apical spines (Fig. 4d).

Larva

Measurements and colouration

Male last instar larva: body length 2.7–3.2 mm. Female larva of last instar, body length 3.8–5.0 mm. Cerci not complete.

Colouration of cuticle yellowish brown. Epidermal pigmentation: brown pigments in a transverse band between lateral ocelli, with an oval or triangular mark behind frontal ocellus; two spots or star-like marks on vertex. Pronotum with a median anvil-shaped mark, laterally with irregular spots and dashed. Mesonotum with angled dark-brown dashes on anterolateral corners, few spots behind them. Visible abdominal terga with diffuse sublateral marks. Operculate gills slightly shaded.

Morphology

Cuticle: inconspicuous, operculate gill and dorsal surface of femora with small denticles, partly net-meshed.

Head: Genae slightly bulged. Pedicel with 3–4 strong and pointed bristles, the apical one often bifid. Mandibles with a dorsolateral row or band of strong, bowed bristles. Three to four long, strong, blunt bristles in front of the eyes. Ratios of maxillary and labial palps and their parts see Table 1.

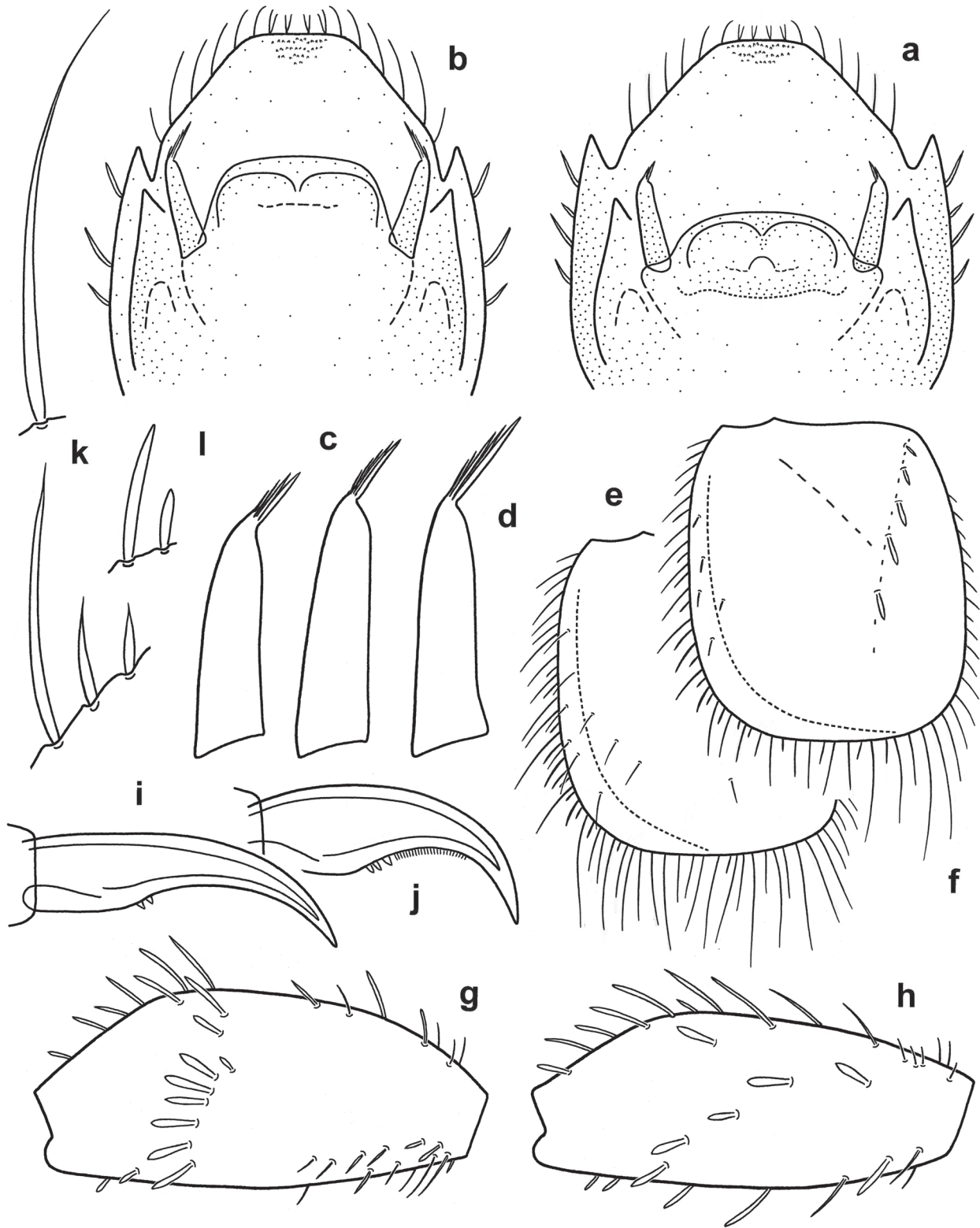
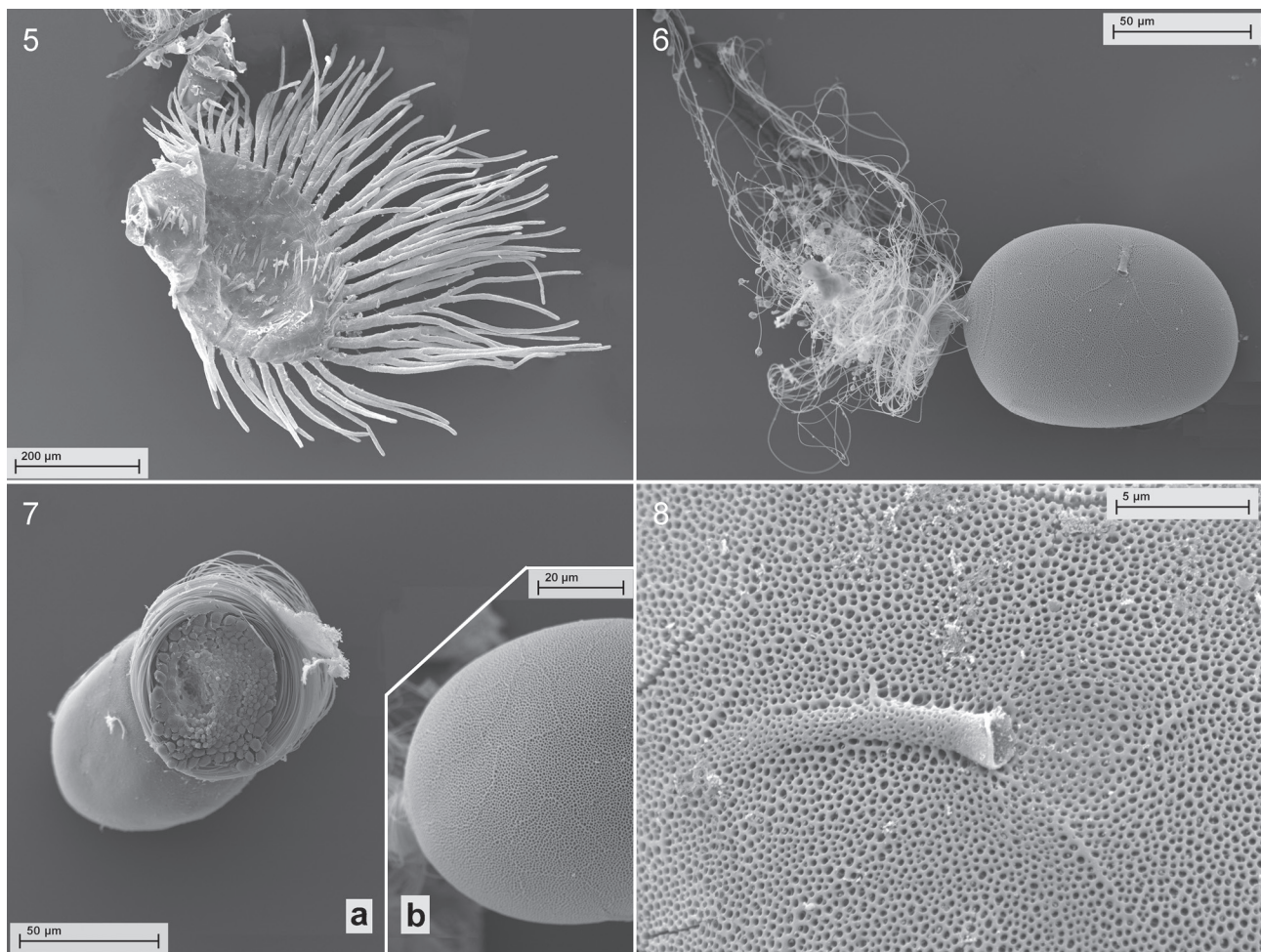


Figure 4. *Caenis ulmeriana*, larva (a, c, f, g–k), *Caenis ulmeriana* group, larva, differing type (b, d, e, l). – a, b. Sternite IX, ♂, with subimaginal genitalia. – c, d. Forcipes. – e, f. Operculate gill. – g. Forefemur. – h. Mid femur. – i. Foreclaw. – j. Hind claw. – k, l. Marginal bristles from operculate gill.



Figures 5–8. *Caenis ulmeriana*, larva. – **5.** Gill 3. **6.** Egg. **7.** Egg, epithema (a), chorion structure (b). **8.** Egg, micropyle.

Thorax: Sides of pronotum straight, more or less diverging anteriorly, smooth or with few small denticles, without setation. Sides of mesonotum without an anterior-lateral nose-shaped projection. Few thin bristles anteriorly from coxae. Coxal processes sickle-shaped. Forefemur on dorsal side with a transverse row of conspicuous, broadly spatulate bristles in two groups (4–6 anterior + 2–3 posterior); somewhat longer bristles on hind margin apically from the transverse row (Fig. 4g). Mid and hind femora with moderate or long marginal bristles. Dorsal side of mid femora with 5–6 irregularly arranged spatulate bristles (Fig. 4h), hind femora with 3–4 bristles. Foretarsus ventrally with 2–3 simple bristles. Mid tarsus with a row of about 5–6 simple bristles, the apical one often pinnate, hind tarsus with an inner row of 5–6 simple bristles and 1–2 pinnate bristle as a rest of the outer row. Foreclaw thin and slender, with 2–3 small basal denticles (Fig. 4i); mid claw broader and bowed with about 3 small basal denticles; hind claw with strongly bent tip, 2–3 basal denti-

cles, and a dense row of microdenticles or pins, becoming shorter to the apical end of the row (Fig. 4j).

Abdomen: Abdominal segments with posterolateral processes of moderate length, on segment VIII and IX shorter. Segment VII with 7–9 short, moderate and long bristles, the short ones blunt, the moderate and longer ones pointed. Segment VIII with 5–7 short or moderate, blunt or shortly pointed bristles; segment IX with 3–5 short, blunt or pointed bristles (Fig. 4a). Tergum II with a broadly triangular posteriomedian process, hind margin with denticles. Dorsolateral group of bristles on tergum VII composed of about 15 moderate, thin pinnate bristles. Hind margin of tergum VII with about 18–25 bristles, moderate or long, apically more or less hair-shaped. The row of about 12–14 moderate bristles on hind margin of tergum VIII without median gap. Hind margin of tergum IX and X with small denticles. Hind margin of sternum IX broadly or triangularly rounded, sometimes posteriorly more or less cut, laterally with few

moderate and thin bristles, medially with short bifurcated bristles (Fig. 4a). Tergum IX of females posteriorly more elongated. Dorsal side of sternite IX with more or less triangular shagreen field, consisting of irregular transverse rows of denticles. Operculate gill (Fig. 4f) with moderate or long bristles on lateral margin and long or very long ones on hind margin, between moderate or long bristles, on postero-lateral corner a few short, more or less spatulate bristles can be found (Within the *ulmeriana* group there are also gills with long marginal bristles only). All these bristles are basally broadened and apically strongly pointed, but of different length. The longest bristles have a hair-like appearance. Y-shaped ridges weakly developed, the inner one posteriorly reduced, with 5–6 spatulate bristles in the apical half or two third (Fig. 4f). Ventral row of microtrichia reaches more or less the posteromedial corner, becoming smaller and smaller towards the end of the row. Microtrichia short and rounded, sometimes a little elongated. Gill I about half as long as gill II. Gill III with moderate filaments, half of them with 3–4 branches (Fig. 5)

Egg

Broadly oval (Fig. 6). Chorion with fine pores and irregular, weakly developed net-meshes (Fig. 7b, 8). One epithema; initial stage flat, forming a coil of fine threads, ending in knobs of different size, surrounded by the coil (Fig. 7a). Later on, epithemata become more or less uncoiled (Fig. 6). Micropyle of moderate length, with a scarcely visible circular sperm-guide (Fig. 8).

Caenis karenae Malzacher, n. sp.

(Figs 9, 11)

Material examined

Holotype. ♂ larva (on microslide): CYP 1.5, Thailand, Chaiyaphum Prov., Huai Tat Fa Noi, N 16° 27' 24.50" E 101° 47' 41.10", 23.03.2000. **SMNS_EPH_007787_M.**

Paratypes. Same data as holotype, 1♀ larva. – CYP 1.2, Thailand, Chaiyaphum Prov., Huai Tat Fah Noi, 16° 27' 24.50"N, 101° 47' 41.10"E, 28.03.2000, 1♂ larva – CYP 1.6, Thailand, Chaiyaphum Prov., Huai Tat Fah Noi, 16° 27' 24.50"N, 101° 47'

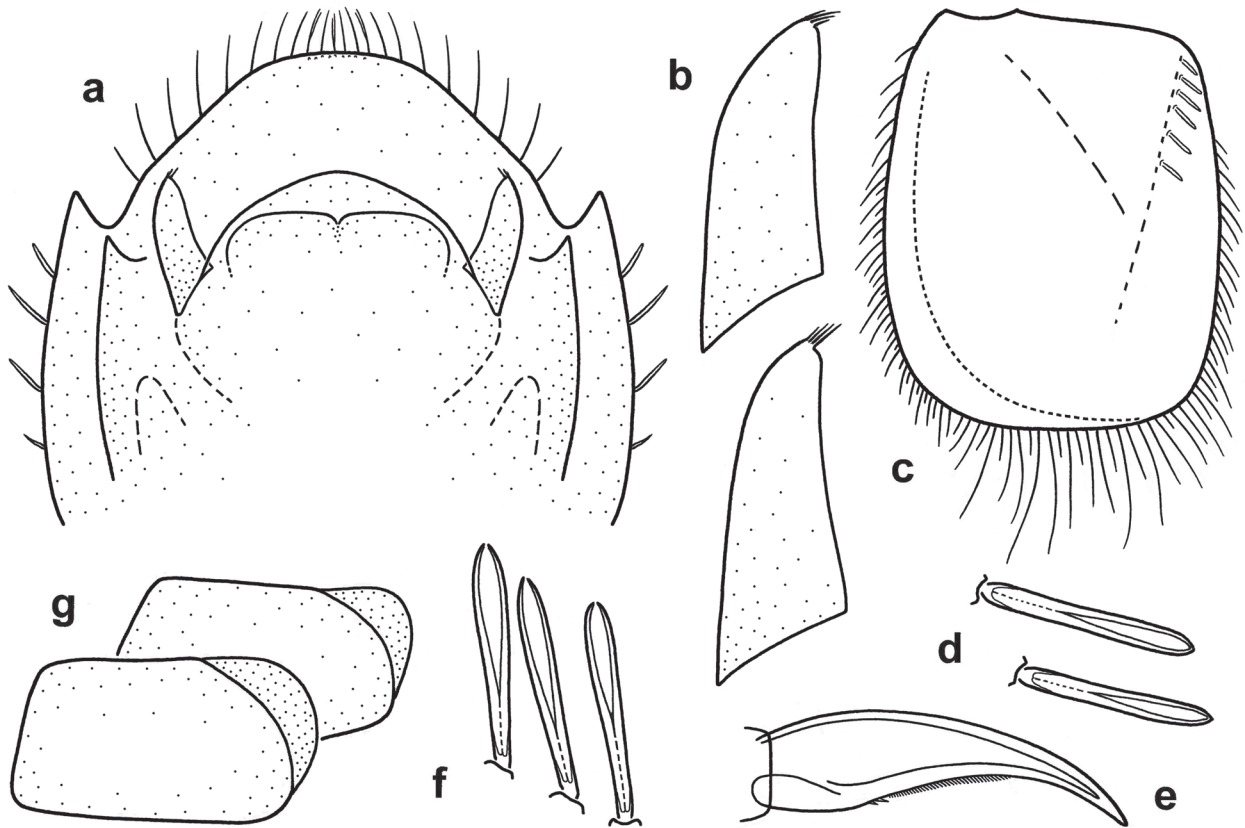


Figure 9. *Caenis karenae* n. sp., larva. – **a.** Sternite IX, ♂, with subimaginal genitalia. – **b.** Forceps. – **c.** Operculate gill. – **d.** Bristles from base of median ridge on dorsal side of operculate gill. – **e.** Hind claw. – **f.** Bristles from transverse row on forefemur. – **g.** Coxal processes from mid leg (right) and hind leg (left).

41.10"E, 28.03.2000, 2♀ larvae. –CYP 1.8, Thailand, Chaiyaphum Prov., Huai Tat Fah Noi, 16° 27' 24.50"N, 101° 47' 41.10"E, 28.03.2000, 1♀ larva –

Other material: MUN 2.1, Thailand, Buriram Prov., Tha Sai Ban Wang Plad, Mun River, 15° 26' 04.00"N, 103° 00' 49.90"E, 23.02.2003, 1♀ larva. – LAO 1.1, Laos, Nam Tou, N 18° 54' 00.01", E 102° 50' 06.21", 01.02.2009, 2♂ larvae. – LAO 1.2, Laos, Nam Mo, N 18° 51' 17.90", E 102° 50' 32.40", 01.02.2009, 1♂ larva, 2♀ larvae. – all N. Sangpradub leg.

Etymology

The species is dedicated to my dear friend and colleague Karen Bühler.

Male subimago

Three specimens are last instar male larvae. The following subimaginal features are therefore visible:

Base of antennal flagellum dilated, dilated part 0.4 times as wide and about as long as pedicel. Prosteral ridges forming a relatively short trapezoid. Segments 2 and 3 of foretarsus each with a moderate apico-median projection, segment 4 with two projections, a lateral and a median one. Abdominal segments with short triangular posterolateral processes. Sternite IX and subimaginal genitalia as in Fig. 9a. Penis broadly rounded. Forcipes short and broad, with a short tuft of thin spines (Fig. 9b).

Larva

Measurements and colouration

Male last instar larva: body length 2.7–3.5 mm, Sub-mature female larva, body length 5.0 mm.

Colouration of cuticle light yellowish brown to yellowish white. Only traces of pigments on head and pronotum.

Morphology

Cuticle: head and pronotum moderately granulated. Operculate gill densely provided with small denticles, partly net-meshed. Mesonotum with transitional structure.

Head: Genae not bulged. Pedicel with 1–3 small, pointed bristles. Mandibles with a broad dorsolateral field of very long, thin and bowed bristles. Two strong and pointed bristles in front of the eyes. Ratios of maxillary and labial palps and their parts see Table 1.

Thorax: Sides of pronotum straight, slightly diverging anteriorly, denticulated, with 2–3 long and thin bristles. Sides of mesonotum without an anterior-lateral nose-shaped projection. Bristles anteriorly of coxae sparse and very thin. Coxal processes semi-elliptical (Fig. 9g). Fore-femur on dorsal side with a transverse row of elongated moderately spatulate bristles (4–5 anterior + 2–3 posterior) (Fig. 9f); somewhat longer bristles on hind margin apically from the transverse row. Mid and hind femora with thin, moderate or long marginal bristles. Dorsal side with 3–4 short spatulate bristles, some mid femora

basally with few short thin bristles. Foretarsus ventrally with 4–6 small simple bristles. Mid tarsus with a row of about 6–7 simple bristles, the apical one pinnate, hind tarsus with an inner row of 6–8 simple bristles and an outer row of 3–5 pinnate bristles. All claws slender and slightly bowed, basally 0–2 very small denticles, hind claw with a dense row of microdenticles or pins, basal often with one or two small denticles (Fig. 9e).

Abdomen: Abdominal segments with posterolateral processes of moderate length, on segments VIII and IX shorter. Segment VII with 7–8 long bristles. Segment VIII with 4–5 shorter and segment IX with 2–4 short bristles (Fig. 9a). Tergum II with a broadly rounded, flat posteriomedian process. Hind margin of tergum VII with about 20 thin bristles, most of them long. Tergum VIII with about 15 moderate to long bristles, few short and blunt. Hind margin of tergum IX and X with small denticles. Hind margin of sternum IX broadly rounded, with moderate bristles, the apical ones bent medially, some of them bifurcated. Shagreen on dorsal side composed of few denticles immediately on hind margin (hardly visible) (Fig. 9a). Operculate gill (Figs 9c, 11 right) with moderate and short bristles on lateral margin. Hind margin with long and very long bristles, moderate ones between them. On postero-lateral corner 8–10 short and blunt bristles can be found between moderate ones. Y-shaped ridges weakly developed, median ridge posteriorly reduced, with 6–7 moderate, blunt and parallel-sided bristles in their basal third (Figs 9c, d). Ventral row of microtrichia almost reaching the postero-medial corner of the gill (Figs 9c, 11, left). Microtrichia oval with very fine filaments (Fig 11, right). Gill I a little more than half as long as gill II.

Differential diagnosis

Caenis karenae can be distinguished from all other *Caenis* species by the following combination of characters:

Male: Base of antennal flagellum dilated. Segments 2 and 3 of foretarsus each with an apico-median projection. Penis lobes broadly rounded (Fig. 9a). Forcipes short and very broad, with a short tuft of thin spines (Fig. 9b).

Larva: Claws slender, slightly bowed, basally with 0–2 very small denticles, hind claw additionally with a long, dense row of microdenticles or pins (Fig. 9e). Median ridge on operculate gill in its basal fourth with about 6 moderate spatulate bristles directed postero-laterally (Fig. 9c). Shagreen on dorsal side of sternum IX with few denticles immediately on hind margin (hardly visible) (Fig. 9a).

Caenis picea Kimmins, 1946
(Figs 10, 12–14)

KIMMINS (1947: 99)

MALZACHER (2015: 383)

Material examined

CHI 1.1, Thailand, Yasothon Prov., Tha Sai Mae Su Jin, Chi River, 15° 48' 23.90"N, 104° 07' 09.80"E, 24.06.2003, 1♂ larva. – POG 1.7, Thailand, Khon Kaen Prov., Ban None Karm Phae, Phong River, 16° 43' 52.43"N, 102° 46' 16.55"E, 10.02.1996, 1♂ larva. – POG 1.8, Thailand, Maha Sarakham Prov., Ban Kui Pang, Phong River, 16° 23' 31.70"N, 102° 57' 19.20"E, 1♂ larva, 1♀ larva. – POG 2.10, Thailand, Khon Kaen Prov., Ban Kut Kwang, Phong River, 16° 42' 16.70"N, 102° 49' 29.40"E, 24.02.2011, 1♀ larva. – POG 3.3, Thailand, Khon Kaen Prov., Ban Or Noi, Phong River, 16° 44' 01.41"N, 102° 49' 09.07"E, 13.07.2013, 1♂ larva, 1♀ larva. – MRC 1.3, 1.4, 1.5, Thailand, Nakorn Phanom Prov., Nam Kham River, 17.06.2013, 4 larvae ♀. – MRC 2.2, Thailand, Ubon Ratchathani Prov., Kong Chiam District, Mun River, 04.04.2015, 1♀ larva. – POG 1.11, Thailand, Khon Kaen Prov., Ban Kut Kwang, Phong River, 16° 42' 16.70"N, 102° 49' 29.40"E, 24.02.2011, 1♀ larva. – all N. Sangpradub leg.

Male subimago

Two specimens are male last instar larvae. The following subimaginal features are therefore visible and can be compared with males (see description in MALZACHER 2015: pp. 38):

Base of antennal flagellum not dilated. Prosternal ridges forming a cone-shaped figure, sides slightly convex. Segments of foretarsus apically not broadened, without small spines. Abdominal segments with short posterolateral processes. Sternite IX and subimaginal genitalia as in Fig. 10a. Penis with rounded lobes and a broadly v-shaped ventral sclerite. Styli ger sclerite brownish, medially pale, with two apophyses of moderate length. Forcipes straight, apically with few short thin spines.

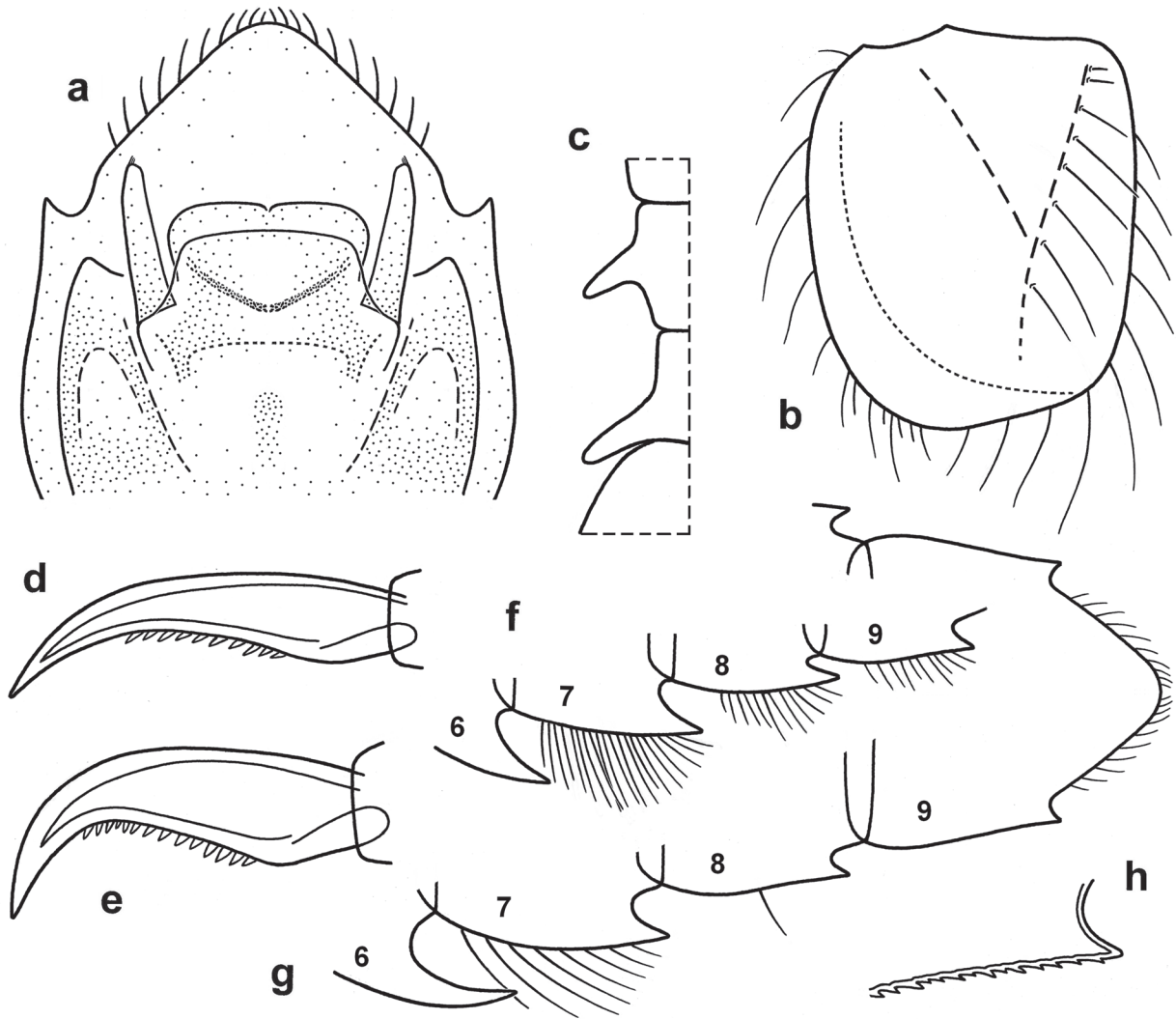


Figure 10. *Caenis picea*, larva (a–e, g, h), *Caenis lactea*, larva (f). – a. Sternite IX, ♂, with subimaginal genitalia. – b. Operculate gill. – c. Posteromedian process on abdominal terga I and II. – d. Foreclaw. – e. Hind claw. – f, g. Marginal setation on abdominal segments VII–IX. – h. Lateral margin of segment IX, higher magnification.

Larva

Measurements and colouration

Male larva of last instar, body length 2.8–3 mm.
Female larva of last instar, body length 5.0 mm.

Colouration of cuticle: A relatively pale species, from whitish beige to light yellowish brown.

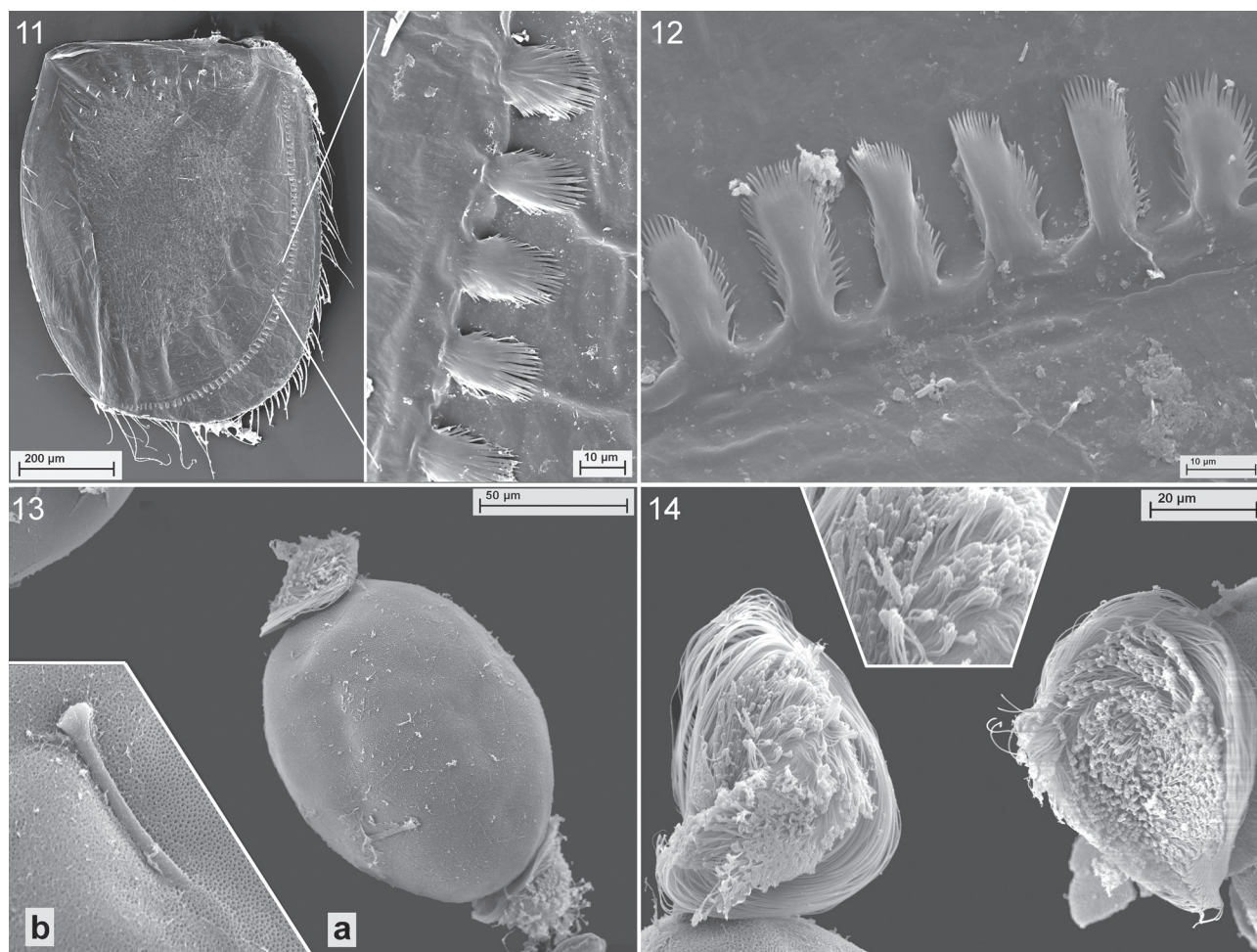
Epidermal pigmentation: There are few small brown pigment spots: two paramedian pairs on pronotum and mesonotum, two spots near inner margin and base of wing buds, three in a line parallel to postero-lateral margin of operculate gill and three in a transverse row on abdominal terga IX and X. Pigment spots also on paraterga. In strongly coloured specimens they are enlarged to longitudinal dashes. Those specimens also show pigments on hind margin of head and pairs of marks on abdominal sterna.

Morphology

Cuticle: Scattered with granules, on operculate gills and abdominal terga more or less denticulated. Surface scattered with long thin bristles.

Head: Genae scarcely bulged. Pedicel with few very thin and short bristles. Mandibles dorsolateral with thin, moderate and bowed bristles. No bristles in front of the eyes. Ratios of maxillary and labial palps and their parts see Table 1.

Thorax: Sides of pronotum straight, converging anteriorly, sometimes slightly concave or with a flat indentation near forecorner; nearly smooth, one or two thin bristles. Sides of mesonotum without an antero-lateral nose-shaped projection. No bristles anteriorly from coxae. Coxal processes inconspicuous, sickle-shaped. Forefemur on dorsal side with a longitudinal row of thin or long bristles, no transverse row. All femora with thin, moderate or



Figures 11–14. *Caenis karenae* n. sp., larva (11). – Operculate gill, ventral view (left), operculate gill, microtrichia from ventral side (right). *Caenis picea*, larva (12–14). – **12.** Operculate gill, microtrichia from ventral side. **13.** Egg, total (a). Egg, micropyle (b). – **14.** Egg, epithemata. Frame: higher magnification.

long bristles on hind margin and shorter ones on foremargin. Dorsal side of mid and hind femora with few long thin bristles, sometimes lacking. Tibiae marginally with moderate bristles, some longer ones on dorsal side. Foretibia additionally with a dorsomedial row of long thin bristles. Fore- and mid tarsus ventrally with 8–10 more or less pinnate bristles, clearly longer than in other species. Hind tarsus with an inner row of 6 short simple bristles and an outer row of 8 long pinnate bristle. Foreclaw slender and slightly bowed, with about 10 strong denticles (Fig. 10d). Mid and hind claw broader, apically strongly bowed with 12–15 strong denticles (Fig. 10e).

Abdomen: Posterolateral processes on abdominal segments VII–IX short to moderate, the anterior ones abruptly longer (VI 3 times as long as VII); segments V–VII with 8–10 long, thin bristles, segment VIII with 1(–2), segment IX without (Fig. 10g). Terga I and II each with a cone-shaped posteromedian process, on tergum I a little shorter (Fig. 10c). Hind margin of tergum VII with about 20 thin bristles, most of them long. Hind margin of terga VIII, IX and X with small denticles. Sternum IX triangularly protruding posteriorly, with moderate bristles laterally, the apical ones shorter and bent medially, some of them bifurcated. Shagreen not visible (Fig. 10a). Operculate gill (Fig. 6b) marginal with about 100 moderate and long thin bristles (in other species the number is 55–85, in Fig. 6b only one in four bristles are figured), the longest on lateral and hind margin. Few shorter bristles on postero-lateral corner. Y-shaped ridges weakly developed. Median ridge a little stronger, with 6–8 very long pointed bristles in its basal two third. Median hind corner of operculate gill more or less protruding posteriorly. Ventral row of microtrichia ends near posteromedial corner of the gill (Fig. 10b). Microtrichia elongated, parallel-sided, or more or less rounded, with filaments all over the outline (Fig. 12). Gill I 0.7 times as long as gill II.

Egg

Broadly oval (Fig. 13a). Chorion with fine pores and scarcely visible irregular net-meshes. Two epithemata; initial stage flat, forming a coil of fine threads, ending in very tiny knobs, surrounded by the coil (Figs 13a, above, 14). Later on, epithemata become more or less uncoiled (Fig. 13a, below). Micropyle long and thin, without visible sperm-guide (Fig. 13b).

Remarks: The species seems to be related to the West Palearctic *Caenis lactea* (see MALZACHER 2015), supported also by larval features e. g. anteriorly converging sides of pronotum and hind margin of sternite IX triangular, posteriorly elongated (Fig. 10g). Both larvae can be distinguished by shape and setation of abdominal segments (compare Figs 10f and g).



Figure 15. *Caenis obtusostilata* n. sp., male. – Habitus.

Caenis obtusostilata Malzacher, n. sp. (Figs 15, 16a–g)

Material examined

Holotype. ♂ (on microslide): **SMNS_EPH_007789_M**, PCB 2.3, Thailand, Petchabun Prov., Huai Hin Lad, Nam Nao National Park, 11.02.1998.

Etymology

The species epithet refers to the blunt apex of forcipes, from Latin *obtusus*, blunt.

Male imago

Measurements, ratios and colouration

Body length: 2.2 mm; wing length: 2.0 mm; length of foreleg: 2.0–2.3 mm. Ratio of forefemur : foretibia = 0.56–0.58; ratio of foretibia : foretarsus = 1.20–1.27; ratio of foreleg : hind leg = 1.98–2.00; ratio of first segment of foretarsus : 2nd : 3rd : 4th : 5th = 1 : 3.9–4.3 : 1.9–2.0 : 1.1–1.2 : 0.8–1.0.

Colouration of cuticle: Thorax brownish-yellow, scutellum and sutures yellowish-brown; other parts yellow to white. Epidermal pigmentation: Vertex with two more or less intense grey transverse bands. Abdominal terga

laterally shaded with brown, terga III–VI with narrow transverse brown bands. Other parts without pigments. (Fig. 15).

Morphology

Head (Fig. 16d): Foremargin between lateral and frontal ocelli convex. Eyes and lateral ocelli relatively small. Eyes spherical. Frons strongly bent ventrally, frontal ocellus nearly invisible in dorsal view. Pedicel elongated, length about 2.7x width. Base of antennal flagellum not dilated (Fig. 16c).

Thorax: Prosternal ridges narrow, forming an anteriorly open trapezoid with concave sides (Fig. 16e). Segments 2–3 of foretarsus each with an apico-median tongue-shaped projection, segment 4 additionally with a short lateral projection: projections with few very small and thin spines or without (Fig. 16f).

Abdomen: Tergum II without finger-like process. Lateral filaments short or very short.

Genitalia and sternum IX as in Fig. 16a. Penis lobes short, broadly rounded. Styliger sclerite broad with short apophyses. Forcipes relatively short, slender, apically rounded and more or less bent medially; surface scattered with small short bristles (Fig. 16b). Distance between the most lateral points of the forceps bases about 2.5 times of forceps length. Sides of sternum IX strongly convex. Postero-lateral processes very short. Basolateral sclerites posteriorly with a small bump.

Differential Diagnosis

Caenis obtusostilata can be distinguished from all other species of *Caenis* by the following combination of characters: Forcipes apically rounded, without spines (Fig. 16b). Penis lobes short and rounded (Fig. 16a). Base of

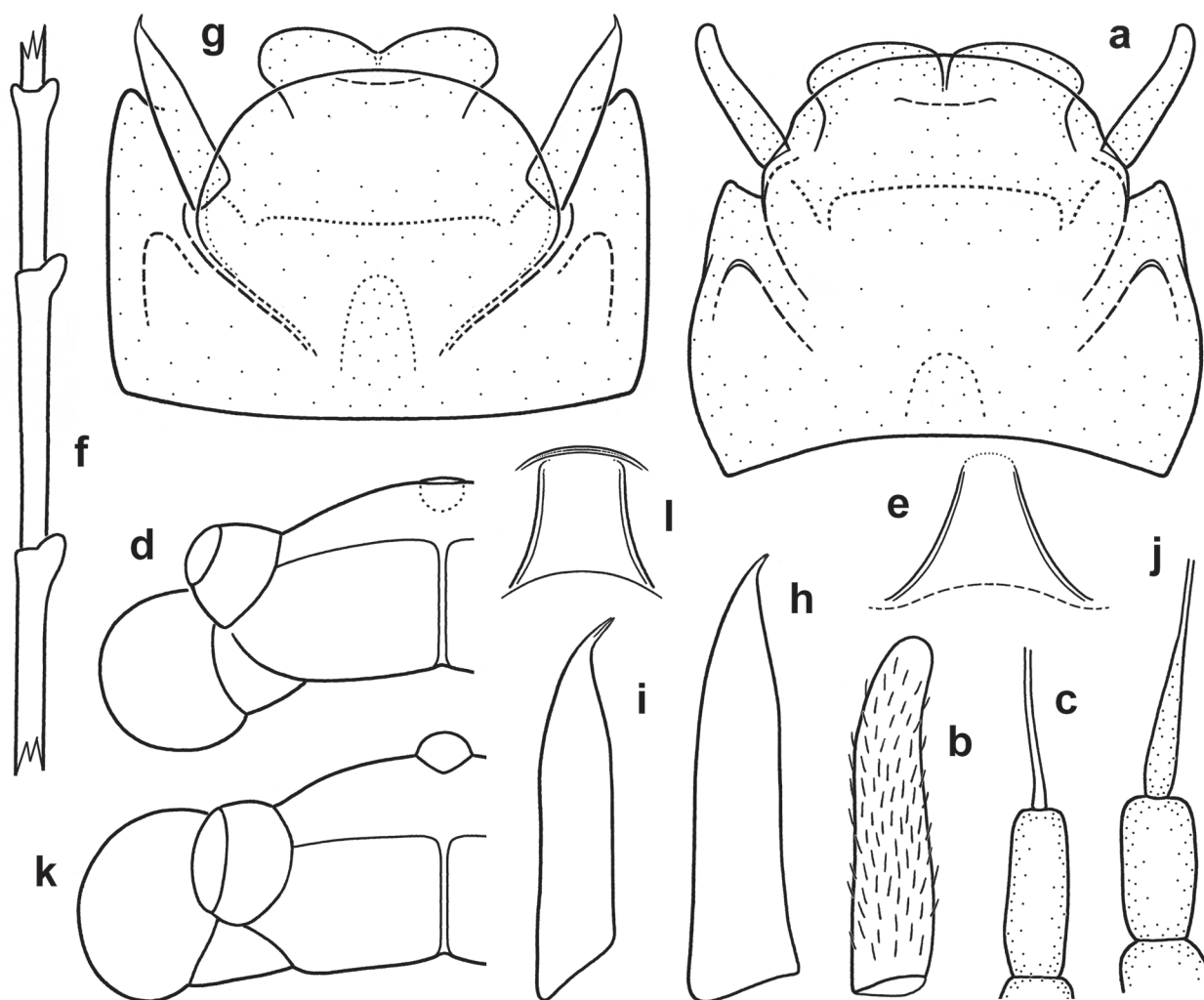


Fig. 16. *Caenis obtusostilata* n. sp., male (a–f), *Caenis acutostilata* n. sp., male (g–l). – a, g. Sternite IX with genitalia. – b, h, i. Forcipes. – c, j. Antennal scape, pedicel and base of flagellum. – d, k. Head, dorsal view. – e, l. Prosternal ridges. – f. Tarsomeres 2–4 of foretarsus.

antennal flagellum not dilated (Fig. 16c). Tarsomeres 2–3 of foretarsus each with an apico-median tongue-shaped projection, segment 4 with two projections, a lateral and a median one; projections with few very small and thin spines or without (Fig. 16f). Frons strongly bent ventrally, frontal ocellus nearly invisible in dorsal view (Fig. 16d).

Caenis acutostilata Malzacher, **n. sp.**
(Fig. 16g–l)

Material examined

Holotype. ♂ (on microslide): **SMNS_EPH_007788_M** SKK 2.1, Thailand, Sakon Nakhon Prov., Keng Mod Dang, Phu Phan National Park, 12.02.1998.

Paratype: same data as Holotype, 1♂ SI.

Etymology

The species epithet refers to the acute apex of forceps, from Latin *acutus*, pointed, acute.

Male subimago

Measurements, ratios and colouration

Body length: 2.5–2.7 mm; wing length: 2.3–2.5 mm; forelegs lacking: Cerci about 2 times as long as body, terminal filum about 3 times.

Colouration of cuticle: Thorax brownish-yellow, other parts yellow to white.

Epidermal pigmentation: no pigments can be observed.

Morphology

Head (Fig. 16k): Foremargin between lateral and frontal ocelli convex. Outline of eyes elliptical. Base of antennal flagellum dilated, dilated part 0.4 times as wide and a little longer as pedicel (Fig. 16j).

Thorax: Prosternal ridges narrow, forming a broad trapezoid with slightly concave sides; anteriorly with a transverse strip (Fig. 16l). Segments 2–4 of foretarsus each with an apico-median tongue-shaped projection, segment 4 without a short lateral projection (visible in foreleg of subimago).

Abdomen: Tergum II without finger-like process. Lateral filaments short or very short.

Genitalia and sternum IX as in Fig. 16g. Penis lobes short, broadly rounded; penis heart-shaped. Styli sclerite broad with very short apophyses, foremargin slightly convex. Forceps straight, of moderate length, basal part more or less parallel sided, evenly narrowed towards the tip that consists of 1–2 (3) short spines (Figs 16h, i); the whole surface densely provided with small short bristles. Distance between the most lateral points of the forceps bases about 1.7 times the forceps length. Sides of sternum IX straight, slightly convex. Postero-lateral processes short and broadly rounded. Lateral and basolateral sclerites anteriorly strongly converging (Fig. 16g).

Differential Diagnosis

Caenis acutostilata can be distinguished from all other species of *Caenis* by the following combination of characters: Forceps straight, basally parallel-sided, apically converging, with 1–3 short spines (Fig. 16h, i). Penis heart-shaped (Fig. 16g). Base of antennal flagellum dilated (Fig. 16j). Segments 2–3 of foretarsus each with an apico-median tongue-shaped projection, segment 4 with two projections (as in Fig. 16f). Lateral and basolateral sclerites anteriorly strongly converging (Fig. 16g). Pale species, genitalia uncoloured.

3.2 Genus *Elatosara* Malzacher, **n. gen.**

Type species: *Elatosara phanomensis* Malzacher, **n. sp.**

Differential Diagnosis

Elatosara can be characterised and distinguished from all other genera of *Caenidae* by the following combination of characters:

Males: Prosternal ridges divided in several thin ones, forming a bell-shaped figure (Fig. 17c). – Forceps of moderate length, apically converging and rounded, without longitudinal folds or ridges (Fig. 17b). – No functional unit of forceps and lateral sclerite.

Table 1. Ratios of larval maxillary (Pmax) and labial (Plb) palps of the herein described *Caenis* species.

	<i>Caenis ludovici</i>	<i>Caenis nasuta</i>	<i>Caenis longiforcipata</i>	<i>Caenis ulmeriana</i>	<i>Caenis karenae</i>	<i>Caenis picea</i>
Pmax segment length: 3/2	1.3	1.4	1.7	1.2–1.4	1.3–1.4	1.7–1.8
Plb segment length: 2/3	2.0	1.8–2.0	2.0	2.0–2.3	1.7–1.8	0.8–1.0
Length Pmax 2+3 / Plb 2+3	1.3	1.4	1.2	1.4	1.4	1.05
Length Pmax / Plb	1.15	1.2	1.15	1.15–1.2	1.2	1.0
Pmax segment 3: length / width	5–5.5	5.5	5.5–6	4.5–4.8	5.0	5.5

Larva: Thorax not broadened. – Head without ocellar tubercles and microscopic pits. – Outline of head slightly bulged in lateral view (Fig. 17f). – Clypeus scarcely protruding anteriorly, without setation (Fig. 17f). – Maxillar and labial palps three-segmented, short. – Segments 2 and 3 of labial palp subequal in length. – Legs not narrow and slender. – Fore tibia and fore tarsus without filtering setae. – Mid and hind tibia ventrally without long bristles. – Femora marginal with long or very long thin bristles (Fig. 17e); similar bristles forming transverse row on fore femur (Fig. 17d) – Operculate gill ventrally with an irregular band of simple scale-shaped microtrichia, clusters of spines and single spines (Figs 18, 19). – Band does not reach hind margin of gill (Fig. 18). – Number of more-branched filaments on gill III(-V) reduced, only 7–9 filaments with 3 or more branches. – Lateral spines of abdomen not bent dorsally. – Posterior part of sternum IX rounded, not shortened (Fig. 17a). – Abdominal terga VII–IX without mediolongitudinal ridge. – Hind margin

of sternum IX without a bi-pointed process with concave margin between the points.

Etymology

Elatos, a figure of the Greek mythology, was the father of Caenis. The ending “-ara” is common in the tribe Clypeocaenini, to which the genus has to be added.

Elatosara phanomensis Malzacher, **n. sp.**

(Figs 17–19)

Material examined

Holotype. ♂ larva (on microslide): MRC 2.3, Thailand, Nakhon Phanom Prov., Mekong River, 01.04.2015, **SMNS_EPH_007793_M**.

Paratypes. MRC 2.3, Thailand, Nakhon Phanom Prov., Mekong River, 01.04.2015, 1♀ larva. MRC 1.5, Thailand, Nakhon Phanom Prov., Nam Kham River, 17.06.2013, 1♂ larva. – all N. Sangpradub leg.

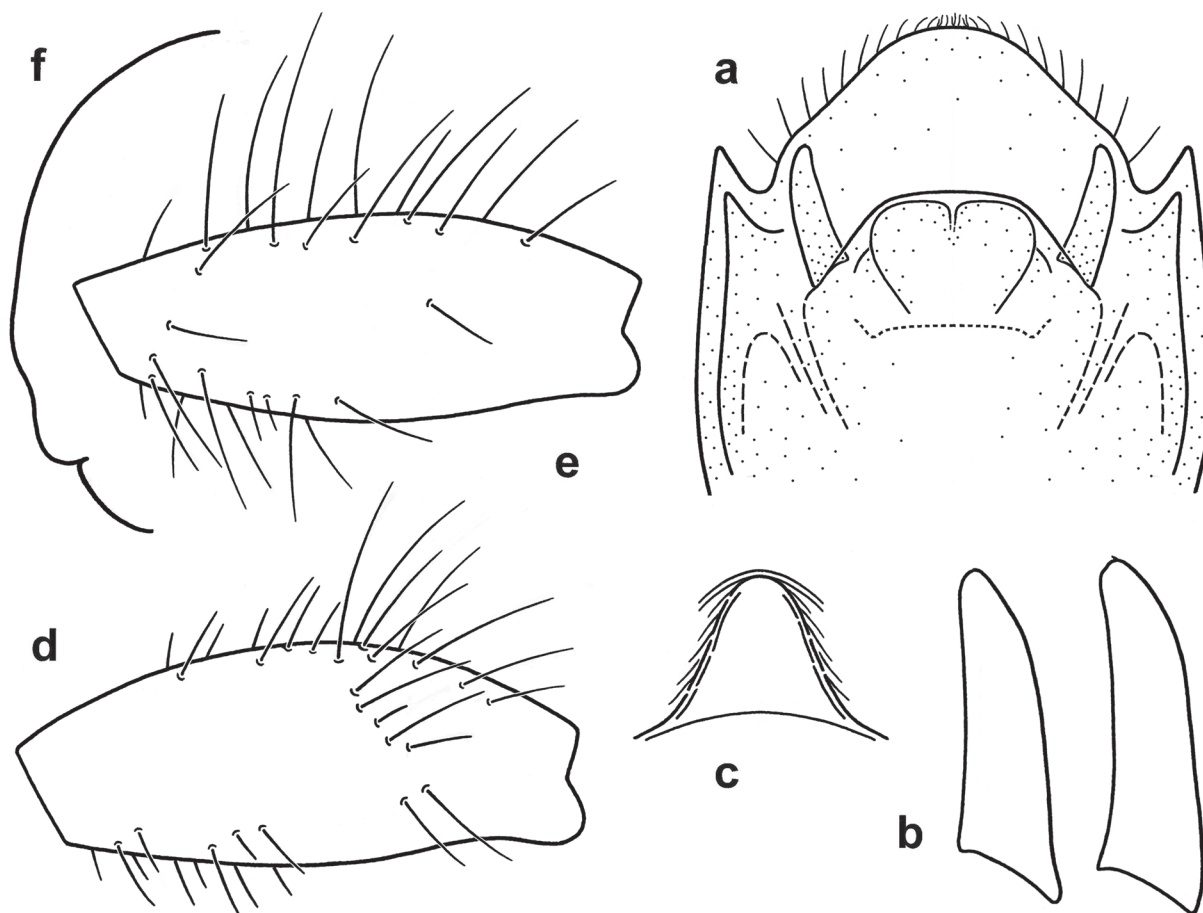
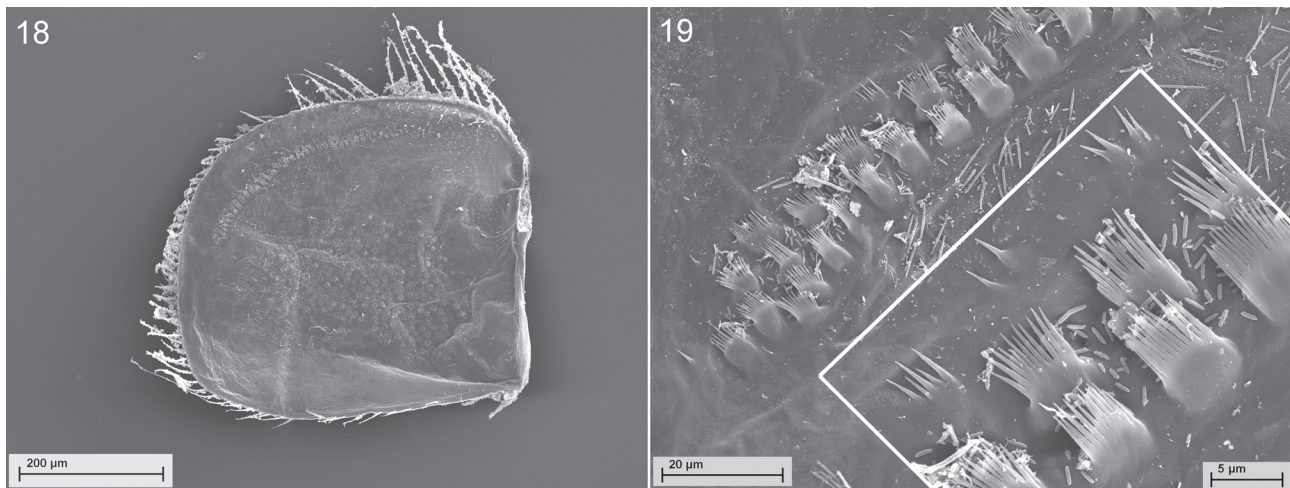


Fig. 17. *Elatosara phanomensis* n. gen., n. sp., larva. – **a.** Sternite IX, ♂, with subimaginal genitalia. – **b.** Forceps. – **c.** Prosternal triangle. – **d.** Forefemur. – **e.** Mid femur. – **f.** Outline of head, lateral view.



Figs 18, 19. *Elatosara phanomensis* n. gen., n. sp., larva. – **18.** Operculate gill, ventral view. **19.** Operculate gill, microtrichia from ventral side. Frame: higher magnification.

Etymology

The species name refers to the Thai word *phanom* that means hill, because of the hilly region where the specimens are found.

Male subimago

Two specimens are male last instar larvae. The following subimaginal features are therefore visible:

Base of antennal flagellum not dilated. Prosteral ridges divided into several thin ones, forming a bell-shaped figure. (Fig. 17c). Segments of foretarsus apically not broadened, without small spines. Abdominal segments with very short posterolateral processes. Subimaginal genitalia as in Fig. 17a. Penis narrow, with broadly rounded lobes, apico-ventral part heart-shaped. Styliger sclerite with two inconspicuous short apophyses. Forceps of moderate length, apically converging and rounded (Fig. 17b).

Larva

Measurements and colouration

Male larva of last instar, body length 2.5–2.8 mm, cerci length 1.5 mm.

Colouration of cuticle: Head, pro- and mesonotum and operculate gill brownish yellow. Other parts whitish.

Epidermal pigmentation: not visible.

Morphology

Cuticle: Head, pro- and mesonotum slightly granulated. Abdominal terga denticulated. Surface scattered

with long thin bristles. Operculate gill with denticles joint by net meshes.

Head: Outline of head slightly bulged in lateral view (Fig. 17f). Genae slightly bulged. Pedicel with 3–4 moderate bristles. Mandibles dorsolateral with relatively short, thin and bowed bristles. No conspicuous bristles in front of the eyes. Maxillary palp short, length to width ratio of segment 3: 3.5–4.0 (5.0–6.0 in most other *Caenis* species). Labial palp segments 2 and 3 subequal in length.

Thorax: Sides of pronotum diverging anteriorly, slightly concave, denticulated, with few thin bristles. Sides of mesonotum without an antero-lateral nose-shaped projection. Coxal processes inconspicuous, sickle-shaped. Forefemur on dorsal side with an oblique transverse row of long or moderate thin bristles (Fig. 17d). Mid and hind femora with long or very long thin bristles on hind margin and somewhat shorter ones on foremargin; dorsal side with few long thin bristles (Fig. 17e). Tarsi ventrally with 5–7 moderate, strong and simple bristles. Foreclaw slender and slightly bowed. Mid and hind claw basally broader, apically more or less bowed. All claws with 5–7 small or very small denticles, often nearly invisible.

Abdomen: Posterolateral processes on abdominal segments short and triangular, V and VI a little longer. Segments V–VII with 6–7 long bristles, segment VIII with about 5 bristles of moderate length, segment IX with about 3 shorter ones. Sides of segment IX nearly parallel, straight or slightly convex (Fig. 17a). Tergum II with a cone-shaped, erect, posteromedian process. Hind margin of tergum VII with about 12, of tergum VIII with

about 8 thin long bristles. Hind margin of terga IX and X with small denticles. Hind part of sternum IX obtuse angled triangular, with broadly rounded tip, marginally with long to moderate bristles, the apical ones shorter and bent medially, at the top a couple of short bifurcated bristles (Fig. 17a). Shagreen not visible. Operculate gill square-shaped, with very broadly rounded postero-lateral corner; this part with short, often spatulate bristles; lateral margin with moderate and long thin bristles, the longest towards the basal end; other long bristles on postero-median corner; inner margin with moderate bristles (Fig. 18). Y-shaped ridges well developed, particularly the median one; base of the latter with about 4 strong pointed bristles of moderate length. Ventral side of operculate gill with an irregular band of simple, scale-shaped microtrichia, clusters of spines and single spines that do not reach hind margin of gill (Figs 18, 19). Gill I about three fourth the length of gill II. Gill III–V with about 8 filaments with 3 branches each.

3.3 Genus *Thainis* Malzacher, **n. gen.**

Type species: *Thainis kalimaenoides* Malzacher, **n. sp.**

Differential Diagnosis

Thainis can be characterised and distinguished from all other genera of Caenidae by the following combination of characters:

Larva: Body slender and elongated, outline evenly curved (Fig. 20). – Head without ocellar tubercles and microscopic pits. – Besides a slight anterior protrusion of clypeus, forming a straight foremargin (Fig. 20, frame), outline of head not bulged in lateral view. – Clypeus without setation. – Maxillar and labial palps three-segmented (Figs 22, 30). – Maxillary palps elongated and narrowed with a conical segment I and more or less s-shaped, coiled segments II and III (Figs 22a, 30a). – Segment 3 of labial palp very short, with oblique dividing line to segment 2; 2 and 3 together oval (Fig. 22b, 30b) – Legs not narrow and slender. – Claws very narrow and slender (Figs 24, 32). – Only hind claws with basal denticles. – Operculate gill ventrally with a regular row of well-developed scale-shaped microtrichia, reaching hind margin of gill; basal area with long pinnate bristles (Figs 25, 27; 33). – Gill III(–V) with very long filaments, most of them with 3 or 4 branches (Fig. 36), dorsal and ventral side densely provided with long thin bristles. – Lateral spines of abdomen not bent dorsally. – Posterior part of sternum IX not shortened, with an apical indentation (Figs 21a, e). – Abdominal terga VII–IX without mediolongitudinal ridge.

Etymology

The genus name is a combination of Thailand and *Caenis*.

Thainis kalimaenoides Malzacher, **n. sp.**

(Figs 20, 21a–d, 22, 23, 24a, 25, 26, 27a, 28, 29)

Material examined

Holotype. ♀ larva (on microslide): CHI 3.1, Thailand, Maha Sarakham Prov., Ban Muang, Chi River, N 16° 14'03.72", E 103° 25' 15.32", 17.06.2003, **SMNS EPH_007790_M**.

Other material. CHI 1.2, Thailand, Yasothon, Tha Sai Mae Su Jin, Chi River, N 15° 48' 23.90", E 104° 07' 09.80", 28.02.2003, 1 ♀ larva. – all N. Sangpradub leg.

Etymology

The species name refers to similarities with the genus *Kalimaenis*.

Larva

Measurements and colouration

Female larva, subadult, body length 7.0 mm, cerci length 3.0 mm.

Colouration of cuticle: yellowish-brown. Epidermal pigmentation: specimens are badly preserved so that pigmentation is not visible.



Fig. 20. *Thainis kalimaenoides* n. gen., n. sp., larva. – Habitus.

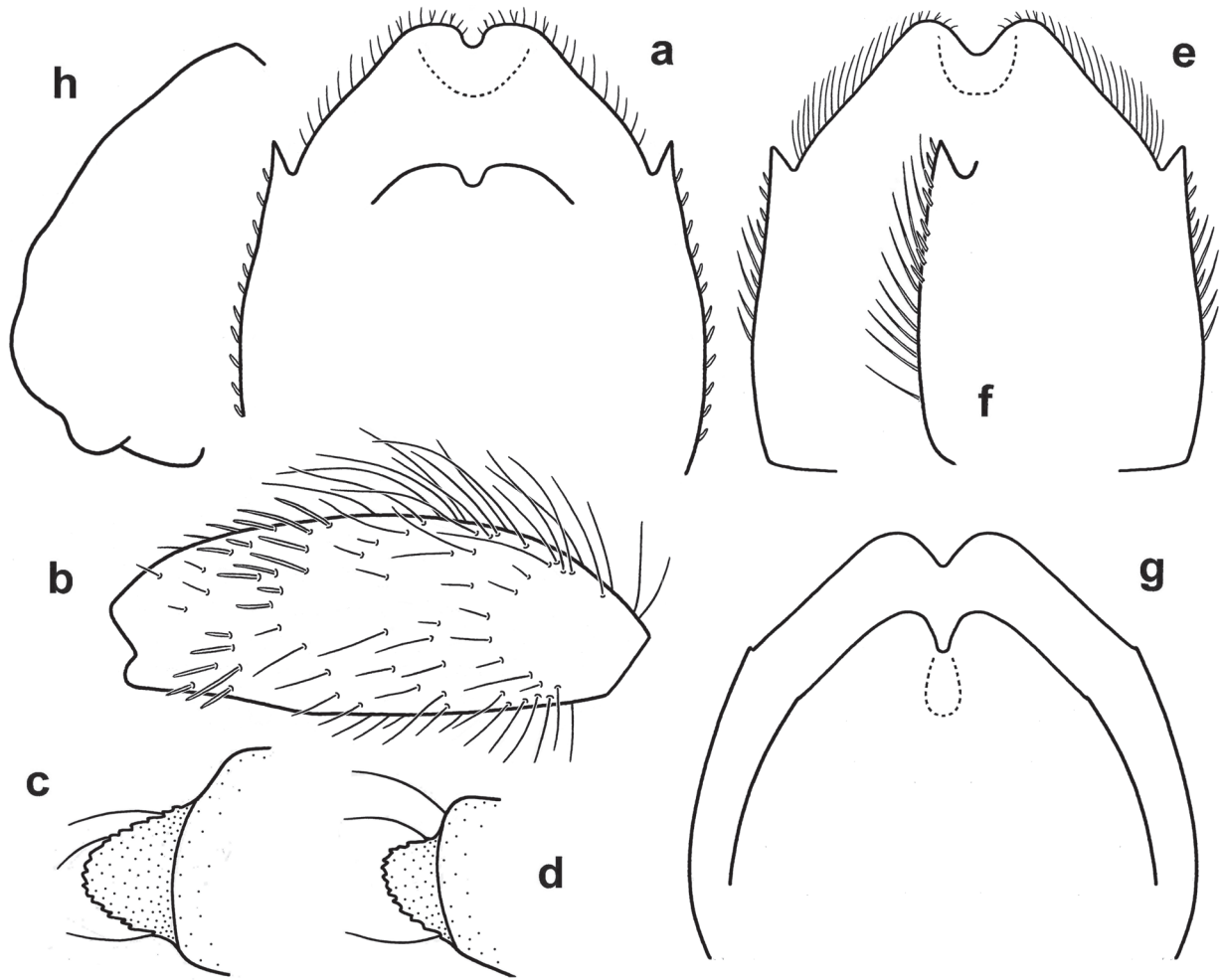


Fig. 21. *Thainis kalimaenoides* n. gen., n. sp., larva (a–d), *Thainis munensis* n. gen., n. sp., larva (e, f), *Kalimaenis procera* n. sp., larva (g). – a, e, g. Sternite IX – b. Forefemur. – c. Coxal process from hind leg. – d. Coxal process from mid leg. – f. Marginal setation of abdominal segment 7. – h. Outline of head, lateral view.

Morphology

Cuticle: Head, pro- and mesonotum granulated, without chloride cells and fine bristles (compare next species). Abdominal terga denticulated, with few blunt or spatulate bristles. Tergum VII densely provided with moderate, nearly parallel sided blunt bristles. Operculate gill with sharp denticles, scattered with moderate blunt bristles.

Habitus: slender, elongated. Outline of body evenly curved (Fig. 20).

Head: Besides a slight anterior protrusion of clypeus, forming a straight foremargin (Fig. 20, frame), outline of head not bulged in lateral view. Genae long, slightly bulged. Pedicel covered with short thin bristles. Mandibles dorsolateral without conspicuous bristles. Two blunt bristles in front of the eyes. Segments 2 and 3 of maxillary palp very long, as long as forefemur; segment 1 apically slightly converging; segment 2 and 3 coiled (Fig. 22a).

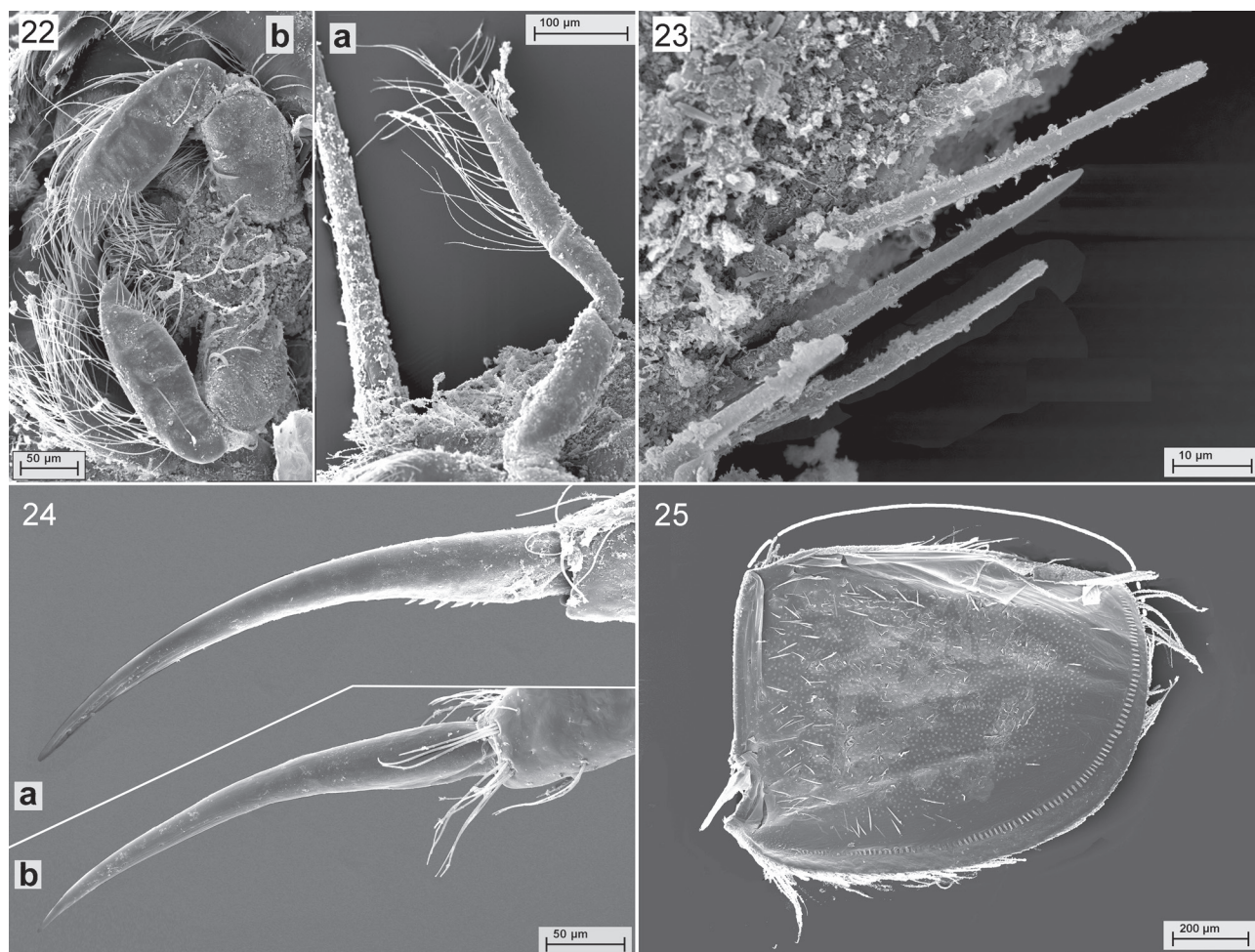
Labial palp segments 2 and 3 together oval, with oblique dividing line; about 3 times as long as wide (Fig. 22b).

Thorax: Sides of pronotum more or less converging anteriorly (Fig. 20), nearly smooth. Foreleg a little shorter than hind leg (Foreleg / hind leg = 0.8). Coxal processes semicircular, margins denticulated with few thin bristles (Figs 21c, d). Forefemur on dorsal side with irregular transverse band of moderate, flat, blunt, and parallel-sided bristles; hind margin basally from transverse row with numerous very long hair-like bristles, as long as femur width; dorsal side basally from transverse band scattered with moderate and long, very thin bristles (Fig. 21b). Hind margin of mid and hind femora densely provided with long to moderate bristles, the longest hair-like, the shorter ones blunt. Those blunt bristles also on foremargin (Fig. 23) and on anterior part of dorsal side. Foretibia on foremargin with a row of long to moderate pointed

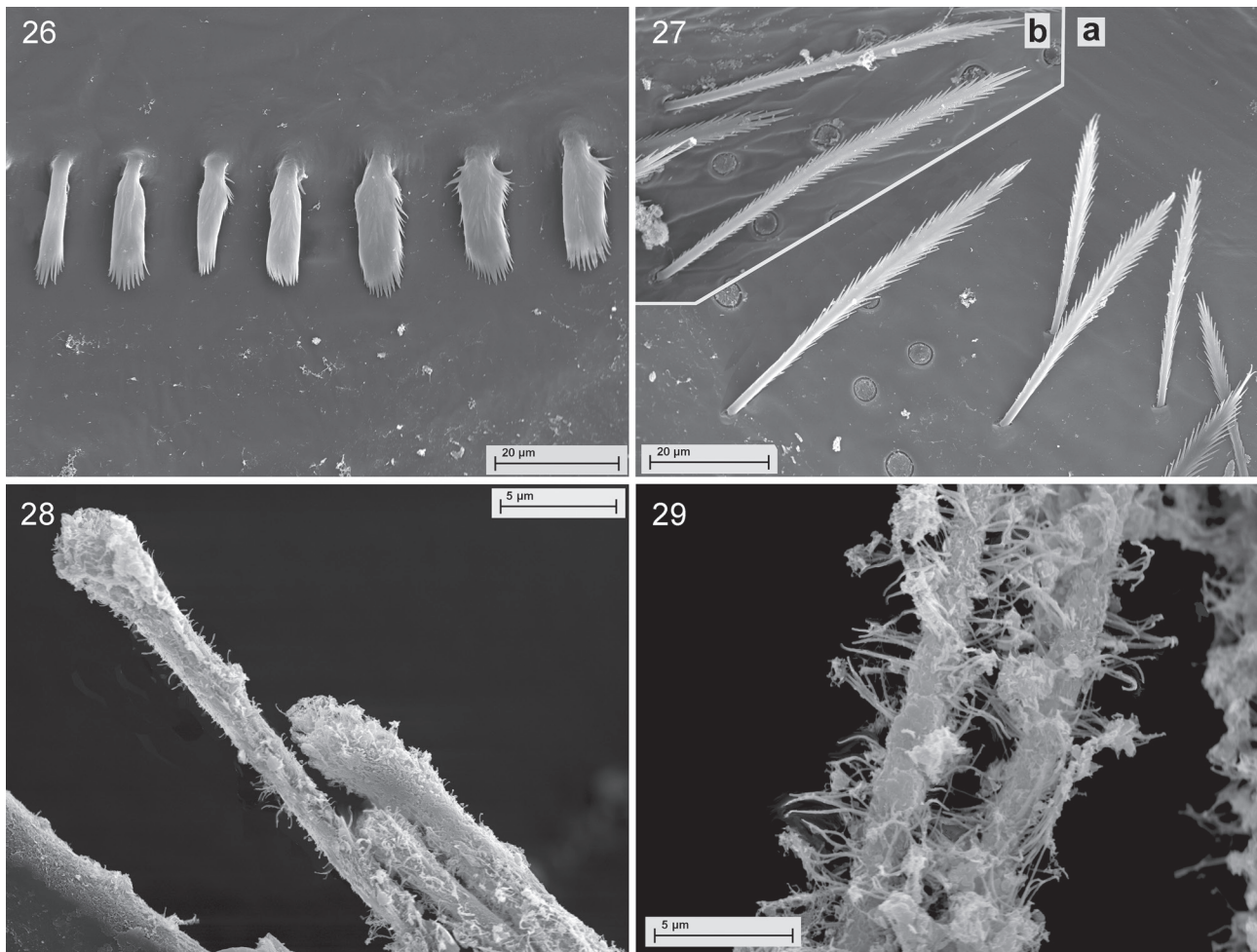
bristles apically ending in a group of shorter, more or less pinnate ones. Few similar bristles neighboured on tarsus base. Tibia on antero-dorsal side with about 10 long and thin bristles, the longest nearly half as long as tibia. Hind tibia marginally with long and moderate bristles. Foretarsus ventrally with a row of about 10 moderate pinnate bristles, the basal ones only slightly pinnate. Mid tarsus with a row of about 13 simple bristles, hind tarsus with an irregular row or band of 14–17 slightly pinnate bristles. All claws very long, slender and slightly bowed. Foreclaw without denticles (as Fig. 24b). Mid claw basally with about three very small denticles. Hind claw basally with 5–8 small denticles (Fig. 24a).

Abdomen: Posterolateral processes on abdominal segments short (Fig. 20). Segments V–VII on lateral margin densely provided with moderate to long blunt bristles, between them a couple of short strong and blunt ones. Segments VIII and IX with shorter bristles, on IX often

very short (Fig. 21a). Tergum II with a flat, triangular, dorsally lifted posteromedian process. Tergum VII dorsally with short to moderate blunt bristles, tergum VIII with fewer short, blunt ones. Hind margin of tergum VI densely provided with about 60 moderate, pointed bristles, of tergum VII with short to moderate blunt bristles, of tergum VIII with few very short blunt to spatulate bristles, and small rounded denticles. Hind margin of terga IX and X with denticles more or less pointed. Hind part of sternum IX triangular, broadly rounded, apically with a small semicircular indentation, marginally with moderate, thin bristles, the apical ones shorter, a few of them bifurcated (Fig. 21a). A large dorsal shagreen field consists of densely arranged, very sharp denticles (dotted line in Fig. 21a). Operculate gill nearly as long as wide (Fig. 25), marginally with long, pointed, thin bristles, the longest ones on posteromedial corner and on basal part of lateral margin. The latter also with moderate, blunt, often



Figs 22–25. *Thainis kalimaenoides* n. gen., n. sp., larva. – 22. Mouthparts: maxillary palp (a), labium (b). 23. Mid femur, bristles from foremargin. – 24. *Thainis kalimaenoides* n. gen., n. sp. Hind claw (a). – *Thainis munensis* n. gen., n. sp. Foreclaw (b). – 25. *Thainis kalimaenoides* n. gen., n. sp., larva. – Operculate gill, ventral view (median margin reconstructed).



Figs 26–29. *Thainis kalimaenoides* n. gen., n. sp., larva. – 26. Operculate gill, microtrichia from ventral side. – 27. *Thainis kalimaenoides* n. gen., n. sp. (a). – *Thainis munensis* n. gen., n. sp. (b). Operculate gill, bristles from ventral side. – 28. *Thainis kalimaenoides* n. gen., n. sp., larva. – Operculate gill, bristles from lateral margin. 29. Operculate gill, bristle from hind margin, sector.

apically broadened bristles, on posterior part all of them broadened (Fig. 28). Bristles on hind margin densely provided with fine filaments (Fig. 29). Basal part of median ridges well developed with about 6 moderate, strong bristles, other parts of Y reduced. Ventral side of operculate gill with a regular row of elongated scale-shaped microtrichia (Fig. 26), relatively close to lateral margin, which nearly reaches posteromedial corner (distance to margin length of one microtrichium) (Fig. 25); basal area with long, pinnate bristles (Fig. 27a). Gill I very short, only about 0.2 times as long as gill II, without bristles. Gill III(–V) with very long filaments, the longest nearly twice as long as gill corpus; widely projecting hind margin of operculate gill; most filaments with 3 or 4 branches; gill corpus dorsally and ventrally densely provided with very long and thin bristles.

Thainis munensis Malzacher, **n. sp.**
(Figs 21e, f, 24b, 27b, 30–35)

Material examined

Holotype. ♀ larva (on microslide): **SMNS_EPH_007791_M**, MUN 1.2, Thailand, Nakorn Ratchasima Prov., Ban Muang, Mun River, N 15° 13' 40.00", E 102° 28' 53.80", 10.12.2003.

Paratypes. MUN 1.1, MUN 1.2, same data as Holotype, 3 larvae.

Other material: POG 1.2, Thailand, Khon Kaen Prov., Ban Nong Chik, Phong River, 03.02.1996, 2♀ larvae. – POG 1.4, Thailand, Loei Prov., Ban Na Noi, Phong River, 16° 48' 59.41"N, 101° 48' 23.91"E, 21.08.1996, 1♀ larva. – all N. Sangpradub leg.

Etymology

The species name refers to Mun River, where the holotype has been found.

Larva

Measurements and colouration

Female larva, submature, body length 8.0 mm, cerci length 4.5 mm.

Colouration: specimens are badly preserved so that colouration cannot be described.

Morphology

Only characters that differ from the species above are described.

Cuticle: Head, pro- and mesonotum more or less granulated with numerous chloride cells and fine bristles. Abdominal terga slightly denticulated, with numerous very thin bristles of different length. Tergum VII densely provided with long thin bristles apically more or less pinnate. Operculate gill more or less denticulated, scattered with very thin bristles.

Head: Genae short, slightly bulged. Segments 2 and 3 of maxillary palp shorter, 0.7–0.8 times as long as forefemur; segment 2 and 3 scarcely coiled or not (Fig. 28a). Labial palp segments 2 and 3 together broadly oval, about 2.6 times as long as wide (Fig. 30b).

Thorax: Ratio Foreleg / hind leg length = 0.75. Bristles of transverse row on dorsal side of forefemur long and pointed. Foretibia apicomedia with a tuft of about 15 strong, pointed and pinnate bristles more or less bent medially, few similar bristles neighboured basally on first tarsal segment (Fig. 31). Dorsal side of tibia without long and thin bristles. Hind tibia without long and moderate bristles on hind margin. All tarsi ventrally with a band of numerous pinnate bristles. Number of bristles: foretarsus 14–20 (24), mid tarsus 17–22 (26), hind tarsus 20–30 (37). Mid claw with about 7 small, basal denticles. Hind claw basally with numerous very small denticles, most of them serrated with two or three tips (Fig. 32).

Abdomen: Longer bristles on lateral margin of abdominal segments pointed, between them 6–10 short strong and blunt bristles. Tergum VII dorsally with moderate to long thin, apically slightly broadened bristles, tergum VIII with long, hair-like bristles. Hind margin of tergum VI without bristles, of tergum VII and VIII with moderate bristles, basally relatively broad and apically very thin. Hind margin of terga IX and X with denticles. Hind margin of sternum IX apically with a broad, v-shaped indentation (Fig. 21e). A relatively narrow shagreen field composed of densely arranged sharp denticles (dotted line in Fig. 21e). Operculate gill clearly longer than wide (Fig. 33). Row of microtrichia on ventral side of operculate gill runs close to lateral and hind margin; often microtrichia extend gill margin (Fig. 34a, b). Pinnate bristles from basal area with two long strong apical spines (Fig. 27b). Gill I one third the length of gill II, with 8–10 long thin bristles. Gill III(–V) with long filaments, the longest 1.5–1.7 times as long as gill corpus (Fig. 35).

3.4 Genus *Kalimaenis* Malzacher, 2013

MALZACHER (2013: 32)

Type species: *Kalimaenis sibylliana* Malzacher, 2013

The genus can be characterised and distinguished from all other genera of Caenidae by the following combination of characters:

Larva. Surface (dorsal and ventral side) strongly granulated. – Head without ocellar tubercles and microscopic pits but with ridges or bulges. – Clypeus anteriorly protruding, without setation (Fig. 36). – Maxillar and labial palps three-segmented. – Maxillary palp very slender, segment I apically converging, segments II and III coiled (Fig. 37). – Segment III of labial palp very short, with oblique border to segment II (Fig. 37). – Legs narrow and slender. – Foreleg clearly shorter than hind leg. – Foretibia and foretarsus without very long bristles. – Hind claws with groups of micro-denticles fused together (in the here described species less visible, Fig. 39). – Gill I very short. – Operculate gill ventrally with a regular row of microtrichia, row ends well apart from hind margin of gill (Fig. 40). – Number of filaments on gills III–VI reduced; only about 7 filaments with 3 or more branches on gill III. – Lateral spines of abdomen not bent dorsally. – Abdominal terga VII–IX without mediolongitudinal ridge. – Hind margin of sternum IX without a bi-pointed process with concave margin between the points.

Kalimaenis procera Malzacher, **n. sp.**
(Figs 21g, h, 36–42)

Material examined

Holotype. ♀ larva (on microslide): **SMNS_EPH_007792_M**, KKJ 1.6, Thailand, Kanchanaburi Prov., Pa La Au6, Kaeng Krachan National Park, 03.04.2008, KKJ 1.5, Thailand, Kanchanaburi Prov., Pa La Au5, Kaeng Krachan National Park, 10.02.2009, 1♀ larva. – all N. Sangpradub leg.

Etymology

The species epithet refers to the slender body-shape, from Latin *procerus*, slender.

Larva

Measurements and colouration

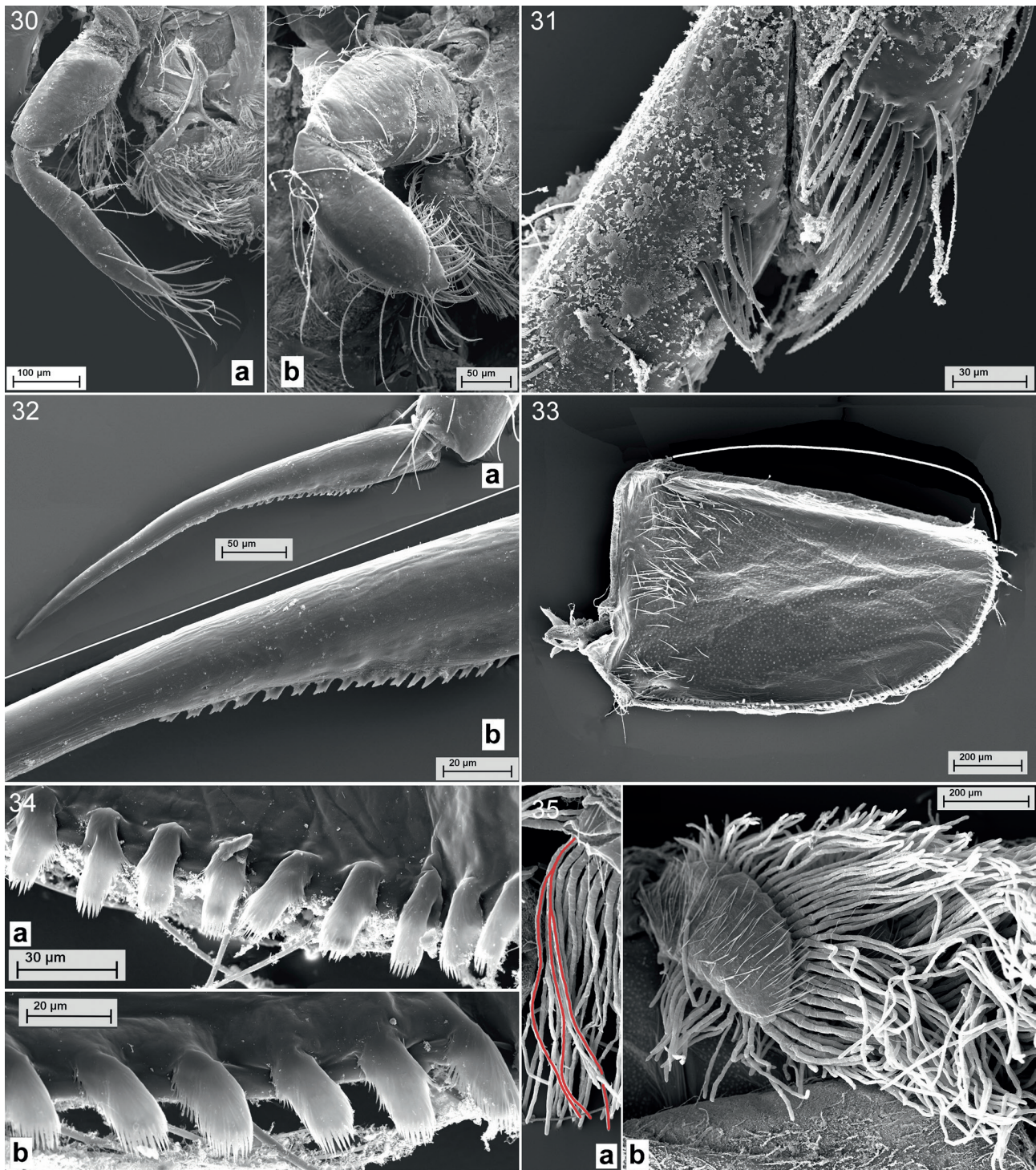
No last instar or submature larva available.

Colouration of cuticle: yellowish-brown Epidermal pigmentation: apart from eyes and ocelli no pigments visible.

Morphology

Body: slender and narrow (Fig. 36).

Surface: dorsal and ventral side strongly granulated, head and thorax mainly with round knobs and square



Figs 30–35. *Thainis munensis* n. gen., n. sp., larva – **30.** Mouthparts: maxillary palp (a), labial palp (b). **31.** Foreleg, setation of area between tibia and tarsus. **32.** Hind claw (a), detail (b). **33.** Operculate gill, ventral view (median margin reconstructed). **34.** Operculate gill, microtrichia from ventral side, hind margin (a) and lateral margin (b). **35.** Gill III: marked filament (a), total view (b).



Fig. 36. *Kalimaenis procera* n. sp., larva. – Habitus.

or pentagonal elevations, abdomen with scaly triangular denticles, also on femora, and modified, very short, club-shaped bristles (Fig. 38). Because of these triangular denticles, body outlines appear strongly granulated or denticulated.

Head (Fig. 37, ventral side): Genae broadly bulging out. Mouthparts shifted posteriorly. Clypeus slightly protruding anteriorly, protrusion with straight foremargin (Fig. 21h, 36). Labrum broadly elliptically rounded. Mandibles without setation. Maxillary palp very slender, segment I apically converging, segments II and III coiled. Segment III of labial palp very short, with oblique border to segment II; segment I short and rounded (Fig. 37).

Thorax: Pronotum broadly rectangular, lateral sides parallel, straight, forecorners protruding anteriorly; fore- and hind margin in dorsal view straight and parallel (Fig. 36); foremargin of prosternum medially strongly emarginate. Legs narrow and slender. Forelegs clearly shorter than hind legs (Fig. 36). Coxal processes forming inconspicuous, denticulated ridges. Femora and tibiae with very short and tiny marginal bristles looking like small knobs. Transverse row on forefemur composed of only 3–5 very short spatulate bristles. Fore- and mid tarsus ventrally with inner row of about 9–11 bristles, the basal

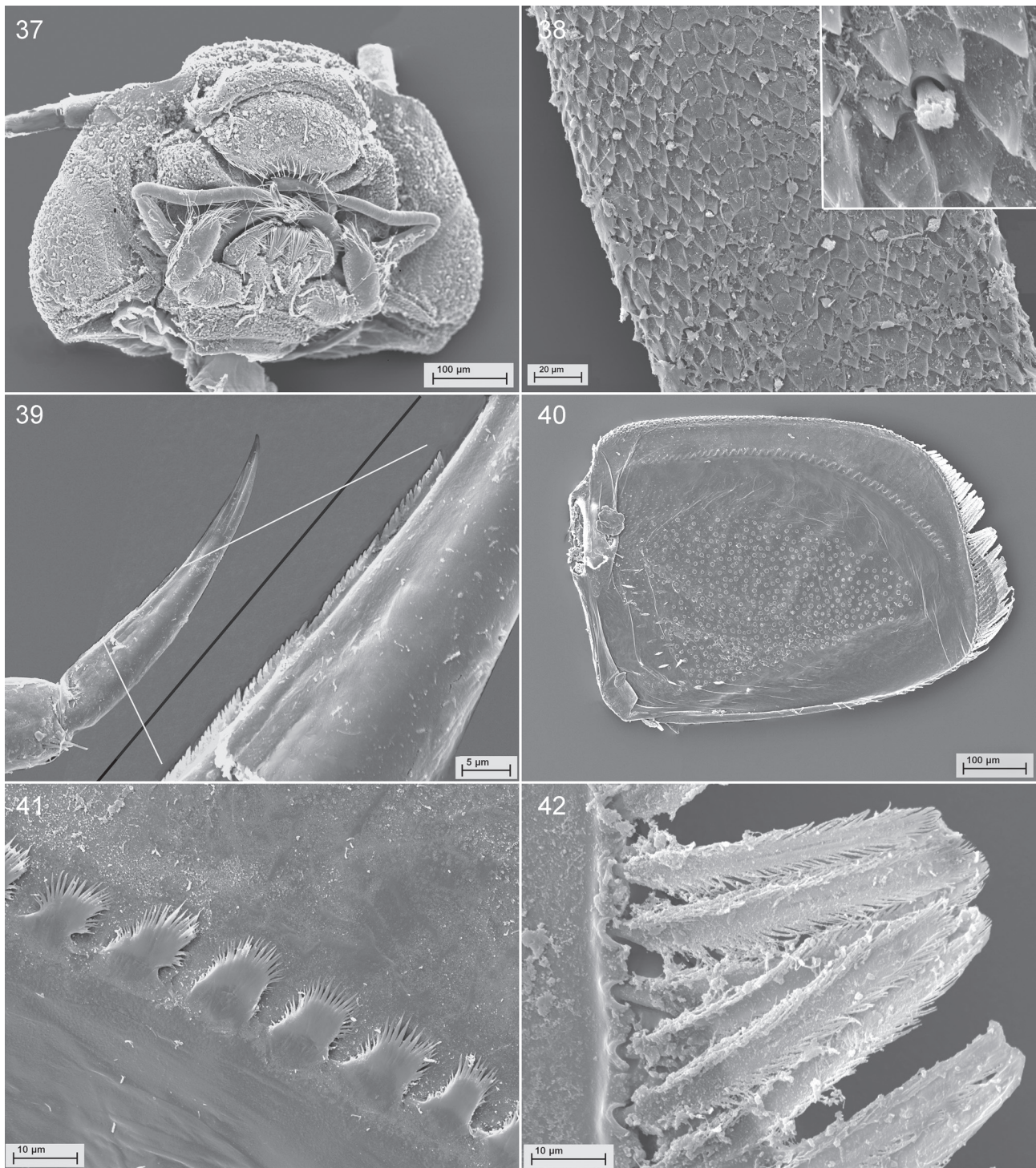
ones short and pointed, the apical long and pinnate. Hind tarsus additionally with an outer row of 4–6 unipinnate bristles, pinnae directed medially; both rows lie very close to each other. Claws slender and scarcely bowed; fore- and mid claws without denticulation; hind claws with very fine micro-denticles forming blurred groups (Fig. 39).

Abdomen: Abdominal segments with short postero-lateral processes; on segment IX nearly totally reduced (Fig. 36). Lateral bristles very short and blunt, on segment VIII and IX knob-like, often nearly invisible. Posteriomedian process of tergum II short, triangular and pointed. Hind margin of tergum VII–X strongly denticulated. Hind margin of sternum IX domed, with a deep indentation of different width (Fig. 21g). Gill I very short, about 0.2x the length of gill cover. Operculate gill (Fig. 40) without bristles on lateral margin, but with few short and thin bristles on median margin. Hind margin densely provided with moderate, broad and flat bristles, increasing in length from posterolateral to posteromedial corner; lateral margins densely provided with fine filaments; filaments of neighbouring bristles overlapping (Fig. 42). Y-shaped ridges well developed, connected in the middle of the gill; medial ridge moderately keeled with about 8 blunt bristles at base of keel. Ventral row of microtrichia not reaching hind margin of gill (Fig. 40). Microtrichia inconspicuous, more or less semicircular, with broad bases (Fig. 41). Small single spines on basal half of ventral surface. Number of filaments on gills III–VI reduced; gill III with about 26 filaments, only 6–7 with 3 or more branches.

4 Determination Keys

4.1 Key to the larvae of Caeninae from Thailand

- 1 Microtrichia on ventral side of operculate gill forming a row or band that does not reach hind margin of the gill (Figs 18, 40). Most filaments on gill 3(–5) one- or two-branched (Clypeocaenini) **2**
- Microtrichia on ventral side of operculate gill forming a regular row that reaches hind margin of the gill (Figs 11, 25, 33). At least half of filaments on gill 3(–5) with three or more branches (Caenini) **3**
- 2 Body nearly without bristles. Legs thin, foreleg clearly shorter than hind leg. Mouth parts shifted posteriorly (Fig. 37). Maxillary palp elongated, coiled (Fig. 37). Operculate gill ventrally with a single row of short, basally broadened microtrichia (Fig. 41) *Kalimaenis procera*
- Body with long thin bristles. Legs, particularly femora, broad, foreleg not shorter than hind leg. Mouth parts not shifted posteriorly. Maxillary palps neither elongated nor coiled. Operculate gill ventrally with a duplicated row or band of short microtrichia (Figs 18, 19) *Elatosara phanomensis*
- 3 Body slender and elongated. Claws very narrow and slender (Figs 24, 32). Filaments of respiratory gills (Fig. 35) widely projecting hind margin of operculate gill. Hind margin of sternum IX medially with deep incision (Fig. 21a and e). Maxillary palps strongly elongated, more or less coiled



Figs 37–42. *Kalimaenis procera* n. sp., larva. – **37.** Head, lateral view, with mouthparts. **38.** Hind femur, surface structure. Frame: sector in high magnification with modified bristle. **39.** Hind claw (left). Sector in higher magnification with microdenticles (right). **40.** Operculate gill, ventral view. **41.** Operculate gill, microtrichia from ventral side. **42.** Operculate gill, bristles from hind margin.

- (Figs 22a, 30a). Segment 3 of labial palp short, with oblique border to segment 2 (Figs 22b, 30b) (*Thainis*)..... 4
- Body broader and shorter. Claws not narrow and slender. Filaments of respiratory gills shorter, projecting operculate gill posteriorly only slightly or not. Hind margin of sternum IX medially without incision. Maxillary palps neither elongated nor coiled. Segment 3 of labial palp without oblique border to segment 2 (*Caenis*) 5
- 4 Maxillary palp as long as forefemur. Hind margin of tergum VI densely provided with acute bristles. Row of microtrichia on ventral side of operculate gill runs well separated from lateral and hind margin (Fig. 25) *Thainis kalimaenoides*
- Maxillary palp 0.7–0.8 times as long as forefemur. Hind margin of tergum VI without bristles. Row of microtrichia on ventral side of operculate gill runs immediately on lateral and hind margin. (Figs 33, 34) *Thainis munensis*
- 5 Mesonotum with anterolateral, nose-shaped process (Figs 1e, 2g) 6
- Mesonotum without anterolateral, nose-shaped process 8
- 6 Nose-shaped process without bristles. Posteromedian process on abdominal tergum II broadly triangular, flat. Operculate gill dorsally along the very flat inner ridge basally with about 4 short blunt bristles and posteriorly with two or three long and thin ones (Fig. 3d). Coxal processes inconspicuous *Caenis longiforcipata*
- Nose-shaped process with short or long bristles 7
- 7 Nose-shaped process with long, thin bristles (Fig. 1e). Operculate gill marginally and dorsally with numerous very long bristles (Fig. 1f). Lateral margin of segment IX with about 7 long or moderate strong bristles, hind margin medially cut or slightly concave, with long thin bristles (Fig. 1a) *Caenis ludovici*
- Nose-shaped process with short blunt bristles (Fig. 2g). Posteromedian process on abdominal tergum II cone-shaped. Operculate gill dorsally only with about 5 moderate, blunt bristles on the base of inner ridge, without long bristles posteriorly (Fig. 2h). Coxal processes long tongue-shaped (Fig. 2f) *Caenis nasuta*
- 8 Segments 2 and 3 of labial palp subequal in length. Forefemur dorsally with longitudinally arranged bristles, without transverse row. All claws with numerous denticles (Fig. 10d, e). Sternum IX posteriorly more or less triangularly protruding (Fig. 10a) 9
- Segments 2 of labial palp clearly longer than segment 3. Forefemur dorsally with a transverse row of more or less spatulate bristles. Claws basally with 0–3 small denticles, hind claw with a dense row of microdenticles or pins (Figs 4j, 9e) 10
- 9 Cuticle without shield- or tongue-shaped microtrichia. Sides of pronotum anteriorly more or less converging. Terga I and II each with a cone-shaped posteromedian process (Fig. 6c). Hind margin of tergum VII with moderate to long bristles. Hind margin of terga VIII, IX and X with small denticles ... *Caenis picea*
- Cuticle with shield-shaped microtrichia on head, pro- and mesonotum, and operculate gills; on femora with tongue-shaped microtrichia (MALZACHER 2015, figs 12, 14). Sides of pronotum parallel or anteriorly slightly diverging. Tergum II with a short, broadly triangular, flat process; tergum I without. Hind margin of tergum VII and VIII with long bristles. Hind margin of terga IX and X with small denticles *Caenis nigropunctatula*
- 10 Bristles from transverse row on forefemur and from dorsal side of mid femur slender and only slightly spatulate (Fig. 9f). Hind claw slightly or moderately bowed (Fig. 9e). Median ridge on operculate gill in its basal third with about 6 moderate spatulate bristles directed postero-laterally (Fig. 9c). Shagreen on dorsal side of sternum IX consists of few denticles immediately on hind margin (hardly visible) (Fig. 9a) *Caenis karenae*
- Bristles from transverse row on forefemur and from dorsal side of mid femur broad, strongly spatulate (as Fig. 2e). Hind claw strongly bowed (Fig. 4j). Median ridge on operculate gill anteriorly with 5–6 spatulate bristles in the apical half or two third (Fig. 4f). Shagreen on dorsal side consists of irregular transverse rows of denticles, forming a triangular or oval field (Fig. 4a, b) *Caenis ulmeriana* group

4.2 Key to the Males of *Caenis* from the Oriental Region

- 1 Segments II and III of foretarsus each with an apico-median projection (Figs 1c, 16f, MALZACHER 2013, fig. 1f) 2
- Segments II to IV of foretarsus apically with a lateral and a median projection or broadening (MALZACHER 2015, figs 1k, 1, 3j, k, 4i, j) or without 8
- 2 Forceps apically rounded (Fig. 16b) *Caenis obtusostilata*
- Forceps apically pointed, with tuft of spines or with a group of short bristles 3
- 3 Forceps apically pointed 4
- Forceps with an apical tuft of spines or with a group of short bristles 6
- 4 Forceps apically with one or 2–3 short spines close together forming a single tip, shaped as in Fig. 16h and i *Caenis acutostilata*
- Forceps differently shaped 5
- 5 Forceps very long, slender, and pointed. Penis rectangular, penis shaft inflated laterally MALZACHER 2013, fig. 3a, b) *Caenis fregatula*
- Forceps shorter and broad, apically with long, stepped, sclerotized tip (Fig. 1b) *Caenis ludovici*
- 6 Forceps short and very broad, apically with few short and thin bristles (Fig. 9b) *Caenis karenae*
- Forceps with a long apical tuft of spines (Figs 2d, 4c, d) 7
- 7 Forceps long (length to basal width about 7), slightly curved laterally (MALZACHER 2013, fig. 1b). Styliger sclerite without apophyses *Caenis unidigitata*
- Forceps of moderate length and width (length to basal width about 5) (Fig. 2d, MALZACHER 2013, fig. 2b) *Caenis nasuta* and *Caenis sebastiani*
(From *C. nasuta* only subimaginal genitalia are known, which are very similar to those of *C. sebastiani*. The larvae however are clearly distinguishable.)
- 8 Forceps apically with a very long spine angled to the short and broad shaft. Ratio shaft to spine about 1.5 (MALZACHER 2015, fig. 6b). Styliger sclerite elongated, anterior margin far away from the base of forceps (MALZACHER 2015, fig. 6a) ... *Caenis guttata*
- Forceps with clearly shorter apical spine, with a tuft of spines, or bristles, or without any spines or bristles. Anterior margin of styliger sclerite approximately on the same line with forceps bases 9
- 9 Forceps very long and narrow, about 9 times longer than wide, with a short apical tuft of spines (Fig. 3b) *Caenis longiforcipata*
- Forceps shorter and broader or without tuft of spines 10

- 10 Apophyses of styliger sclerite curved medially (MALZACHER 2015, fig. 7d). Sides of forceps evenly converging, ending apically in a short, thin spine (MALZACHER 2015, fig. 7e). Lateral abdominal filaments of moderate length..... *Caenis incurva*
- Apophyses of styliger sclerite straight or lacking. Sides of forceps not evenly converging. Lateral abdominal filaments short or very short11
- 11 Basal half of forceps very broad, with parallel sides, apical part abruptly narrowed to the tip, apically with a strong spine, with about 2 short and very thin bristles near the tip (MALZACHER 2015, fig. 5b). Penis narrow, semicircular, lobes laterally not protruding, ventral side covered with a broad lamella; anterior margin of styliger sclerite convex (MALZACHER 2015, fig. 5a)..... *Caenis maratha*
- Forceps and penis with different shape 12
- 12 Forceps apically with tuft of long spines, or with a long strong spine and few thin spines, or more or less fused bristles..... 13
- Forceps with short bristles, a short spine, or a more or less rounded tip.....14
- 13 Genital sclerites and forceps brown. Central sclerite large and round. Forceps with a tuft of long spines (MALZACHER 2015, fig. 5c, d). Penis with short, broadly triangular lobes and with a group of round sensillae (MALZACHER 2015, fig. 5c)..... *Caenis annulata*
- Genital sclerites and forceps not or only weakly coloured. Forceps apically with tuft of spines, consisting of a strong spine and few more or less thinner ones, often basally fused (variable, compare Fig. 4c, d and MALZACHER 2015, fig. 4c–f). Penis with broadly rounded and laterally slightly protruding lobes and with a tongue-shaped ventral lamella (MALZACHER 2015, figs 4a, b). Segments II to IV of foretarsus with tongue-shaped projections (MALZACHER 2015, figs 4i, j)..... *Caenis ulmeriana*
- 14 Penis anvil-shaped, hind margin straight with two narrow transverse sclerites (MALZACHER 2013, fig. 4a). Forceps long and narrow, slightly bent medially; 2–3 nearly totally fused spines forming a tip, more or less bent medially (MALZACHER 2013, figs 4b, c). Foretarsus with a very long segment II and long tongue-shaped apical processes. (MALZACHER 2013, fig. 4f)..... *Caenis bidigitata*
- Penis and forceps with different shape. Segment II of foretarsus shorter15
- 15 Forceps long, with more or less parallel sides, slightly bent laterally, with a short broad spine inserting medially (MALZACHER 2013, fig. 6c). Prosternal ridges straight, forming a broad trapezoid (MALZACHER 2013, fig. 6d)..... *Caenis abdita*
- Forceps differently shaped16
- 16 Small species, body length at last 2.1 mm, wing length at last 1.7 mm, fore leg length at last 1.6 mm. Outlines of prosternal triangle vague, without clear lateral ridges (MALZACHER 2015, fig. 6g). Forceps short and broad, with an apical spine (MALZACHER 2015, fig. 6f). Penis narrow, apical width about half the distance of the extreme lateral points of the forceps bases (MALZACHER 2015, fig. 6d)..... *Caenis gephyria*
- Body longer than 2.4 mm, wing longer than 2.0 mm, foreleg longer than 2.1 mm. Poststernal triangle with clear lateral ridges. Apical width of penis at least 0.7 the distance of the extreme lateral points of the forceps bases.....17
- 17 Penis broad, without a v-shaped brown sclerite (MALZACHER 2015, figs 1a, b). Forceps small, apically with a short acute spine or hook (MALZACHER 2015, figs 1c–i)..... *Caenis nigropunctatula*
- Penis ventrally with a v-shaped brown sclerite. (MALZACHER 2015, figs 3a, 7a, b).....18
- 18 Forceps tip rounded, very different shapes, often with a small bump or tip (MALZACHER 2015, fig. 3c–h). Abdominal tergum II without finger-like process..... *Caenis ranauensis*
- Forceps apically with few short or very short bristles often fused together (MALZACHER 2015, fig. 7c). Sclerites more or less brownish. Abdominal tergum II with a short finger-like process *Caenis picea*

5 Discussion

5.1 *Caenis*

KANG & YANG (1994) described 7 new *Caenis* species from Taiwan: *C. argillosa*, *C. nitida*, *C. bella*, *C. corpulenta*, *C. cornigera*, *C. granifera*, and *C. montana*. From all species, only larvae were described. Like in the *Caenis* species from Thailand there are species with anterolateral processes on mesonotum and others without. The species with those processes are *C. cornigera*, *C. granifera*, and *C. montana*.

Three of the herein described species also show nose-shaped processes on the mesonotum, namely *C. ludovici*, *C. longiforcipata*, and *C. nasuta*. *C. ludovici* cannot be conspecific with one of the three Taiwanese species, because these neither show a protruding and cut sternite IX with very long medially bent bristles (Fig. 1a) nor an operculate gill with numerous long bristles on the dorsal side (Fig. 1f). *C. granifera* and *C. montana* each show characters that cannot be observed in the remaining Thai species with nose-shaped processes: *C. granifera* has about 10 bristles on the sides of abdominal segment IX, a dense row of blunt bristles on the hind margin of sternum IX, and very long thin bristles dorsally on mid and hind femur (KANG AND YANG 1994, figs 6k, f, g). *C. montana* has strongly bulged genae, a dense setation on the lateral and hind margin of segment IX and no spatulate bristles dorsally on mid and hind femur (KANG AND YANG 1994, figs 7e, l, g, h). Moreover, in both species the operculate gills are equipped with shield-shaped microtrichia (KANG & YANG 1994, figs 12–15) that cannot be found in the species from Thailand. *C. cornigera*, the third species with mesonotal processes described by KANG & YANG, can be distinguished from *C. longiforcipata* by a different setation of the operculate gill (compare Fig. 3d and KANG & YANG 1994, fig 5i). From *C. longiforcipata* and *C. nasuta* it can be distinguished by pinnate and differently shaped spatulate bristles on the femora (compare Fig. 2e and KANG & YANG 1994, fig 5f).

The group without mesonotal processes is represented in Taiwan by *C. argillosa*, *C. nitida*, *C. bella*, and *C. corpulenta*, and in Thailand by *C. karenae*, *C. ulmeriana*, *C. picea*, and *C. nigropunctatula* (the species *C. guttata* and *C. gephyria*, also recorded from Thailand, are only known

from males). *C. corpulenta* differs from all Thai species in the dorsal setation of operculate gills (KANG & YANG 1994, figs 12–15). Larvae of *C. picea* and *C. nigropunctatula* can be separated from Taiwanese species by the triangularly protruding hind margin of sternum IX (Figs 10a, g and MALZACHER 2015 figs 2a, b) and the strongly denticulated claws (Figs 10d, e and MALZACHER 2015 figs 2d, e). *C. ulmeriana* can be distinguished from the remaining species *C. argillosa*, *C. nitida*, and *C. bella* by the dorsal setation of operculate gills and setation of hind margin of sternite IX (compare Figs 4e, f and 4a, b with corresponding figures in KANG & YANG 1994). *C. kareniae* can also be distinguished from the three species by the latter character and by its elongated bristles on the forefemur (compare Figs 9a and f with corresponding figs in KANG & YANG 1994).

HWANG & BAE 1999 described the larvae of *C. moe* and *C. tuba*. Both species cannot be conspecific with one of the Thailand species because in contrary to the latter they possess shield-shaped microtrichia (HWANG & BAE 1999: figs 11, 12).

C. pycnacantha (Jia et. al., 2010) shows forcipes with an apical tuft of short strong spines, strongly bent medially and basally more or less fused together (JIA et. al., 2010: figs 11, 17, 18), which distinguishes it from all other *Caenis* species.

C. yangi Kang & Yang, 1996 can be distinguished from the Thai species by the following combination of characters: lateral and hind margin of operculate gill and lateral margin of abdominal segment IX densely provided with short spatulate bristles, a very flat hind margin of sternum IX with moderate, frayed bristles and a small semicircular indentation on hind margin of sternum IX.

Finally, *C. parviforcipis* and *C. sinensis*, both species described by ZHOU & ZHENG (2004), show forcipes with sclerotized pointed tips. From the Thai species, only *C. ludovici* possesses forcipes with such tips, but the genitalia can be clearly distinguished from those of the above-mentioned species (compare Figs 1a, b with ZHOU & ZHENG, 2004, figs 8, 9, 11).

The assignment of *C. moe* Hwang & Bae, 1999 and *C. melanoleuca* Zhou & Zheng, 2004 to the genus *Caenis* seems to be questionable. The arrangement of microtrichia on the ventral side of the operculate gill in *C. moe* could indicate a placement within the tribe Clypeocaenini. Accordingly, larvae of *C. moe* should be checked for the synapomorphies of the tribe (No. 1 and 2 in Table 1).

ZHOU & ZHENG (2004) described males of *C. melanoleuca* with totally contracted forcipes, an indication that they are provided with well-developed forceps muscles, which are otherwise not present in *Caenis*. Very long abdominal processes of the larvae and sickle-shaped forcipes of the males could thus suggest a placement within *Tigrocercus*.

In the Oriental region, species with anterolateral processes on the mesonotum seem to be more common than in other regions, where a more or less bulged anterolateral margin can only be observed in few species, e.g. *C. pycnacantha* from China, or the European species *C. luctuosa* and *C. macrura* (MALZACHER 1984, table 12, figs 2 and 3). Clear anterolateral processes are present in the closely related species *C. horaria* (MALZACHER 1984, table 12, fig. 1) and *C. sinensis* (ZHOU & ZHENG, 2004, fig. 6). On the other hand, anterolateral processes on mesonotum are a generic character in the Australian *Wundacaenis*. These processes are semicircular in *Wundacaenis dostini* and *Wundacaenis flabellum*. The third species of the genus, *Wundacaenis angulata*, however is provided with strongly protruding angular and pointed processes (SUTER 1993, figs 7, 32, 57). Also, *Brachoculis acutalis*, a species of the new tribe Brachoculini (MALZACHER & SANGPRADUB 2017), shows triangular pointed anterolateral processes (see ZHOU et. al. 2003, sub. *Caenoculis acutalis*, fig. 1).

Species of *Caenis* with apically rounded forcipes so far are only recorded from West Africa and South America. Besides *Caenis martensis* MALZACHER, 2018 from the Nepalese Himalaya, the herein described *Caenis obtusostilata* is the only species with this forceps shape that occurs in Asia.

5.2 *Kalimaenis*

So far, only two species of *Kalimaenis* were known from Borneo: *Kalimaenis sibylliana* and *Kalimaenis staniczeki* (MALZACHER 2013). The larvae of the latter species are unknown, so that there is a theoretical possibility that *K. procera* represents the larval stage of *K. staniczeki*. However, all other so far described Caenidae from Borneo have not been found outside of the island, so they are probably all endemic. On the other hand, all species from the remaining Oriental region are not recorded from Borneo. So it seems to be tenable to describe the new larval specimens of *Kalimaenis* from Thailand as a new species.

5.3 Systematic placement of the new genera *Elatosara* and *Thainis*

MALZACHER 2013, 2014 and MALZACHER & STANICZEK 2016 revealed the tribes Clypeocaenini and Caenini + Tasmanocoenini as sister groups within the subfamily Caeninae. Fig. 43 illustrates the phylogenetic position of the herein described genera *Elatosara* and *Thainis* together with the recently described new genus *Liebenauis* (MALZACHER & STANICZEK 2018). Table 2 lists all characters used for the phylogenetic placement.

Genera of Clypeocaenini share following synapomorphies: (1) Number of multiple-branched filaments on gill III(–V) reduced, only 7–9 filaments with 3 or more branches. (2) Outline of head bulged in lateral view.

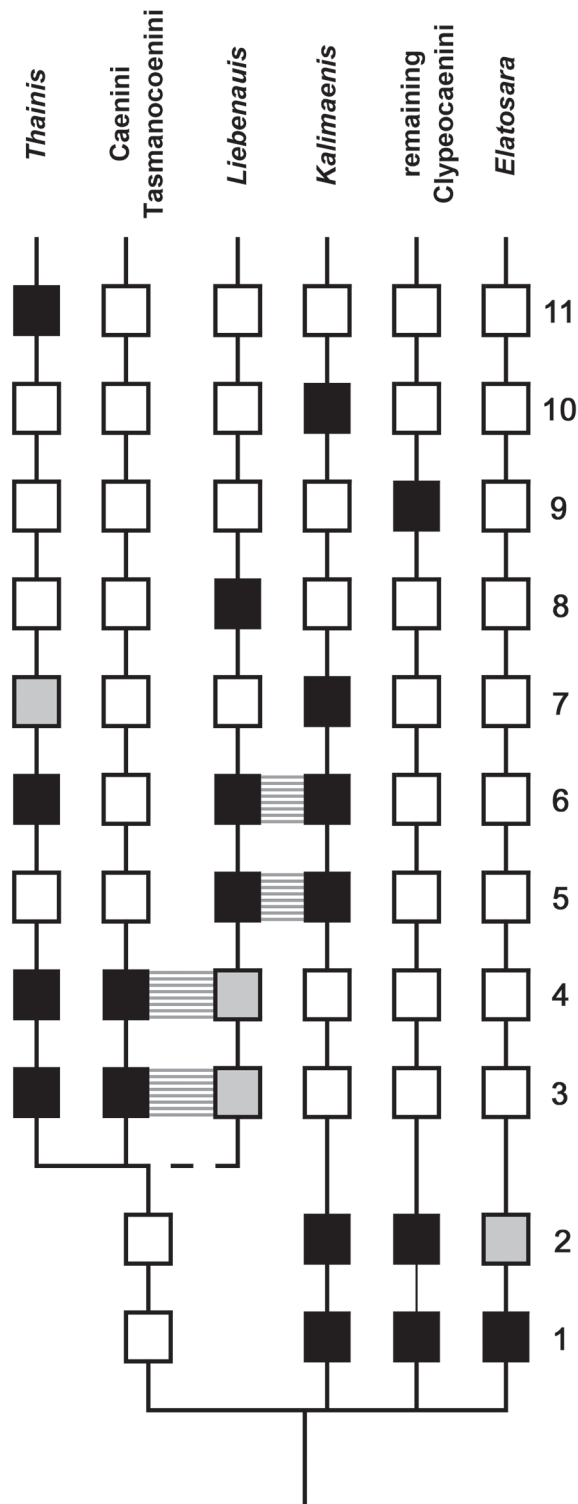


Fig. 43. Phylogenetic tree with herein described genera. White squares denote plesiomorphic character states, black squares apomorphic character states, grey squares denote intermediate character state, grey lines indicate possible synapomorphies. For explanation see also phylogenetic discussion and Table 2.

Caenini + *Tasmanocoenini* share following synapomorphies: (3) Row of microtrichia on ventral side of operculate gill reaching hind margin of the gill. (4) The regular row consists of complex, scale-shaped microtrichia. For additional discussion of these characters see MALZACHER & STANICZEK 2016.

Thainis shares synapomorphies (3) and (4) with *Caenini* + *Tasmanocoenini*. Additionally, it has three autapomorphic characters: (6) Claws very narrow and slender (Figs 24, 32). This is not an unique apomorphy, but seems to be a parallel development in *Kalimaenis*, *Liebenauis*, and at least one *Caenis* species, namely *Caenis unguolata* (MALZACHER & STANICZEK 2018). The elongated hind claws of the above mentioned genera show different types of denticulation (compare Figs 24a, 32, 39, MALZACHER 2013 fig. 8e, f; 2017b figs 1f, 2d). The claws of *Thainis* are the narrowest though (compare Figs 24a and 32 with 39). (7) Maxillary palps elongated, with a conical segment I and more or less s-shaped coiled segments II and III (Figs 22a, 30a). Previously, this character was regarded as unique apomorphy of *Kalimaenis* (MALZACHER & STANICZEK 2016). However, this might be a parallel development in *Thainis* and *Kalimaenis*. (11) Gill III(–V) with very long filaments. In *Thainis munensis* the longest are 1.5–1.6 times as long as gill corpus, in *Thainis kalimaenoides* they are nearly twice as long. Most of the filaments show 3 or 4 branches (Fig. 35). Dorsal and ventral side of the gill corpus are densely provided with very long thin bristles. In *Caenis* and the remaining Caeninae, filaments are clearly shorter, in most species 0.7–1.1 the length of gill corpus, in few species 1.2–1.3. The same ratios can be found in the outgroups Clypeocaenini, Brachycercinae and Neoephemeridae. In none of them very long bristles on gill corpus are present.

The character (10), hind claw with groups of microdenticles, is still regarded an apomorphy of *Kalimaenis*, as *Kalimaenis procera* shows a similar arrangement of microdenticles in groups, even if those groups in the latter species are not as clearly separated from each other as in *Kalimaenis sibylliana* (compare fig. 8e, f. in MALZACHER 2013 with Fig. 39). A simple arrangement of denticles can be found in *Liebenauis tenuipes*, with only about 5 denticles in the basal half of the claw (MALZACHER & STANICZEK 2018, fig. 3e). Species of *Caenis* often have heterodont hind claws, i.e. claws with few basal larger denticles and an apical row of smaller microdenticles. In *Caenis unguolata*, only the apical row is present. The *Thainis* species however show a different arrangement: In *Thainis kalimaenoides* only few denticles are visible (Fig. 24a), whereas in *Thainis munensis* a long row of two- or three-pointed denticles can be observed (Fig. 32), which may be interpreted as transitional stage to the claws of *Kalimaenis*.

Elatosara can be regarded as a member of the tribe Clypeocaenini by presence of synapomorphies (1) and (2).

Table 2. Phylogenetic characters used in Fig. 43

	character	plesiomorphic character state	apomorphic character state
1	Gill III	more than 15 up to 25 filaments	at most 9 filaments with 3 or more branches
2	Outline of head, lateral view	evenly bowed	with bulges, clypeus $\pm$ protruding
3	Gill II, ventral row of microtrichia	row not reaching hind margin	reaching hind margin of gill
4	Gill II	bands or irregular rows of spines, clusters of spines or simple scales	with regular row of complex, scale-shaped microtrichia
5	Legs	all parts shorter, femora broad	long and slender, femora narrowed
6	Claws	shorter	long and slender
7	Maxillary palp	shorter and not coiled	elongated, segment 1 conical, segments 2+3 coiled
8	Operculate gill, ventral side	without modified chloride cells	with modified chloride cells
9	Mesonotum	not broadened, outline $\pm$ irregular	broadened, outline of body more or less evenly curved
10	Claws	shorter and broader	long and slender
11	Gill III–VI	not enlarged, corpus with short bristles or without	enlarged, filaments elongated, corpus with very long bristles

The bulged outline of head is however only slightly developed; compare however Fig. 16f with figs 14a, b in MALZACHER 2013. *Elatosara* shares with many species of Clypeocaenini the plesiomorphic irregular arrangement of microtrichia on the ventral side of the operculate gill (Fig. 19).

However the relationship of *Elatosara* to *Kalimaenis* and to the remaining Clypeocaenini remains unresolved, as *Elatosara* does not share any of their apomorphies (5, 6, 7, 9, 10).

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