Caenidae from East Kalimantan, Borneo (Insecta: Ephemeroptera). With a discussion on phylogeny of the new tribe Clypeocaenini, subfamily Caeninae

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Abstract

The here examined Caenidae material from a relatively small area (10 × 6 km), about 140 km W of Tarakan, East Kalimantan, includes representatives of five genera: *Caenis* Stephens, 1835, *Kalimaenis* **n. gen.**, *Clypeocaenis* Soldan, 1978 (all Caeninae), *Tigrocercus* Malzacher, 2006 (Madecocercinae) and *Oriobrachys* Sun & McCafferty, 2008 (Brachycercinae), with the species: *Caenis unidigitata* **n. sp.**, *C. sebastiani* **n. sp.**, *C. fregatula* **n. sp.**, *C. bidigitata* **n. sp.**, *C. abdita* **n. sp.**, *Kalimaenis sibylliana* **n. sp.**, *K. staniczeki* **n. sp.**, *Clypeocaenis soldani* **n. sp.**, *Tigrocercus nastassjae* **n. sp.**, and *Oriobrachys* sp. The system of the subfamily Caeninae, particularly the new tribe Clypeocaenini, is discussed.

K e y w o r d s : Caenidae, new tribe Clypeocaenini, new genus *Kalimaenis*, new species, phylogeny, Borneo, Kalimantan.

Zusammenfassung

Das hier untersuchte Caenidae-Material stammt von einem relativ kleinen Areal (10 × 6 km), ungefähr 140 km westlich von Tarakan im Nordosten von Kalimantan. Es enthält fünf verschiedene Gattungen: *Caenis* Stephens, 1835, *Kalimaenis* **n. gen.**, *Clypeocaenis* Soldan, 1978 (alle Caeninae), *Tigrocercus* Malzacher, 2006 (Madecocercinae) und *Oriobrachys* Sun & McCafferty, 2008 (Brachycercinae), mit den Arten: *Caenis unidigitata* **n. sp.**, *C. sebastiani* **n. sp.**, *C. fregatula* **n. sp.**, *C. bidigitata* **n. sp.**, *C. abdita* **n. sp.**, *Kalimaenis sibylliana* **n. sp.**, *K. staniczeki* **n. sp.**, *Clypeocaenis soldani* **n. sp.**, *Tigrocercus nastassjae* **n. sp.** und *Oriobrachys* sp. Das System der Unterfamilie Caeninae wird – unter besonderer Berücksichtigung des neuen Tribus Clypeocaenini – diskutiert.

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1 Introduction

The only species of the family Caenidae from Borneo known so far was *Oriobrachys mahakam* Sun & McCafferty, 2008. The genus belongs to the subfamily Brachycercinae. From the surrounding archipelago only a few species are known. *Caenis nigropunctata* seems to be widely distributed from Sumatra to the Philippines (Ulmer 1939), so that it could also be expected in Borneo, but it is not included in the material described herein. A redescription of the latter species is in preparation, based on the Ulmer material from Java and Sumatra deposited in the Zoologisches Museum Hamburg.

Acknowledgements

My special thanks go to Michel Sartori (Musée cantonal de Zoologie, Lausanne) for leaving me the material for investigation. Thanks are also due to Arnold Staniczek, Susanne Leidenroth and Milan Pallmann (Staatliches Museum für Naturkunde, Stuttgart) for help, making the SEMs and the microphotographs. Michel Sartori and Arnold Staniczek kindly read the manuscript.

2 Material and methods

The investigated material is preserved in 75 % ethanol. It contains several hundred male and female imagines and subimagines

(abbreviated SI) and about 180 larvae, collected between June 2000 and April 2001. Whereas the larvae were collected in an area of about 50 km², 140 km West of Tarakan in the East Kalimantan Province near Malinau, all imagines were light-trapped at only one place within this area. On details of the sampling sites see DERLETH (2003).

The majority of the material, including the types of the newly described species, is stored in the Musée cantonal de Zoologie, Lausanne, Switzerland. Some paratypes are deposited in the Museum of Zoology, Bogor, Indonesia. A small number of specimens is preserved in the author's collection.

Specimens used for SEM were dehydrated through a stepwise 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. Macrophotographs were taken with a Leica Z16 APO Macroscope, processed with Leica Application Suite™ Version 3.1.0 to obtain combined photographs with extended depth of field. Digital photographs were enhanced by using PhotoFiltre.

3 Systematic account

3.1 Genus *Caenis* Stephens, 1835

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

I m a g o . Prosternum with ridges forming a triangle or trapezoid. – Forceps without longitudinal folds or ridges. – Forceps morphologically and functionally not fused together with the styliger plate. – Without a functional unit of forceps, forceps muscle and enlarged lateral sclerite.

E g g . Chorion without longitudinal grooves or rowed structures.

L a r v a . Thorax not broadened. – Head neither with ocellar tubercles nor with ridges, bulges and/or microscopic pits. – Clypeus anteriorly not protruding. – Maxillary and labial palps three-segmented. – Fore tibia and fore tarsus without very long bristles. – Femora longer than broad and clearly broader than tibiae, without extended plates. – Operculate gill ventrally with a regular row of scale-shaped microtrichia. – A large number (15–26) of filaments on gill III with 3 or more branches. – Lateral spines of abdomen not bent dorsally. – Posterior part of sternum IX dorsally with shagreen field. – Abdominal terga VII–IX without mediolongitudinal ridge. – Hind margin of sternum IX without a bi-pointed process with concave margin between the points.

Caenis unidigitata **n. sp.**
(Fig. 1)

H o l o t y p e , ♂ (on microslide): B1313PLM, Seturan, Seturan River, tributary, 116°30'48"E, 3°00'05"N, 17.IV.2001, P. DERLETH & M. SARTORI.

P a r a t y p e s : Same data as holotype, several hundred ♂♂ and ♂♂ SI.

Etymology

The species name refers to the single finger-like projections of the median fore tarsal segments.

Description

M a l e i m a g o

Measurements, ratios and colouration

Body length 2.3–2.7 mm; wing length 1.6–1.8 mm; length of fore leg 1.7–1.8 mm. – Ratios: Fore femur to fore tibia length = 0.50–0.53; fore tibia to fore tarsus length = 1.38–1.55; fore leg to hind leg length = 1.88–2.00; $1^{st} : 2^{nd} : 3^{rd} : 4^{th} : 5^{th}$ fore tarsal segments length = 1 : 3.7–4.5 : 2.9–3.1 : 2.2–2.4 : 1.0–1.1; fore tarsal segments length 3–5 : 1+2 = 1.1–1.6; body length to length of cercus to length of terminal filament = 1 : 1.6 : 2.6; terminal filum to cercus length = 1 : 1.63.

Colouration of cuticle: Metanotum beige; other parts white.

Epidermal pigmentation: Vertex and frons shaded with greyish-brown. Sometimes traces of pigments on prosternal trapezoid, mesosternum and anterior paraterga.

Morphology

Head: Base of antennal flagellum slightly dilated, dilated part nearly as long as and one-third as wide as the pedicel, with surface slightly bumpy, distally more or less abruptly narrowed (Figs. 1d, e).

Thorax: Prosternal ridges thin, forming a trapezoid with concave lateral sides; frontal side with tiny pins; a transverse chitinous strip extending dorsally from the fore margin, nearly reaching the fore coxae (Fig. 1c). Segments II and III of fore tarsus each with an apico-median projection, segment IV with two projections, a lateral and a median one; segment V extremely short (Fig. 1f). Scutellum broad, rounded, only slightly pointed.

Abdomen: Lateral filaments of abdominal segments very short. Without finger-like process on tergum II.

Genitalia and sternum IX as in Fig. 1a. Penis broadly rounded. Sclerites uncoloured. Anteriolateral points of forceps bases and anterior margin of styliger sclerite along the same line (Fig. 1a). Apophyses of styliger sclerite very short, often invisible. Apical part of forcipes slightly bent laterally, lateral sides concave; apical spines thin (Fig. 1b).

Female imago and larva unknown.

Differential diagnosis

Caenis unidigitata can be distinguished from all other *Caenis* species by the following combination of charac-

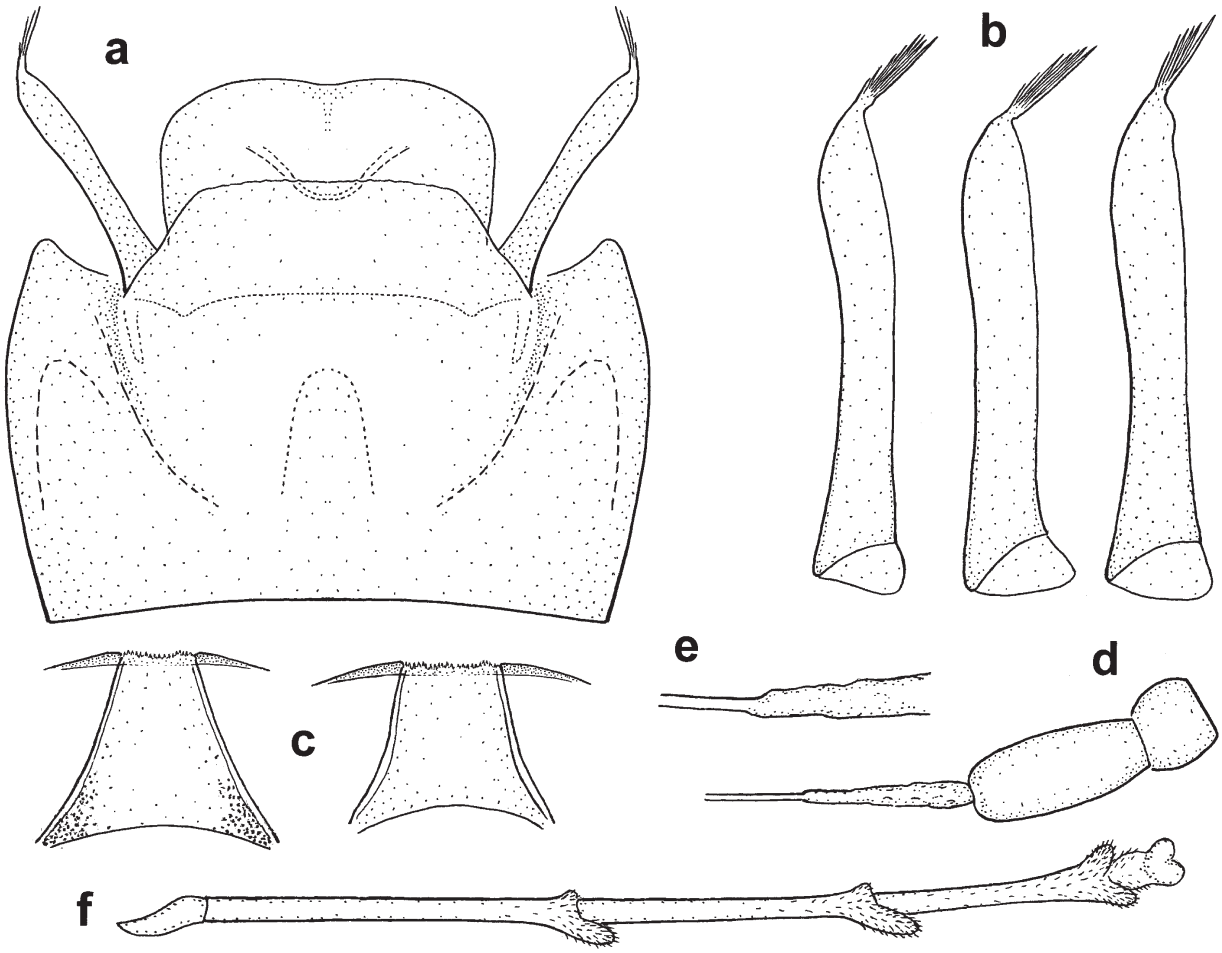


Fig. 1. *Caenis unidigitata* n. sp., ♂. – **a**. Genitalia. **b**. Different shape of forcipes. **c**. Different shape of prosternal trapezoid. **d**. Antennal scape, pedicel and base of flagellum. **e**. Base of flagellum in higher magnification. **f**. Fore tarsus.

ters: Base of antennal flagellum slightly dilated. Forcipes with apical tuft of long spines. Penis without triangular lobes. Abdominal tergum II without finger-like process. – Prosternal ridges anteriorly converging. Segment V of fore tarsus extremely short. Segments II and III each with an apico-median projection. Anteriolateral points of forceps bases and anterior margin of styliger sclerite along the same line. Apophyses of styliger sclerite very short, rounded, often invisible. Apical part of forcipes slightly bent laterally, lateral sides concave.

Caenis sebastiani **n. sp.**
(Figs. 2, 45)

Holotype, ♂ (on microslide): B1313PLM, Seturan, Seturan River, tributary, 116°30'48"E, 3°00'05"N, 17.IV.2001, P. Derleth & M. Sartori.

Paratypes: Same data as holotype, about 200 ♂♂, most of them SI. – Same locality and collectors, 20.IV.2001, about 50 ♂♂, most of them SI.

Other material: B0113, Langab Sud, Rian River, Belakau, 116°30'26"E, 3°04'04"N, 20.IV.2001, P. Derleth & M. Sartori, 1 larva. – B1313, Seturan, Seturan River, tributary, 116°30'48"E, 3°00'05"N, 28.III.2001, P. Derleth & B. Feldmeyer, 1 larva. – B0812A, Seturan, Seturan River, Temalat, 116°33'29"E, 2°59'29"N, 2.IV.2001, P. Derleth & M. Sartori, 1 larva.

Etymology

The species is named after my nephew Sebastian because he should not be behind his sister Johanna who lends her name to *Caenis johannae* from Madagascar.

Description

Male imago

Measurements and colouration

Body length 2.3–2.7 mm; wing length 1.5–1.8 mm. – Ratios of fore legs etc. cannot be given because the few imagines all have the fore legs missing.

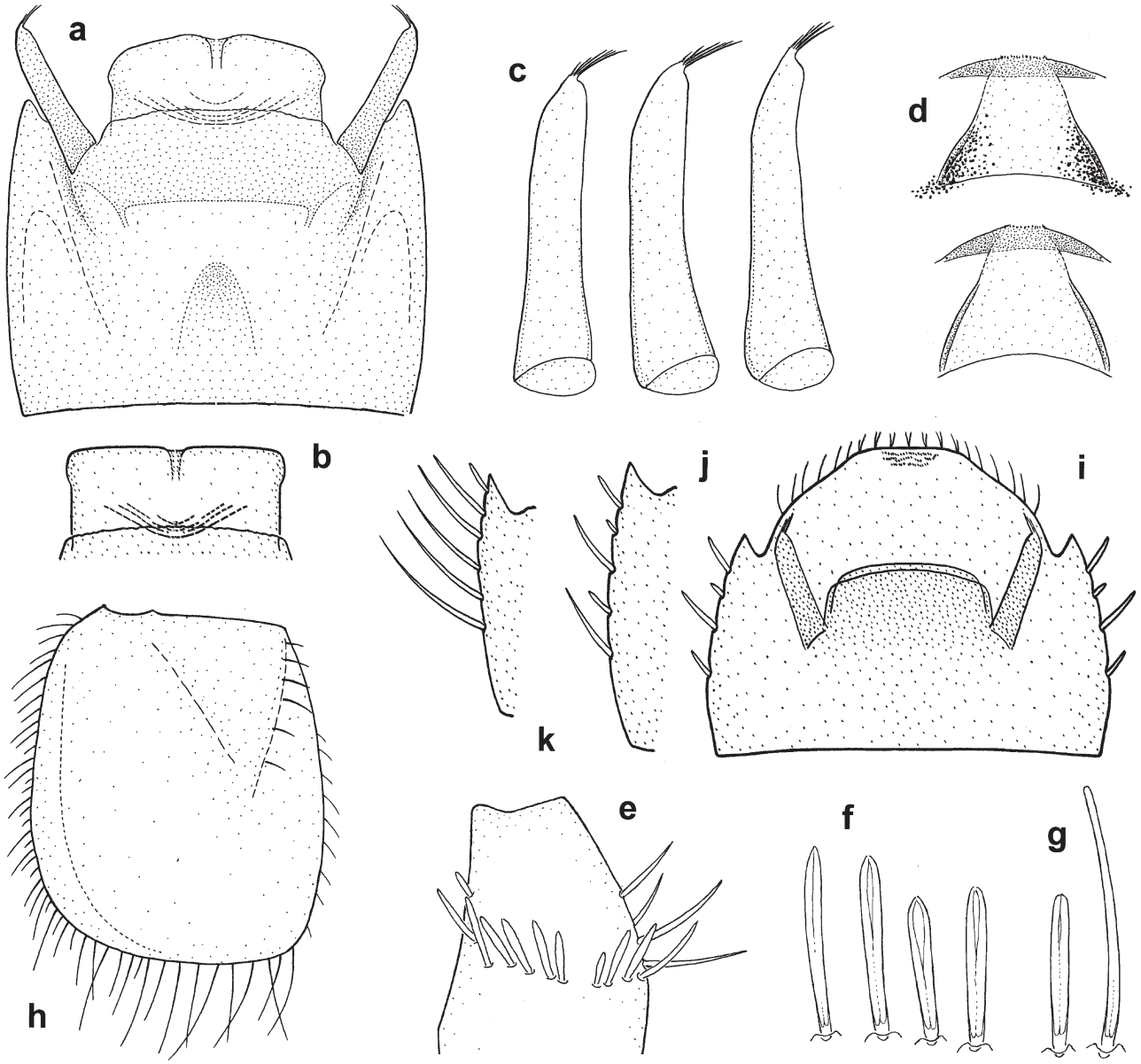


Fig. 2. *Caenis sebastiani* n. sp., ♂ (a–d), larva (e–k). – **a**, **b**. Genitalia (b another penis shape). **c**. Different shape of forcipes. **d**. Different shape of prosternal trapezoid. **e**. Fore femur, distal part with transverse row of bristles. **f**. Bristles from the transverse row. **g**. Bristles from dorsal side of mid and hind femur. **h**. Operculate gill. **i**. Sternum IX, ♂, with subimaginal genitalia. **j**. Marginal setation of abdominal segment VII. **k**. Marginal setation of abdominal segment V.

Colouration of cuticle: Metanotum yellowish- or reddish-brown; other parts yellowish-white.

Epidermal pigmentation: Pigmentation of dorsal and lateral side as in Fig. 45. Vertex and frons evenly intense brown. Pronotum greyish-brown with two paramedian spots and sometimes sublateral lightenings. Abdominal terga with grey transverse bands often medially more or less interrupted. Prosternal trapezoid with basolateral pigmentations, a curved dark line extending from the hind corners laterally.

Morphology

Head: Antennal base similar to that of *Caenis unidigitata,* flagellum slightly dilated, dilated part two-thirds to three-fourths as long as and one-fourth as wide as the pedicel, surface scarcely bumpy, distally more or less abruptly narrowed.

Thorax: Prosternal ridges forming something like a trapezoid or broadly rounded triangle with lateral sides posteriorly convex, frontal side sunken dorsad, transverse chitinous strip often more posteriorly (Fig. 2d). Segments

II and III of fore tarsus with an apico-median projection, segment IV with two projections, a lateral and a median one (as in Fig. 1f).

Abdomen: Lateral filaments of abdominal segments very short. Without finger-like process on tergum II.

Genitalia and sternum IX as in Figs. 2a, b. Penis shape variable, more or less rounded, hind margin straight and slightly angled; sometimes with very short rounded penis lobes. Styliger sclerite slightly beige-coloured, its basal margin extending anterior to the forceps bases. Apophyses of styliger sclerite short and narrow, but clearly visible. Forcipes not bent, lateral sides more or less straight; apical spines long and very thin (Fig. 2c).

Female imago unknown.

Larva

Measurements and colouration

Male larva of last instar, body length 2.7 mm, length of cerci 1.8 mm; female larva of last instar not available.

Colouration of cuticle: Yellowish-brown.

Epidermal pigmentation: Head with a narrow band of grey pigments between the lateral ocelli, surrounding of frontal ocellus shaded with grey. Pronotum with pattern similar to that of the males. Mesonotum with irregular marks anterior to wing pads. Abdominal pigmentation as in the males.

Morphology

Surface: Honeycombed or with net-meshes, often with posterior or lateral denticles (e. g. femora, operculate gills).

Head: Genae slightly bulging out. Pedicel with about 10 strong bristles. Labrum with broadly rounded corners, anterior margin with a strongly denticulated indentation. Mandibles with long bent setae on lateral margin. Second segment of labial palp about twice the length of the third (measured along the centre-line); outer margin with about 8 strong bristles.

Thorax: Sides of pronotum strongly denticulated, diverging anteriorly; fore corners rounded with 4–5 stout bristles slightly bent posteriorly. Coxal processes inconspicuous. Femora and tibiae of mid and hind legs with long, more or less spatulate bristles (the shorter, the more spatulate, Fig. 2g). Transverse row on fore femur consisting of similar bristles, forming a basket (Figs. 2e, f). Fore tibia medially with very long setae. Fore tarsus ventrally with inner row of 4–5 simple bristles; mid tarsus ventrally with inner row of 5–6 simple bristles; hind tarsus with inner row of 6–7 simple bristles and short outer row of 2–3 pinnate bristles. Claws slender, without denticulation.

Abdomen: Abdominal segments with short postero-lateral processes. Lateral bristles long, slightly shorter on segments VIII and IX (Figs. 2i–k). Posteriomedian process of tergum II short, broadly triangular, pointed and moderately erect in lateral view (slightly more erect than in Fig. 4g). Hind margin of terga VII and VIII with very long bristles, of terga IX and X with denticles. Hind margin of sternum IX medially cut or with a very shallow indentation, with short bifurcate bristles (Fig. 2i). Operculate gills with thin bristles on medial margin, hind margin with very long hair-like bristles, lateral margin with more or less blunt bristles of moderate length; medial ridge only anteriorly developed, with about 6 bristles similar to that on lateral margin, posterior part of medial ridge obliterated, ridges medially not connected (Fig. 2h). Ventral row of microtrichia extending to the middle of the hind margin of the gill. Shape of microtrichia similar to that of *Caenis fregatula* (Fig. 17), slightly stronger and clearly visible in light microscopic view. Cerci with strong and pointed spines.

Differential diagnosis

Caenis sebastiani can be distinguished from all other *Caenis* species by the following combination of characters: Base of antennal flagellum slightly dilated. Forcipes with apical tuft of long spines. Penis without triangular lobes. Abdominal tergum II without finger-like process. – Prosternal ridges anteriorly converging, forming a trapezoid with lateral sides posteriorly convex. Segment V of fore tarsus extremely short. Segments II and III each with an apico-median projection. Basal margin of styliger sclerite extending anteriorly from the forceps bases. Apophyses of styliger sclerite short and narrow but clearly visible. Forcipes straight, with very thin apical spines.

For further differential diagnosis of this and the following *Caenis* species see discussion (section 5).

Remarks

The assignment to the males is based on a larva with visible subimaginal genitalia, showing short and straight forcipes (Fig. 2i) and fore tarsi with median projections only on segments II and III.

Caenis fregatula **n. sp.**
(Figs. 3, 14–17)

Holotype, ♂ (on microslide): B1313PLM, Seturan, Seturan River, tributary, 116°30'48"E, 3°00'05"N, 20.IV.2001. P. Derleth & M. Sartori.

Other material: B0513, Seturan, Seturan River, Tamalang, 116°30'29"E, 2°59'22"N, 10.IV.2001, P. Derleth, 3 larvae. – B0812, Seturan, Seturan River, Temalat, 116°33'29"E, 2°59'29"N, 16.VIII.2000, P. Derleth & R. Schlaepfer, 1 larva. – B0833, same locality, 16.IV.2001, P. Derleth & M. Sartori, 1 larva.

Etymology

The species name *fregatula*, a diminutive of *Fregata*, refers to the shape of the forcipes that resembles the long pointed and diverging tails of frigate birds (e. g. *Fregata magnificens*).

Description

Male imago

Measurements, ratios and colouration

Body length 2.5 mm; wing length 1.5–1.6 mm; length of fore leg 1.7–1.8 mm. – Ratios: Fore femur to fore tibia length = 0.55–0.65; fore tibia to fore tarsus length = 1.02–1.19; fore leg to hind leg length = 1.70–1.76; $1^{st} : 2^{nd} : 3^{rd} : 4^{th} : 5^{th}$ fore tarsal segments length = 1 : 4.6–4.8 : 3.0–3.1 : 2.3–2.8 : 1.1–1.2; fore tarsal segments length 3–5 : 1+2 = 1.1–1.3.

Colouration of cuticle: Metanotum beige; other parts yellowish-white.

Epidermal pigmentation: Vertex and frons without pigments. Pronotum laterally with longitudinal, blackish, anteriorly broadened dashes; posteriorly with transverse blackish-grey band with paramedian and sublateral lightenings. Prosternal trapezoid with basolateral pigmentations, a curved dark line extending from the hind corners laterally. Posterior parapsidal sutures on mesonotum and base of scutellum pigmented. Blackish-grey marks on each side of abdominal terga III–VII, I and II with small lateral spots; all segments with blackish paratergal spots or dashes.

Morphology

Head: Base of antennal flagellum slightly dilated, dilated part nearly as long as and one-third as wide as the pedicel, with surface slightly bumpy.

Thorax: Prosternal ridges thin, anteriorly parallel, posterior third converging, rounded; transverse chitinous strip narrow, not reaching fore coxae (Fig. 3c). Segments II and III of fore tarsus each with an apico-median projection, segment IV with two projections, a lateral and a median one; segment V extremely short (as in Fig. 1f).

Abdomen: Lateral filaments of abdominal segments very short. Without finger-like process on tergum II.

Genitalia and sternum IX as in Fig. 3a. Penis with short, broadly rounded lobes, hind margin medially slightly convex; penis shaft inflated, about as wide as penis lobes. Styliger sclerite short and broad, medial part of anterior margin, between the very short apophyses, curved posteriorly. Forcipes very long, slender and pointed, evenly narrowed to the tip, apical part slightly bent laterally; basal

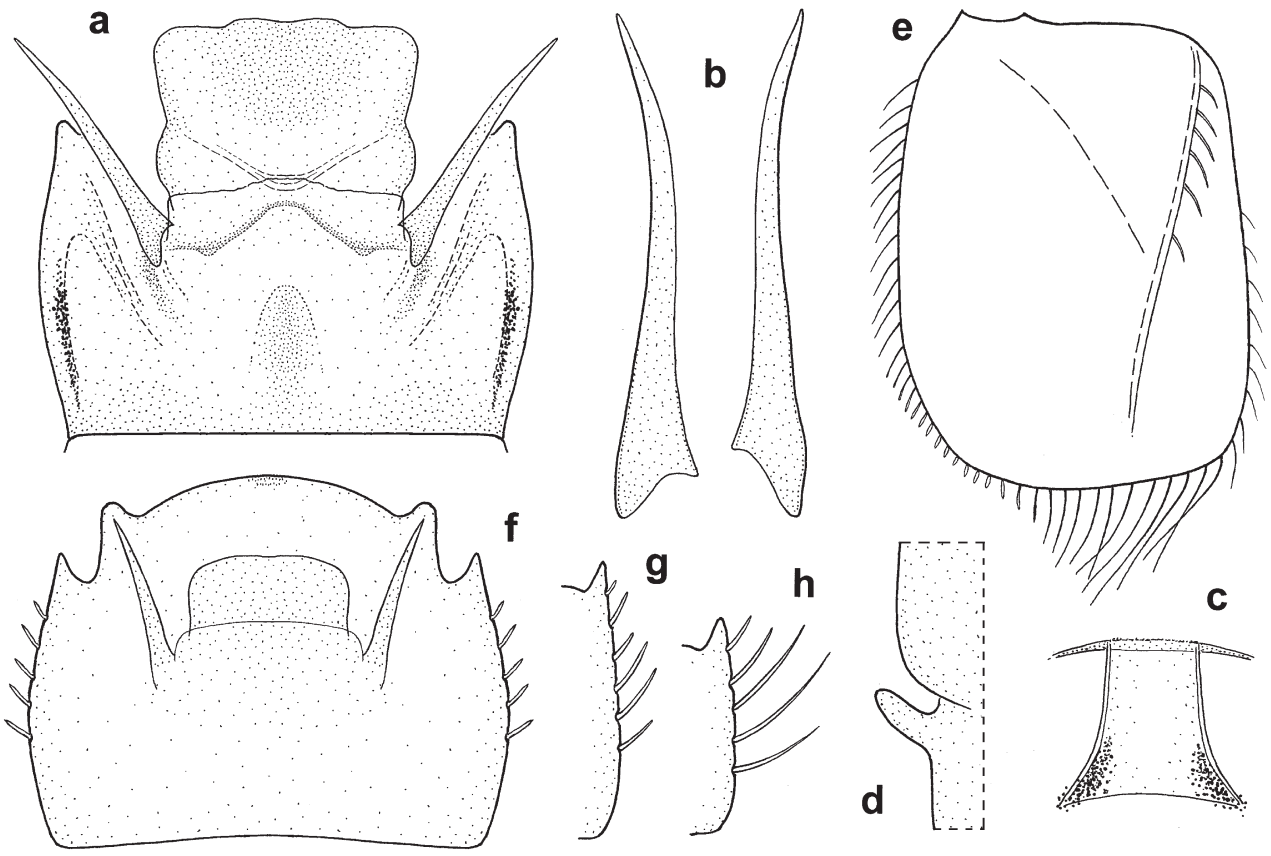


Fig. 3. *Caenis fregatula* n. sp., ♂ (a–c), larva (d–h). – **a**. Genitalia. **b**. Different shape of forcipes. **c**. Posternal trapezoid. **d**. Posteriomedian process of tergum II, lateral view. **e**. Operculate gill. **f.** Sternum IX, ♂, with subimaginal genitalia. **g**. Marginal setation of abdominal segment VII. **h**. Marginal setation of abdominal segment V.

two-thirds with very short trichoma, apical third without (Fig. 3b).

Female imago unknown.

Larva

Measurements and colouration

Male larva of last instar, body length 2.5 mm, length of cerci 1.5 mm; female larva of last instar not available.

Colouration of cuticle: Pale beige with yellowish-brown pattern on the following parts: lateral parts of pronotum, two spots at the base of the wing pads and a double mark posteriorly between them (giving the mesonotum a certain similarity with the frontal view of a lion face), the field between Y-shaped ridges and a posterior round mark on operculate gills and marks on each side of abdominal terga.

Epidermal pigmentation: Apart from eyes and ocelli no pigments visible.

Morphology

Surface: Head, pro- and mesonotum granulated, with paramedian fields of flat round- and net-meshes (Fig. 14), between the granules with small, fragile, branched bristles (Fig. 15). Metanotum, femora and abdominal terga with net-meshes and fine denticles, operculate gills with strong denticles, the field medially from the longitudinal ridge with honeycombs.

Head: Genae slightly bulging out. Labrum with broadly rounded corners, anterior margin with a shallow indentation. Mandibles only with a few very thin bristles on dorsal surface. Second segment of labial palp about 1.8 times the length of the third (measured along the centre-line); strong bristles on lateral side of second segment only basally.

Thorax: Sides of pronotum anteriorly moderately or strongly diverging, straight or slightly convave (Fig. 16), denticulated, fore corner with inconspicuous short bristles. Coxal processes inconspicuous. Femora and tibiae of mid and hind legs with numerous long marginal bristles; femora with a few shorter spatulate bristles on dorsal surface, an additional longitudinal row of long more or less spatulate bristles extending dorsally on tibiae. Bristles of the transverse row on fore femur of moderate length, spatulate. Fore and mid tarsus ventrally with inner row of 7–8 slender and pointed bristles, hind tarsus with inner row of about 7–8 strong simple bristles and outer row of 4–5 unipinnate bristles, pinnae directed medially. Claws slender, without denticulation.

Abdomen: Abdominal segments with short posterolateral processes, lateral bristles long, shorter on segments VIII and IX (Figs. 3f–h). Posteriomedian process of tergum II long, cone-shaped, erect in lateral view (Fig. 3d). Hind margin of tergum VII with numerous long bristles, of tergum VIII with only a few bristles but additionally with denticles in the median part. Hind margin of tergum IX and X with denticles only. Hind margin of sternum IX flatly rounded, with a few very short bifurcate bristles; in adult male larvae (the only one that could be identified with certainty) there are two triangular protrusions where the tips of subimaginal forcipes are situated (Fig. 3f). Operculate gills with short spatulate bristles on postero-lateral corner, followed by long thin bristles on hind margin and bristles of moderate length on lateral margin. Y-shaped ridges well-developed, medial ridge more or less keeled, with about 5 bristles of moderate length in its basal half (Fig. 3e). Ventral row of microtrichia extending to the middle of the hind margin of the gill. Shape of microtrichia as in Fig. 17, delicate and nearly invisible in light microscopic view.

Differential diagnosis

Caenis fregatula can be distinguished from all other *Caenis* species by the following combination of characters: Base of antennal flagellum slightly dilated. Forcipes without tuft of long spines. Penis without triangular lobes. Abdominal tergum II without finger-like process. – Prosternal ridges parallel in the anterior two-thirds. Segment V of fore tarsus extremely short. Segments II and III each with an apico-median projection. Penis with short, broadly rounded lobes, hind margin medially slightly convex; penis shaft inflated. Styliger sclerite short and broad, medial part of anterior margin, between the very short apophyses, curved posteriorly. Forcipes very long, slender and pointed, evenly narrowed to the tip.

Remarks

The assignment to the males is based on a larva with visible subimaginal genitalia, showing the characteristic shape of forcipes (Fig. 3f); fore tarsi with median projections only on segments II and III.

Caenis bidigitata **n. sp.**

(Figs. 4, 5, 18–25)

Holotype, ♂ (on microslide): B1313PLM, Seturan, Seturan River, tributary, 116°30'48"E, 3°00'05"N, 17.IV.2001, P. Derleth & M. Sartori.

Paratypes: Same data as holotype, about 250 ♂♂, most of them SI, 5 ♀♀.

Other material: B0113, Langap Sud, Rian River, Belakau, 116°30'26"E, 3°04'04"N, 20.IV.2001, P. Derleth & M. Sartori, 11 larvae. – B0433, Langap Sud, Rian River, Ngayo, 116°30'58"E, 3°04'56"N, 14.IV.2001; P. Derleth & M. Sartori, 3 larvae. – B0421, same locality, 12.VII.2000; P. Derleth, 1 larva. – B0631, Seturan, Seturan River, Wok, 116°33'30"E, 2°59'11"N, 29.VI.2000, P. Derleth, 17 larvae. – B0713, C, same locality, 5.IV.2001, P. Derleth & B. Feldmeyer, 6 larvae. – B0811, Seturan, Seturan River, Temalat, 116°33'29"E, 2°59'29"N, 18.VI.2000, P. Derleth & J.-L. Gattolliat, 1 larva. –

B0812, same locality, 16.VIII.2000, P. Derleth & R. Schlaepfer, 1 larva. – B0833, same locality, 16.IV.2001, P. Derleth & M. Sartori, 3 larvae.

Etymology

The species name refers to the two projections of the median fore tarsal segments.

Description

Male imago

Measurements, ratios and colouration

Body length 2.2–2.5 mm; wing length 1.5–1.7 mm. – Ratios: Fore femur to fore tibia length = 0.45–0.46; fore tibia to fore tarsus length = 1.61–1.81; fore leg to hind leg length = 2.23–2.31; $1^{st} : 2^{nd} : 3^{rd} : 4^{th} : 5^{th}$ fore tarsal segments length = 1 : 6.4–6.7 : 1.8–1.9 : 1.7–1.8 : 1.0–1.3; fore tarsal segment 2 very long, segments 3–5 : 1+2 = 0.6–0.7.

Colouration of cuticle: Metanotum beige, with brownish median notal suture; other parts yellowish-white.

Epidermal pigmentation: Vertex and frons medium brown, posterior part of vertex lighter. Antero-lateral parts of pronotum greyish, two paramedian dark marks. Scutellum basally pigmented. Abdominal terga with greyish transverse bands often medially interrupted.

Morphology

Head: Base of antennal flagellum slightly dilated, dilated part as long as and one-fourth as wide as the pedicel, surface smooth, transition to the distal part of flagellum smooth (Fig. 4e).

Thorax: Prosternal ridges anteriorly converging, often forming a broadly rounded triangle; transverse strip short or nearly invisible (Fig. 4d). Segments II–IV of fore tarsus each with two projections, a lateral and a median one; segment II extremely long, 1.3 times as long as segments III–V together (Fig. 4f). Scutellum narrow, pointed.

Abdomen: Lateral filaments of abdominal segments very short. Without finger-like process on tergum II.

Genitalia and sternum IX as in Fig. 4a. Penis anvil-shaped, with sclerotized hind margin. Apophyses of styliger sclerite nearly invisible. Forcipes slender, slightly waisted medially, apical part slightly bent (Fig. 4b); 2–3 apical spines fused together to a short tip; basal part of the tip often showing an S-shaped curvature (Figs. 4b, c).

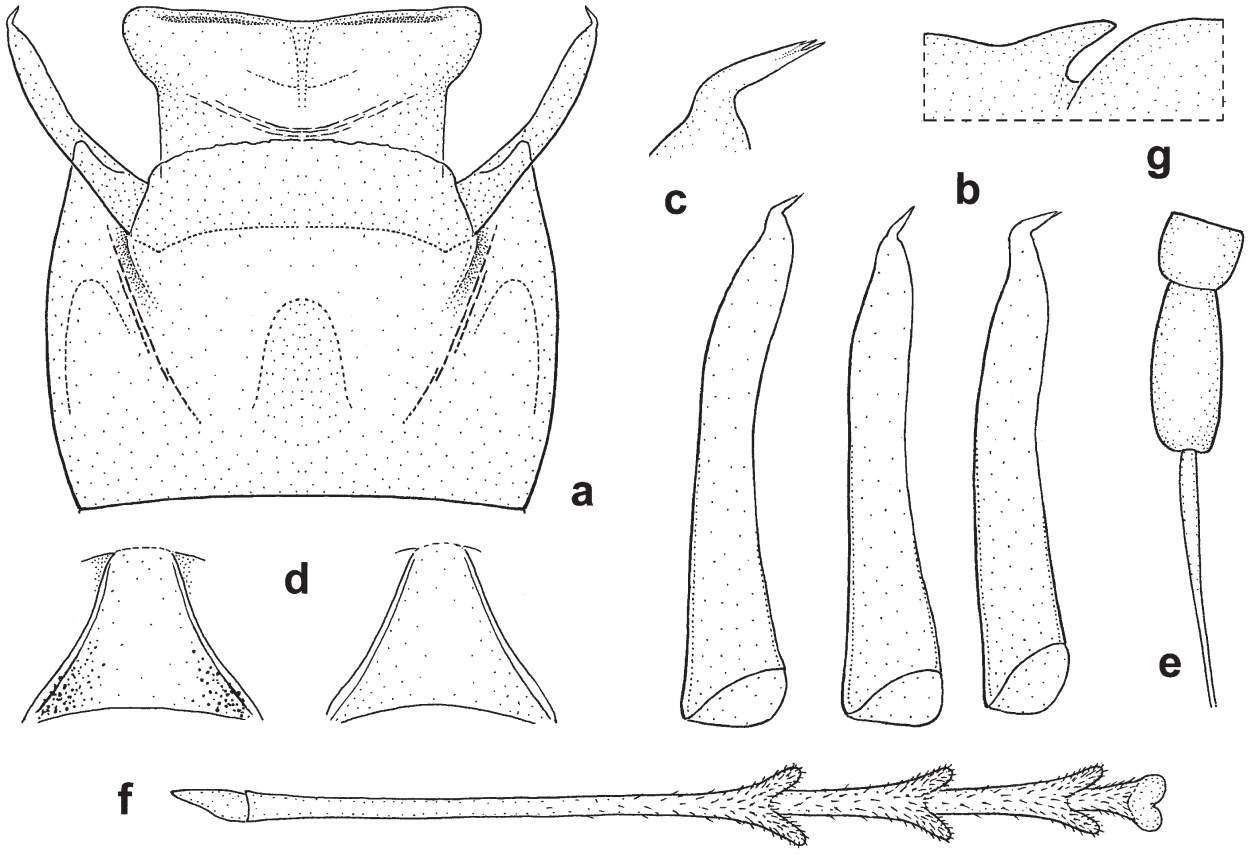


Fig. 4. *Caenis bidigitata* n. sp., ♂. – **a**. Genitalia. **b**. Different shape of forcipes. **c**. Tip of forceps in higher magnification. **d**. Different shape of prosternal trapezoid. **e**. Antennal scape, pedicel and base of flagellum. **f**. Fore tarsus.

Female imago

Measurements and colouration

Body length 2.5–3.2 mm; wing length 2.0–2.2 mm.

Colouration of cuticle: Metanotum brown, with brownish median notal suture not as strongly brown as in males; other parts light yellowish-brown to white. In contrary to females of the other species the hind margin of mesosternum is strongly brown sclerotized.

Epidermal pigmentation: Frons and anterior part of vertex brown, posterior part pale. Basal part of scutellum strongly pigmented, inner margin of lateral sclerites blackish; often with blackish-grey dashes on posterior part of parapsidal sutures. Abdominal terga with grey transverse bands.

Remarks

After the identification of larvae (see below) some females could be assigned to the species by shape and structure of the eggs.

Egg

Chorion finely pored. Micropyle of moderate length, posteriorly broadened (Fig. 19). Two epithemata of coiled-rope-type, with a more or less eccentric position towards the poles (Fig. 18). Epithemata of a modified *C. perpusilla* subtype (see discussion and Malzacher 2011), with 6–8 threads, forming loops by turning about (Fig. 20), and 2–3 tiny terminal knobs hardly visible in light microscopic view. Knobs give end to 1–4 threads (Fig. 21).

Larva

Measurements and colouration

Male larva of last instar, body length 2.2–2.5 mm, length of cerci 1.5 mm; female larva of last instar, body length 2.8–3.2 mm, length of cerci 2.0–2.3 mm.

Colouration of cuticle: Pale, yellow to brownish-yellow.

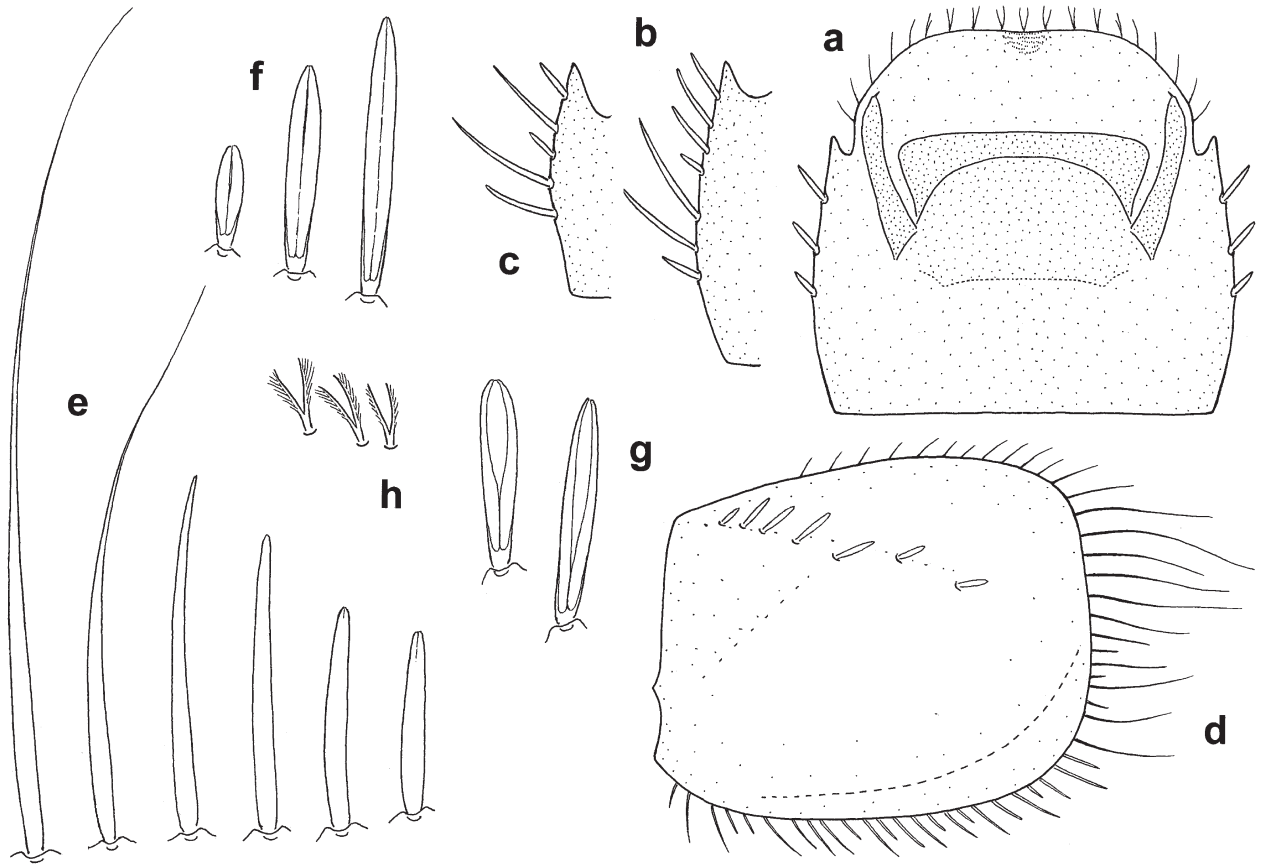


Fig. 5. *Caenis bidigitata* n. sp., larva. – **a**. Sternum IX, ♂, with subimaginal genitalia. **b**. Marginal setation of abdominal segment VII. **c**. Marginal setation of abdominal segment V. **d**. Operculate gill. **e**. Bristles from hind margin (left) and lateral margin (right) of operculate gill. **f**. Bristles from the transverse row on fore femur. **g**. Bristles from dorsal side of mid and hind femur. **h**. Bristles from hind margin of sternum IX.

Epidermal pigmentation: Frons and transverse band on vertex greyish. Pronotum diffusely greyish painted, often with sublateral lightenings. Mesonotum with antero-lateral longitudinal dashes and paramedian spots.

Morphology

Surface: Structure inconspicuous, sometimes with traces of delicate net-meshes and very small denticles (femora); operculate gills with stronger denticles but without distinct meshes.

Head: Genae not bulging out. Pedicel with 10 or more strong bristles. Labrum with broadly rounded corners, anterior margin smooth, slightly concave. Mandibles with a dorso-lateral field of very long bent setae. Second segment of labial palp about 2.3 times as long as third (measured along the centre-line); basal half of outer margin with 4–5 strong bristles.

Thorax: Sides of pronotum straight to convex, diverging anteriorly, smooth or with very delicate denticles; fore corners broadly rounded with 4–5 strong and long spatulate bristles (Fig. 23). Coxal processes inconspicuous. Femora and tibiae of mid and hind legs with long, more or less spatulate bristles (Fig. 22). Bristles on the dorsal surface strong and broad (Fig. 5f). Bristles of the transverse row on fore femur (Figs. 5g, 23) in comparison with *C. sebastiani* stronger and broader (as generally all spatulate bristles). Fore tibia medially with very long setae, the longest sometimes as long as three-fourths of femur width. Fore tarsus ventrally with inner row of 2–4 small bristles; mid tarsus ventrally with inner row of about 5 small bristles; hind tarsus with inner row of 3–4 simple bristles and short outer row of 2–3 pinnate bristles. Claws slender, without denticulation.

Abdomen: Abdominal segments with short postero-lateral processes. Lateral bristles long, slightly shorter on segments VIII and IX (Figs. 5a–c). Posteriomedian process of tergum II very short, broadly triangular, pointed in lateral view (Fig. 4g). Hind margin of terga VII and VIII with very long bristles, of terga IX and X with denticles. Hind margin of sternum IX broadly rounded, medially with a shallow indentation (Fig. 5a), with short bifurcate and frayed bristles (Fig. 5h). Operculate gills (Fig. 5d) with thin bristles on medial margin, hind margin with very long bristles with basal part broadened and apical part very thin hair-like (Fig. 5e, left; this kind of bristles can also be found on hind margin of terga VII and VIII and on lateral margins of anterior abdominal segments); lateral margin of operculate gills with blunt bristles of moderate length (Fig. 5e, right); Y-shaped ridges strongly reduced, medial one lacking, marked only by the row of 6–8 short, broadly spatulate bristles (Fig. 5d). Ventral side of operculate gill basally with frayed bristles (Fig. 24). Ventral row of microtrichia ending lateral to (Fig. 5d) or exceeding the middle of the hind margin of the gill. Microtrichia more or less elongated (Fig. 25).

Differential diagnosis

Caenis bidigitata can be distinguished from all other *Caenis* species by the following combination of characters: Base of antennal flagellum slightly dilated. Forcipes without tuft of long spines. Penis with triangular lobes. Abdominal tergum II without finger-like process. – Prosternal ridges anteriorly converging, forming an open triangle or a narrow trapezoid. Segment V of fore tarsus extremely short. Segments II–IV of fore tarsus each with two projections, a lateral and a median one; segment II extremely long. Penis anvil-shaped with sclerotized hind margin. Apophyses of styliger sclerite nearly invisible. Forcipes with 2–3 apical spines fused together to a short tip. – Egg with two epithemata of coiled-rope type and *perpusilla* subtype.

Remarks

The assignment to the males is based on three larvae with visible subimaginal genitalia, showing the characteristic shape of forcipes and penis; fore tarsi with two apical projections on segments II and III. (Fig. 5a).

Caenis abdita **n. sp.**
(Figs. 6, 26–28, 46)

Holotype, ♂ SI (on microslide): B1313PLM, Seturan, Seturan River, tributary, 116°30'48"E, 3°00'05"N, 20.IV.2001, P. Derleth & M. Sartori.

Paratypes: Same data as holotype, 3 ♂♂ SI.

Other material: B0111, Langap Sud, Rian River, Belakau, 116°30'26"E, 3°04'04"N, 5.VII.2000, P. Derleth, 1 larva. – B0121, same locality, 7.VII.2000, P. Derleth, 31 larvae. – B0123, same locality, 18.IV.2001, P. Derleth & M. Sartori, 1 larva. – B0113, same locality, 20.IV.2001, P. Derleth & M. Sartori, 1 larva. – B0421, Langap Sud, Rian River, Ngayo, 116°30'58"E, 3°04'56"N, 12.VII.2000, P. Derleth, 6 larvae. – B0513, B0521, Seturan, Seturan River, Tamalang, 19.VII.2000, P. Derleth, 2 larvae. – B0513, same locality, 10.IV.2001, P. Derleth, 1 larva. – B0713, Seturan, Seturan River, Wok, 116°32'25"E, 3°00'09"N, 05.IV.2001, P. Derleth & B. Feldmeyer, 3 larvae. – B0811, Seturan, Seturan River, Temalat, 116°33'29"E, 2°59'29"N, 18.VI.2000, P. Derleth & J.-L. Gattolliat, 2 larvae. – B0821, same locality, 21.VI.2000, P. Derleth & J.-L. Gattolliat, 2 larvae. – B0812, same locality, 16.VIII.2000, P. Derleth, 1 larva. – B0812, same locality, 2.IV.2001, P. Derleth & M. Sartori, 3 larvae. – B0823, same locality, 4.IV.2001, P. Derleth, 1 larva. – B0833, same locality, 16.IV.2001, P. Derleth & M. Sartori, 1 larva. – B1211, Langap Sud, Rian River, tributary, 116°31'05"E, 3°01'40"N, 11.VII.2000, P. Derleth, 1 larva. – B1013, Seturan, Rian River, tributary, 116°32'16"E, 3°00'57"N, 30.III.2001, P. Derleth, 1 larva. – B1413/B1423, Seturan, Seturan River, tributary, 116°33'30"E, 2°58'58"N, 24.IV.2001, P. Derleth & M. Sartori, 6 larvae.

Etymology

The species name *abdita* (from Latin abdere = to hide) refers to the larval mud cover which often completely hides the body.

Description

Male subimago

Measurements and colouration

Body length 2.5–2.7 mm; wing length 1.5–1.8 mm. – Ratios of fore legs etc. cannot be given because there are only three subimagines available whose fore legs are not finally developed.

Colouration of cuticle: Metanotum beige; other parts yellowish-white.

Epidermal pigmentation: Vertex and frons brownish. Abdominal terga with weakly greyish-brown sublateral marks.

Morphology

Head: Base of antennal flagellum not dilated.

Thorax: Prosternal ridges thin and straight, strongly converging anteriorly, forming a very broadly rounded triangle; transverse strip invisible (Fig. 6d). Segments II–IV of fore tarsus each with two projections, a lateral and a median one.

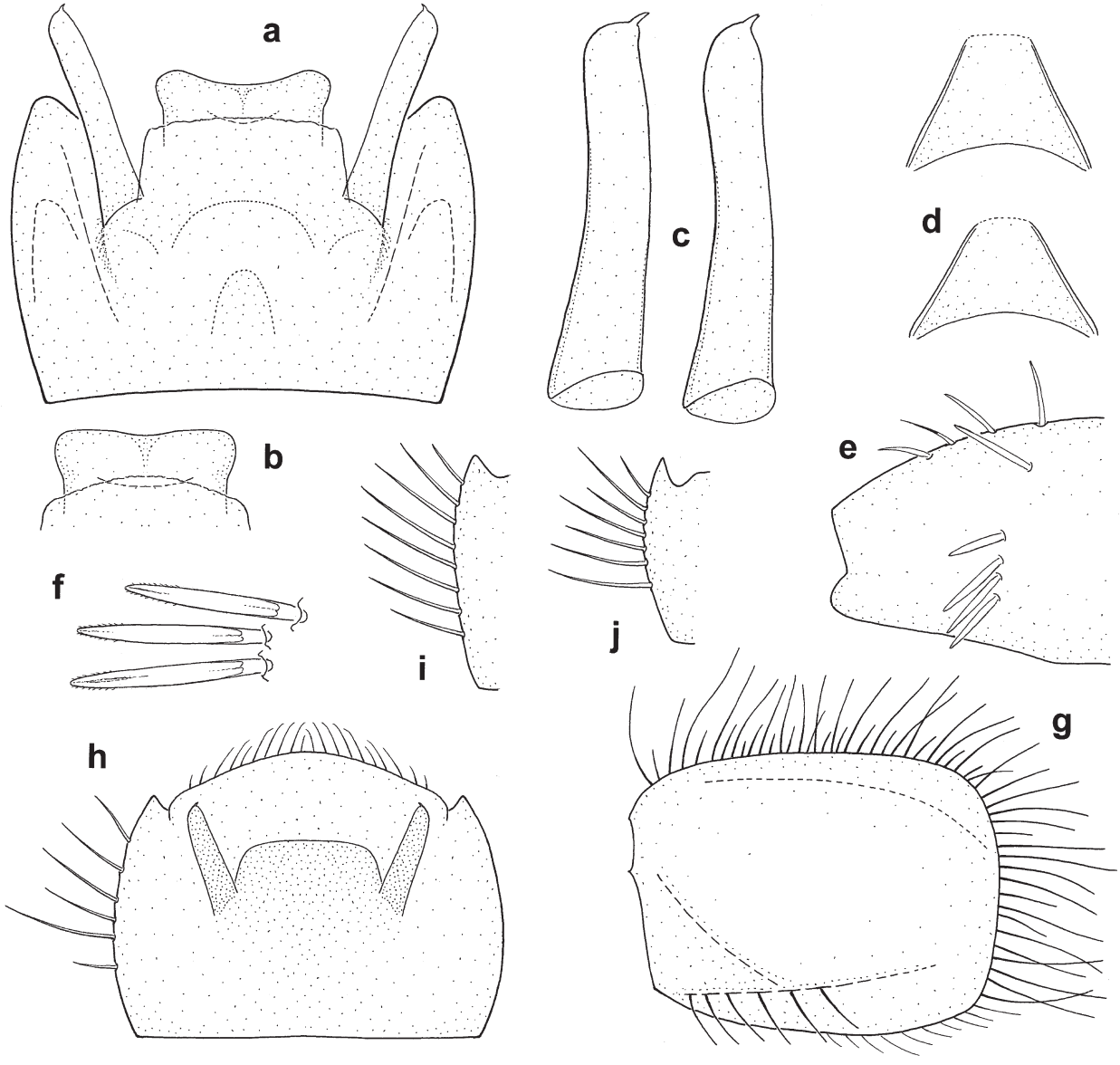


Fig. 6. *Caenis abdita* n. sp., ♂ (a–d), larva (d–h). – **a**, **b**. Genitalia (b another penis shape). **c**. Different shape of forcipes. **d**. Different shape of prosternal trapezoid. **e**. Fore femur, distal part with transverse row of bristles. **f**. Bristles from the transverse row. **g**. Operculate gill. **h**. Sternum IX, ♂, with subimaginal genitalia. **i**. Marginal setation of abdominal segment VII. **j**. Marginal setation of abdominal segment V.

Abdomen: Lateral filaments of abdominal segments lacking. Without finger-like process on tergum II.

Genitalia and sternum IX as in Figs. 6a, b. Penis with short, broadly rounded lobes, hind margin more or less concave. Anterior margin of styliger sclerite curved, apophyses short and broad. Forcipes slightly bent laterally, with more or less parallel sides, apically broadly rounded, with a short, broad spine inserting medially (Fig. 6c).

Female imago unknown.

Egg

Chorion fine and densely pored (Fig. 27). One epithema, very flat and spread towards equator (Fig. 26). One long micropyle, mouth not broadened, sperm-guide small and circular (Fig. 27). – The described egg is from a female last instar larva.

Larva

Measurements and colouration

Male larva of last instar, body length 2.5–2.6 mm, length of cerci 1.8 mm; female larva of last instar, body length 2.7–3.2 mm, length of cerci 2.0–2.3 mm.

Colouration of cuticle: Pale, yellowish-brown.

Epidermal pigmentation: Apart from eyes and ocelli no pigments visible.

Morphology

Surface: Head, pro- and mesonotum coarsely granulated, metanotum, first abdominal tergum and femora with net-meshes and denticles or small spines. Body surface bearing numerous long bristles and hairs with a lot of detritus particles sticking to them, so that the whole larva is entirely covered with mud (Fig. 46). Highly magnified SEM pictures show a network of very fine threads spreading through the detritus particles, the threads seemingly originating from the bristles.

Head: Clypeus with transverse ridge, but not protruding anteriorly. Genae not bulging out. Labrum with broadly rounded corners, anterior margin smooth, slightly concave. Mandibles only with a few very thin bristles on dorsal surface. Second segment of labial palp about 1.7 times as long as third (measured along the centre-line).

Thorax: Sides of pronotum straight and parallel, fore corners slightly curved medially; without lateral flattened areas, margins more or less denticulated. Coxal processes inconspicuous. Femora and tibiae of mid and hind legs with numerous long bristles and sensitive hairs. Fore tibia anteriorly with a row of very long bristles. Bristles of the transverse row on fore femur relatively small, narrow and blunt, tip inconspicuously frayed (Figs. 6e, f). Fore tarsus ventrally with inner row of 4–5 slender and pointed bristles; mid tarsus ventrally with inner row of about 6 stronger bristles; hind tarsus with inner row of about 7 strong simple bristles, no pinnate bristles as in the other herein described *Caenis* larvae. Claws without denticulation, apically slightly more bent than in the above described species.

Abdomen: Abdominal segments with short posterolateral processes, with long and pointed lateral bristles, also on segments VIII and IX (Figs. 6h–j). Posteriomedian process of tergum II very short, broadly triangular, scarcely visible in dorsal view, pointed and more or less erect in lateral view. Hind margin of terga VII and VIII with very long bristles, often longer as the posteriorly following tergum. Hind margin of tergum IX with denticles and about 4 long bristles, of tergum X with spine-shaped denticles about twice or even three times as long as denticles on tergum IX. Hind margin of sternum IX only slightly protruding, medially more or less angled (in female larvae slightly more rounded), with long simple bristles that are apico-medially bent (Fig. 6h). Operculate gills with very thin bristles on medial margin, lateral and hind margin with very long bristles, lateral margin additionally with shorter ones. Y-shaped ridges well-developed, basal half of medial ridge with about 6 long strong and pointed bristles (Fig. 6g). Ventral row of microtrichia not reaching the middle of the hind margin of the gill. Shape of microtrichia square or rounded (Fig. 28).

Differential diagnosis

Caenis abdita can be distinguished from all other *Caenis* species by the following combination of characters: Base of antennal flagellum not dilated. Forcipes without tuft of long spines. Penis without triangular lobes. Abdominal tergum II without finger-like process. – Prosternal ridges strongly converging anteriorly, forming a trapezoid. Segments II–IV of fore tarsus each with two projections, a lateral and a median one. Penis with short, broadly rounded lobes, hind margin slightly concave. Forceps apically broadly rounded, with a short, broad spine inserting medially.

Remarks

The assignment to the males is based on two larvae with visible subimaginal genitalia, showing the characteristic shape of forcipes (Fig. 6h), fore tarsi with two apical projections on segments II and III and base of antennal flagellum not dilated.

3.2 Genus *Kalimaenis* **n. gen.**

Type species: *Kalimaenis sibylliana* n. sp.

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

I m a g o . Prosternum with ridges forming a broad trapezoid or rectangle. – Metanotum elongated. – Lateral filaments of abdominal segments very short. – Forceps very long, with apical tuft of long spines, without longitudinal folds or ridges. – Forceps morphologically and functionally not fused together with the styliger plate. – No functional unit as in the Brachycercinae, but with a well-developed forceps muscle.

E g g . Chorion without longitudinal grooves or rowed structures. – Micropyle very short.

L a r v a . Thorax not broadened. – Head without ocellar tubercles and microscopic pits but with ridges or bulges. – Clypeus anteriorly protruding, protrusion with straight fore margin, without setation. – Maxillary and labial palps three-segmented. – Maxillary palp very slender, segment I apically converging, segments II and III coiled. – Segment III of labial palp very short, with very oblique dividing line to segment II. – Legs, particularly of female larvae, narrow and slender. – Fore leg clearly shorter than hind leg. – Fore tibia and fore tarsus without very long bristles. – Hind claws with groups of micro-denticles fused together. – Gill I very short, one-fourth length of gill-cover. – Operculate gill ventrally with a regular row of microtrichia, row ending away from hind margin of gill. – 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. – Posterior part of sternum IX dorsally with shagreen field. – Abdominal terga VII–IX without mediolongitudinal ridge. – Hind margin of sternum IX without a bi-pointed process with concave margin between the points.

Etymology

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

Kalimaenis sibylliana **n. sp.**
(Figs. 7a–c, 8, 12a, b, 13e, 29–36)

H o l o t y p e , ♂ SI (on microslide): B1313PLM, Seturan, Seturan River, tributary, 116°30'48"E, 3°00'05"N, 17.IV.2001, P. Derleth & M. Sartori.

P a r a t y p e s : Seturan, Seturan River, tributary, 116°30'31"E, 3°00'57"N, 20.IV.2001, P. Derleth & M. Sartori, 2 ♂♂ SI.

O t h e r m a t e r i a l : B0431, Langap Sud, Rian River, Ngayo, 116°30'58"E, 3°04'56"N, 13.VII.2000, P. Derleth, 3 larvae. – B0541, Seturan, Seturan River, Bengahau, 116°30'46"E, 2°59'22"N, 19.VIII.2000, P. Derleth & R. Schlaepfer, 2 larvae. – B0113, Langap Sud, Rian River, Belakau, 116°30'26"E, 3°04'04"N, 20.IV.2001, P. Derleth & M. Sartori, 2 larvae. – B0833, Seturan, Seturan River, Temalat, 116°33'29"E, 2°59'29"N, 16.IV.2001, P. Derleth & M. Sartori, 1 larva. – B1413, Seturan, Seturan River, tributary, 116°33'29"E, 2°58'54"N, 24.IV.2001, P. Derleth & M. Sartori, 2 larvae. – B1513A, Seturan, Seturan River, tributary, 116°31'22"E, 2°59'49"N, 27.IV.2001, P. Derleth & M. Sartori, 1 larva.

Etymology

The new species is named in honour of Maria Sibylla Merian (1647–1717) who discovered and described metamorphosis in Insecta.

Description

M a l e s u b i m a g o

Measurements and colouration

Body length 2.9–3.3 mm; wing length 1.8–2.0 mm. – Ratios of fore legs etc. cannot be given because only three subimagines are available whose fore legs are not finally developed.

Colouration of cuticle: Mesonotum, lateral parts of pronotum and anterior part of metanotum yellowish-brown; other parts yellowish.

Epidermal pigmentation: Frons and vertex strongly blackish-brown, with a transverse light line on vertex. Pronotum greyish-brown with light paramedian longitudinal dashes. All abdominal terga with transverse grey bands, intensity decreasing posteriorly; terga I–III with anteromedian black spots. Blackish spots in area of coxae and pleura. Diffuse greyish pigments in area of mouth part rudiments, base of antennae and fore legs.

Morphology

Head: Fore margin between lateral and frontal ocellus straight. Base of antennal flagellum dilated, dilated part about 1.2 times as long as and less than half as wide as the pedicel, slightly converging and anteriorly more or less abruptly narrowed.

Thorax: Prosternal ridges straight (sometimes slightly concave), anteriorly converging, forming a broad trapezoid, fore margin and transverse chitinous strip lacking (Fig. 7c). Segments of fore tarsus without apical projections.

Abdomen: Lateral filaments of abdominal segments very short. Without finger-like process on tergum II.

Genitalia and sternum IX as in Fig. 7a. Penis with rounded lobes. Styliger sclerite rectangular, with concave anterior margin between long and strong apophyses. Lateral sclerites short, inconspicuous. Forcipes long and slender, sides of median part nearly parallel, apically slightly converging, base weakly broadened; apical tuft consisting of about 5 weakly coiled spines (Fig. 7b). A well-developed forceps muscle inserts at the thickened inner margin of the forceps base.

Female imago unknown.

E g g

Eggs (from a female last instar larva) elongated, about twice as long as wide, with a cap-shaped epithema (Fig. 29). Chorion with densely set, relatively large pores covered by a fine network (maybe the rest of a covering

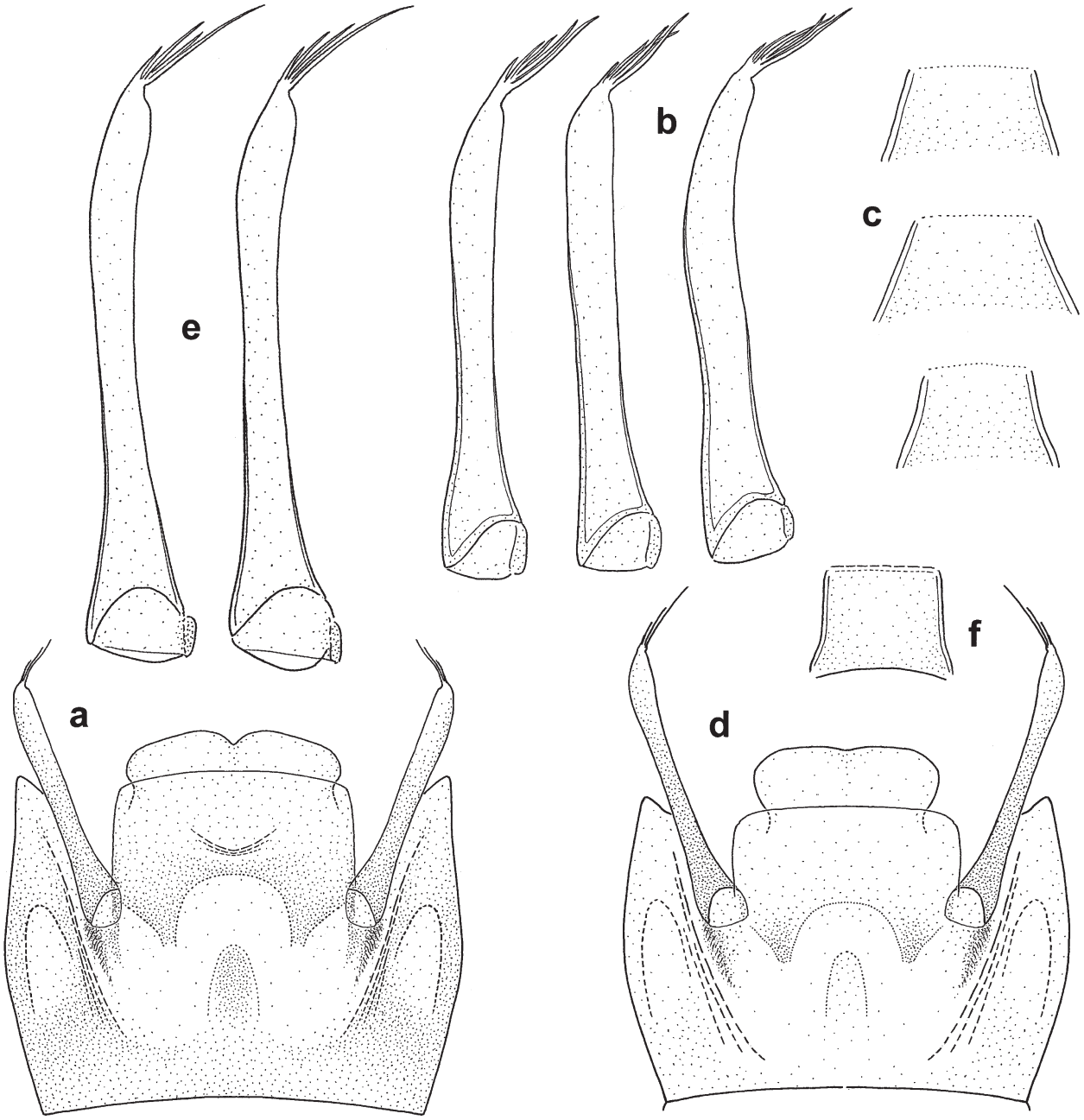


Fig. 7. *Kalimaenis sibylliana* n. sp., ♂ (a–c) and *K. staniczeki* n. sp., ♂ (d–f). – **a**, **d**. Genitalia. **b**, **e**. Different shape of forcipes. **c**, **f**. Prosternal trapezoid.

layer that will be no longer present in adult eggs). One very short micropyle with circular sperm-guide (Fig. 30).

Larva

Measurements and colouration

Male larva of last instar, body length 2.8–3.0 mm, length of cerci 1.5–1.8 mm; female larva of last instar, body length 4.5 mm, length of cerci 2.5 mm.

Colouration of cuticle: Yellowish-brown.

Epidermal pigmentation: Apart from eyes and ocelli no pigments visible.

Morphology

Body slender and narrow (Fig. 31). Surface: Dorsal and ventral side strongly granulated, head and thorax mainly with round knobs, posterior parts with rounded triangular structures or small denticles; femora with a scaly sur-

face. Because of this structure all outlines of the body are strongly granulated or denticulated.

Head: Surface of clypeus and frons slightly bumpy; with longitudinal median ridge (Fig. 32). Genae clearly bulging out. Clypeus slightly protruding anteriorly, protrusion with straight fore margin, without setation (Fig. 32). Labrum with broadly rounded corners, anterior margin with median indentation. Mandibles without setation. Maxillary palp very slender, segment I apically converging, segments II and III coiled (Fig. 12a). Segment III of labial palp very short, with oblique dividing line to segment II; segment I short and round (Fig. 12b).

Thorax: Pronotum broadly rectangular, lateral sides parallel, straight or slightly concave, fore corners protruding anteriorly; fore and hind margin in dorsal view straight and parallel (Fig. 32). Mid and hind coxae with short processes, with scaly surface (Fig. 8a). Legs, particularly of female larvae, narrow and slender (Figs. 8b–d). Fore legs clearly shorter than hind legs. Femora and tibiae of mid and hind legs with very short spatulate marginal bristles; dorsal surface of femora with a few spatulate bristles of the same size or slightly longer. About 4 or 5 slightly longer bristles forming a transverse row on fore femur (Fig. 8b). Fore and mid tarsus ventrally with inner row of about 8–10 thin and pointed bristles, the apical one more or less pinnate. Hind tarsus with inner row of about 10 thin and pointed bristles and outer row of 4–5 unipinnate bristles, pinnae directed medially; both rows are very near and tend to merge with each other. Claws slender and scarcely bowed; fore and mid claws without denticulation; hind claws with groups of micro-denticles fused together (Figs. 8e, f).

Abdomen: Abdominal segments with short posterolateral processes; process of segment II clearly longer (Figs. 8j–l). Lateral bristles short or very short and spatu-

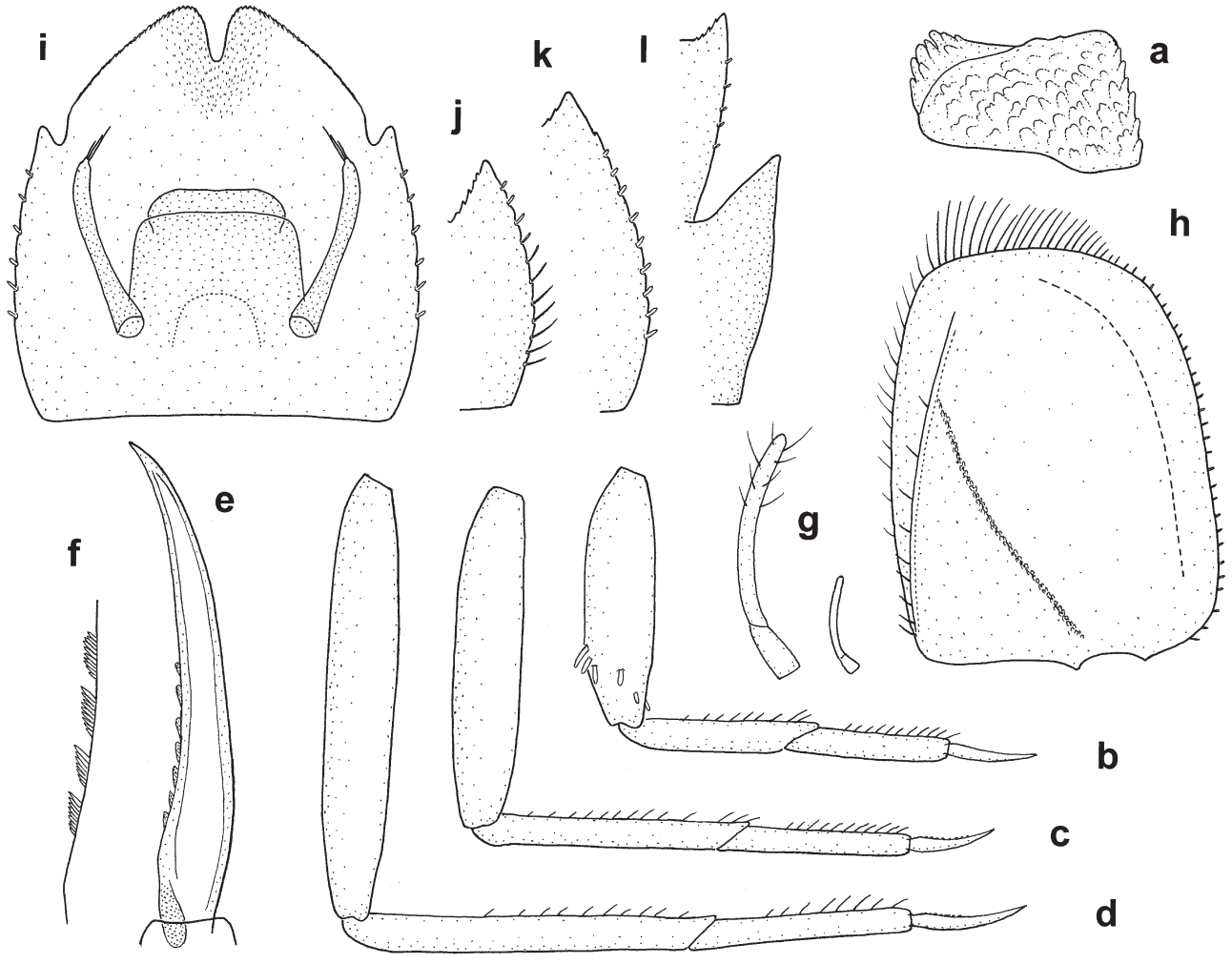


Fig. 8. *Kalimaenis sibylliana* n. sp., larva. – **a**. Coxal process of hind leg. **b**. Fore leg, ♂. **c**. Hind leg, ♂. **d**. Hind leg, ♀. **e**. Claw of hind leg. **f**. Claw of hind leg, inner margin with groups of micro-denticles, higher magnification. **g**. Gill I. **h**. Operculate gill (same magnification as gill I). **i**. Sternum IX, ♂, with subimaginal genitalia. **j**. Marginal setation of abdominal segment V. **k**. Marginal setation of abdominal segment VII. **l**. Margin of abdominal segments II and III.

late, with close-fitting micro-trichoma (Fig. 33), slightly longer on segments IV and V (VI); segments I–III with very short spatulate bristles or without (Figs. 8i–l). Posteriomedian process of tergum II of moderate length, triangular and pointed. Hind margin of terga VII–X strongly denticulated, tergum VII additionally with very short spatulate bristles. Hind margin of sternum IX domed, with a very deep and narrow indentation which is surrounded dorsally by a large shagreen field consisting of micro-spines or denticles (Fig. 8i). Gill I (Fig. 8g) very short, about one-fourth length of gill-cover. Operculate gills with very short spatulate bristles on lateral margin (like those on lateral margins of abdominal segments), changing to longer pointed bristles on hind margin of the gills (Fig. 8h). The short bristles have close-fitting micro-trichoma (Fig. 33), the longer ones numerous fine threads which are catenated with those of the neighbouring bristles similar to radii of a bird feather (Fig. 34). Y-shaped ridges well-developed, connected together posterior to the middle of the gill; medial ridge moderately keeled with about 10 blunt bristles at the base of the keel (Figs. 8h, 33, small frame). Ventral row of microtrichia not reaching the middle of the hind margin of the gill (Figs. 8h, 35). Microtrichia scale-shaped, nearly as well-developed as in Caenini (Fig. 36). Base of the row also with clusters and single spines (Fig. 36, small frame), the latter can be found on nearly the whole ventral surface. Number of filaments on gills III–VI reduced; gill III with 28 filaments (35–60 in other *Caenis* species) and only about 7 filaments with 3 or more branches (14–26).

Remarks

The assignment to the males is based on a larva with visible subimaginal genitalia, showing the characteristic shape of forcipes and prosternal ridges.

Kalimaenis staniczeki **n. sp.**
(Figs. 7d–f)

Holotype, ♂ SI (on microslide): B1313PLM, Seturan, Seturan River, tributary, 116°30'48"E, 3°00'05"N, 20.IV.2001, P. Derleth & M. Sartori.

Etymology

I dedicate the new species to my colleague and dear friend Arnold H. Staniczek (Stuttgart) for his kind help and cooperation.

Description

Male imago

Measurements and colouration

Body length 3.0 mm; wing length 1.7 mm. – Ratios of fore legs etc. cannot be given because only one subimago is available whose fore legs are not finally developed.

Colouration of cuticle: Mesonotum beige, with marginal yellowish-brown bands; pronotum yellowish; abdomen white.

Epidermal pigmentation: Frons and vertex dark brown. Pronotum greyish-brown with light marks and dashes. Scutellum greyish shaded. All abdominal terga with broad transverse grey bands, intensity increasing posteriorly. Blackish spots in area of coxae and pleura. Diffuse greyish pigments on ventral side, anterior mesosternum, prosternum, area of mouth part rudiments, base of antennae, and fore legs.

Morphology

Head: Fore margin between lateral and frontal ocellus slightly convex. Base of antennal flagellum dilated, dilated part nearly as long as and one-third as wide as the pedicel, sides evenly converging.

Thorax: Prosternal ridges forming a square (sides posteriorly slightly diverging); transverse chitinous strip lacking (Fig. 7f). Segments of fore tarsus without apical projections. Mesonotum and median notal membrane elongated; anterior parapsidal sutures nearly invisible; scutellum relatively short and small.

Abdomen: Lateral filaments of abdominal segments very short. Without finger-like process on tergum II.

Genitalia and sternum IX as in Fig. 7d. Penis with short, broadly rounded lobes (in contrary to the other genital structures, the subimaginal penis often does not show its final shape). Styliger sclerite rectangular, with concave anterior margin and short and broad apophyses. Lateral sclerite invisible. Basolateral sclerite basally broadened, weakly longitudinally ridged. Forcipes very long and slender, apically slightly, at the base strongly broadened; apical tuft consisting of a very long and slightly curved spine and 3–4 clearly shorter spines (Fig. 7e). A strongly developed forceps muscle inserts at the thickened inner margin of the forceps base.

Female and larval stage unknown.

3.3 Genus *Clypeocaenis* Soldán, 1978

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

Imago. Prosternum with ridges forming a triangle or trapezoid. – Forceps without longitudinal folds or ridges. – Forceps morphologically and functionally not fused together with the styliger plate. – Without a functional unit of forceps, forceps muscle and enlarged lateral sclerite.

Egg. Chorion without longitudinal grooves or rowed structures.

Larva. Head without ocellar tubercles. – Clypeus anteriorly protruding, protrusion with two or more long and strong bristles. – Mandibles with a group or two transver-

sal rows of long setae. – Maxillary palps two-segmented, labial palps three-segmented. – Segment III of labial palp very long and conical, 3–4 times as long as the short segment II. – Fore tibia with two rows and fore tarsus with one row of very long filtering bristles. – Femora without extended plates. – Operculate gills ventrally with a band or row of microtrichia, ending far away from hind margin of gill. – Nearly all filaments on gill III (IV–V) two-branched or simple. – Lateral spines of abdomen not bent dorsally. – Posterior part of sternum IX dorsally with shagreen field. – Abdominal terga VII–IX without mediolongitudinal ridge. – Hind margin of sternum IX without a bi-pointed process with concave margin between the points.

Clypeocaenis soldani **n. sp.**
(Figs. 9, 12c, d, 13h, 37–44, 47)

Holotype, ♂ larva (on microslide): B0213, Seturan, Seturan River, Temalat, 116°32'24"E, 3°00'10"N, 27.III.2001, P. Derleth.

Paratypes: Same data as holotype, 12 larvae.

Other material: B0121, Langap Sud, Rian River, Belakau, 116°30'26"E, 3°04'04"N, 7.VII.2000, P. Derleth, 1 larva. – B0513, Seturan, Seturan River, Tamalang, 116°30'29"E, 2°59'22"N, 10.IV.2001, P. Derleth, 2 larvae. – B0541, Seturan, Seturan River, Bengahau, 116°30'46"E, 2°59'22"N, 19.VIII.2000, P. Derleth & R. Schlaepfer, 1 larva. – B0533, same locality, 11.IV.2001, P. Derleth & B. Feldmeyer, 4 larvae. – B1013, Seturan, Rian River, tributary, 116°32'16"E, 3°00'57"N, 30.III.2001, P. Derleth, 5 larvae. – B1211, Langap Sud, Rian River, tributary, 116°31'05"E, 3°01'40"N, 11.VII.2000, P. Derleth, 4 larvae.

Etymology

The species is dedicated to Dr. Tomáš Soldán (České Budějovice, Czech Republic) who described the genus *Clypeocaenis* for the first time.

Description

[Male imago]

Among the studied larvae there are two male final instars so that at least genitalia, arrangement of prosternal

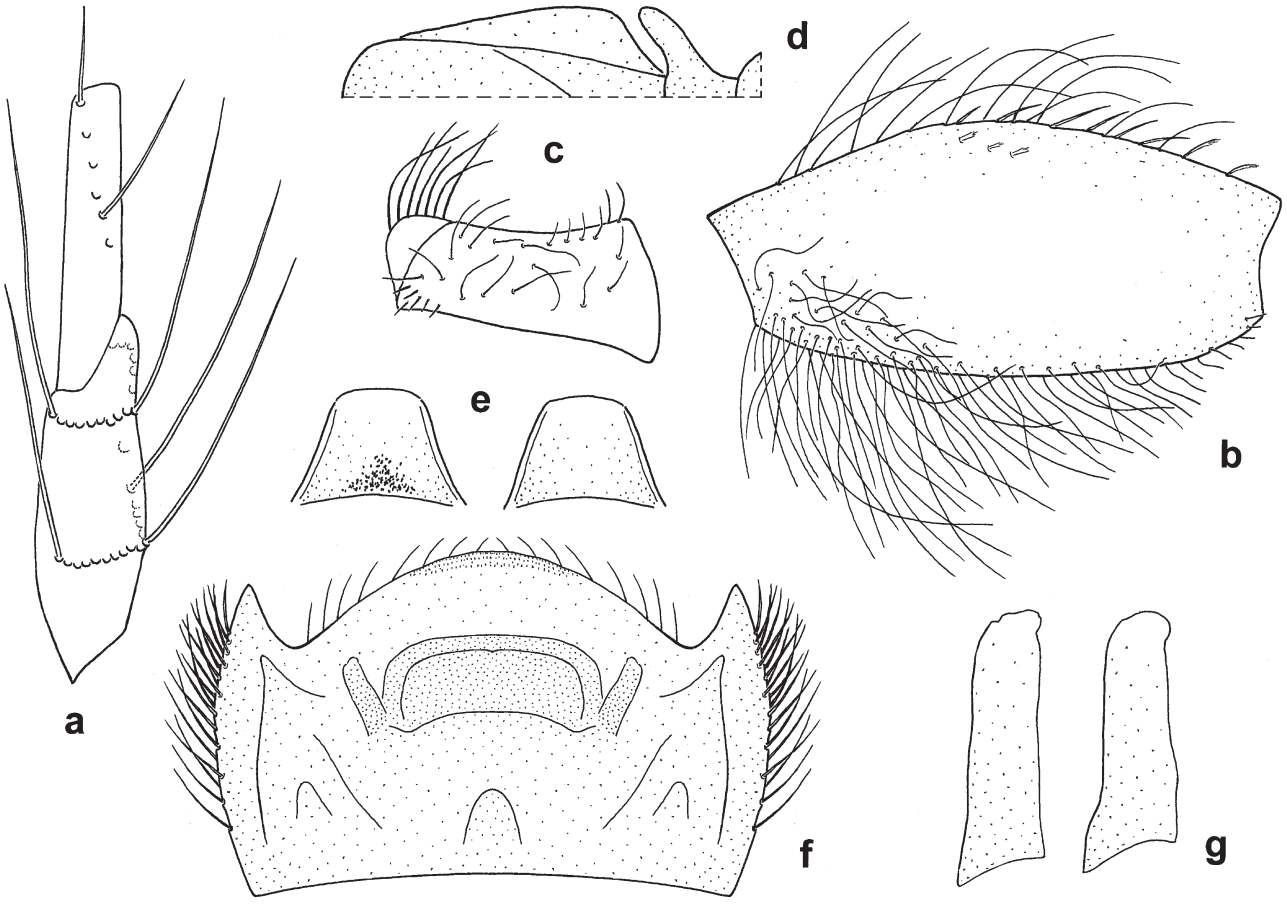


Fig. 9. *Clypeocaenis soldani* n. sp., larva. – **a**. Tibia and tarsus of fore leg, with insertions of filtering setae (explanation see text). **b**. Setation of hind femur. **c**. Coxal process of hind leg. **d**. Posteriomedian process of tergum II and operculate gill, lateral view. **e**. Prosternal trapezoids from last instar larva. **f**. Sternum IX, ♂, with subimaginal genitalia. **g**. Forcipes from subimaginal genitalia.

ridges, shape of antenna and epidermal pigmentation of the otherwise unknown males can be described:

Vertex with grey hind margin and a transverse band between lateral ocelli. Hind margin of pronotum greyish. Abdominal terga with transverse grey bands, on tergum II–VII medially intensified. Prosternum with a median blackish-grey spot; sutures and a median line of mesosternum pigmented. Abdominal sterna I–VII with medial grey spots.

Base of antennal flagellum moderately dilated. Prosternal ridges forming a trapezoid with straight or slightly convex lateral sides, anteriorly open or weakly rounded (Fig. 9e). Sternite IX and subimaginal genitalia as in Fig. 9f. Forcipes short with more or less parallel sides and rounded apex, often with a small apico-medial bump (Fig. 9g).

Larva

Measurements and colouration

Male larva of last instar, body length 3.3–3.5 mm, length of cerci 1.5 mm; subadult female larva, body length about 5 mm, length of cerci about 2 mm.

Colouration of cuticle: Yellowish- or reddish-brown.

Epidermal pigmentation: Vertex with transverse greyish band between lateral ocelli. Abdominal terga with broad transverse greyish bands (Fig. 47, left).

Morphology

Body flat and very broad (Fig. 47). Surface: Dorsal side and femora strongly granulated. More or less covered with multibranched bristles (Fig. 37) and often with so-called sausage-shaped bristles with many thin and irregularly arranged and matted branches (Figs. 38, 39). There are all transitional stages to bristles with only short or very short branches on different places of the body surface e. g. the lateral outline (compare *Caenis abdita*, section 3.1).

Head: Surface of clypeus and frons slightly bumpy. Genae clearly bulging out, outline notched. Clypeus protruding anteriorly, protrusion rounded, with 20–35 long bristles which are more or less covered with matted branches (Fig. 39). Mandibles with a dorso-lateral group of about 15 long bristles, only the basal ones in a curved row, the others irregularly arranged. Galea-lacinia very broad, with a long row of about 10 bristles on inner margin. Segment II of maxillar palp with very dense setation along the inner margin, except on the basal third (Fig. 12c). Segment III of labial palp cone-shaped, 3.5–3.8 times as long as segment II.

Thorax: Pronotum with slightly convex sides, anteriorly more or less converging (Fig. 47). Mesonotum marginally with long and very thin, irregularly curved bristles. Fore tibia (Fig. 40) with two transverse rows of very long filtering setae on dorsal side which are prolonged on ventral side in longitudinal direction; on tarsus another scattered row extending nearly longitudinally (Fig. 9a). Fore femur short and broad, with a transverse band of numerous blunt or spatulate bristles (Fig. 41), long pointed bristles on outer margin and about 4 very long filtering setae on inner margin. Coxal processes semi-elliptical, with very long thin bristles (Fig. 9c). Tufts of about 20 long and thin bristes anteriorly on mid and hind coxae. Femora of mid and hind legs with very long hair-like marginal bristles (Fig. 9b). Marginal bristles on mid and hind tibiae slightly shorter and stronger. Fore tarsus ventrally with inner row of about 7 thin and pointed bristles; mid tarsus with inner row of 5 slightly shorter and weaker bristles; hind tarsus with inner row of about 7 pointed bristles and outer row of 5 bipinnate bristles. Some bipinnate bristles also apico-ventrally on hind tibia. Claws hooked, with about 5 strong denticles. Hind claws homodont (without additional row of very fine micro-denticles).

Abdomen: Posterior abdominal segments with moderate strongly curved postero-lateral processes; processes of segments III–V (VI) very short and broadly rounded, of segment II long and triangular. Lateral bristles long, numerous, densely set (Fig. 9f). Posteriomedian process of tergum II long, triangular, cone-shaped in lateral view (Fig. 9d). Hind margin of terga VII–X strongly denticulated, tergum VII additionally with moderate spatulate bristles. Sternum IX very broad with hind margin flatly rounded; a narrow shagreen band consisting of 2–3 rows of micro-denticles extends very close to the hind margin (Fig. 9f). Gill I short, one-fourth to one-third length of gill-cover. Operculate gill broad (Fig. 42), with bristles of moderate length on lateral margin and shorter, broader and frayed ones on hind margin; inner margin with very thin bristles. Medial ridges strongly developed, forming an elevated triangular keel (Figs. 9d, 43), basally with 7–8 strong bristles; outer oblique ridge formed by a row or narrow band of strong granules. A band of microtrichia on ventral side extends along the lateral margin ending far from hind margin (Fig. 42), consisting of simple spines on lateral side and clusters of 2–6 spines medially (Fig. 44). Gills III (–V) with only 1 filament with 3 branches; all other filaments (35–40 or more) simple or two-branched.

Differential diagnosis

Clypeocaenis soldani can be distinguished from all other *Clypeocaenis* species by the following combination of characters: Larva flat and very broad. Surface with multibranched bristles. Protrusion of clypeus rounded, with 20–35 long bristles which are more or less covered with matted branches. Mandibles with a dorso-lateral group of about 15 long bristles, not arranged in straight rows. Anterior margin of fore femur with about 4 long bristles. Operculate gill with a band of microtrichia on ventral side consisting of simple spines and clusters of 2–6 spines.

3.4 Genus *Tigrocercus* Malzacher, 2006

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

I m a g o . Fore coxae widely separated; prosternum broad, with two transverse ridges. – Trochanter of fore leg elongated. – Metanotum flat, without transverse ridge, with membranous hind margin. – Abdomen with very long lateral filaments, at least on segments V–VII. – Forceps long and sickle-shaped, apical half very narrow, with a longitudinal ridge, basal part strongly broadened. – Articulation of forceps to lateral sclerite more lateral. – Forceps morphologically and functionally not fused together with the styliger plate. – Forceps, forceps muscle and enlarged lateral sclerite forming a functional unit.

E g g . Chorion with longitudinal rows of scale like structures.

Tigrocercus nastassjae **n. sp.**
(Figs. 10a–d, 13i, 48)

H o l o t y p e , ♂ SI (on microslide): B1313PLM, Seturan, Seturan River, tributary, 116°30'48"E, 3°00'05"N, 17.IV.2001, P. Derleth & M. Sartori.

Etymology

The species is dedicated to my second grandchild, Nastassja.

Description

M a l e s u b i m a g o

Measurements and colouration

Body length 3.0 mm; wing length 2.5 mm. – Ratios of fore legs etc. cannot be given because only one subimago is available whose fore legs are not finally developed.

Colouration of cuticle: Mesonotum yellowish-brown; other parts yellowish-white.

Epidermal pigmentation: Pigmentation of dorsal and lateral side as in Fig. 48. Head, pronotum and abdomen strongly pigmented; median suture of mesonotum black. On ventral side transverse blackish lines on hind margin of head and along the prosternal ridges. Mesosternum with a broad longitudinal band of diffuse grey pigments. Abdominal sterna with paramedian and sublateral greyish diffuse smudges; parasternal spots blackish and voluminous, paratergal ones inconspicuous. Pigments also on fore legs and cerci.

Morphology

Head: Both antennal flagella lost. [A specimen of a closely related species from Thailand (see discussion) has the antennal flagellum basally dilated.]

Thorax: Fore coxae widely separated, prosternum broad, with two transverse ridges, the posterior one partly doubled (Fig. 13i). Trochanter of fore leg elongated. Mesonotum in front of the short mesonotal membrane abruptly lowed. Metanotum without transverse ridge, with membranous hind margin.

Abdomen: Very long lateral filaments on abdominal segments V–VII, shorter ones on segment IV (Figs. 10c, 48). Abdominal terga I and II each with a median finger-like process (Fig. 10d).

Genitalia and sternum IX as in Fig. 10a. Penis with moderate broadly rounded lobes, with a median tongue-like structure and two paramedian rounded processes on ventral side. Styliger sclerite inconspicuous. Lateral sclerites parallel and moderately sclerotized, with weakly S-shaped keels. Forcipes long and sickle-shaped, apical half very narrow, with one or two longitudinal ridges, basal part strongly broadened, median part on inner margin irregularly toothed (Fig. 10b). A strongly developed forceps muscle inserts at the inner side of the forceps base.

Female imago and larva unknown.

Differential diagnosis

See discussion (section 5) and Tab. 3.

3.5 Genus *Oriobrachys* Sun & McCafferty, 2008

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

I m a g o . Pedicel about 2.3 times as long as scape, 2.5–2.8 times as long as wide. – Fore coxae widely separated, prosternum broad, with one transverse ridge, divided by two incisions. – Metanotum flat, without transverse ridge, with membranous hind margin. – Abdomen with very short lateral filaments on segments III–VI. – Sternite IX and genitalia elongated, medially waisted by concave lateral and basolateral sclerites. – Forceps grooved, very long and narrow; basal part broadened and covered by the styliger plate. – Apical part of forcipes not fused together with the styliger plate. – Forceps, forceps muscle and enlarged lateral sclerite forming a functional unit.

L a r v a . Operculate gill with a longitudinal ridge in the sublateral area. – Postero-lateral projection of abdominal segment VI distinctly curved medially. – Ocellar tubercles without long setae. – Pedicel about twice as long as scape, 3.5–3.7 times as long as wide. – Maxillary and labial palps two segmented. – Labial palp segment I with long setae ventrally. – Fore tibia without a row of long setae on the posterior surface. – Abdominal tergum II without a postero-medial process. – Operculate gill without a protruding edge at the postero-lateral corner. – Microtrichia

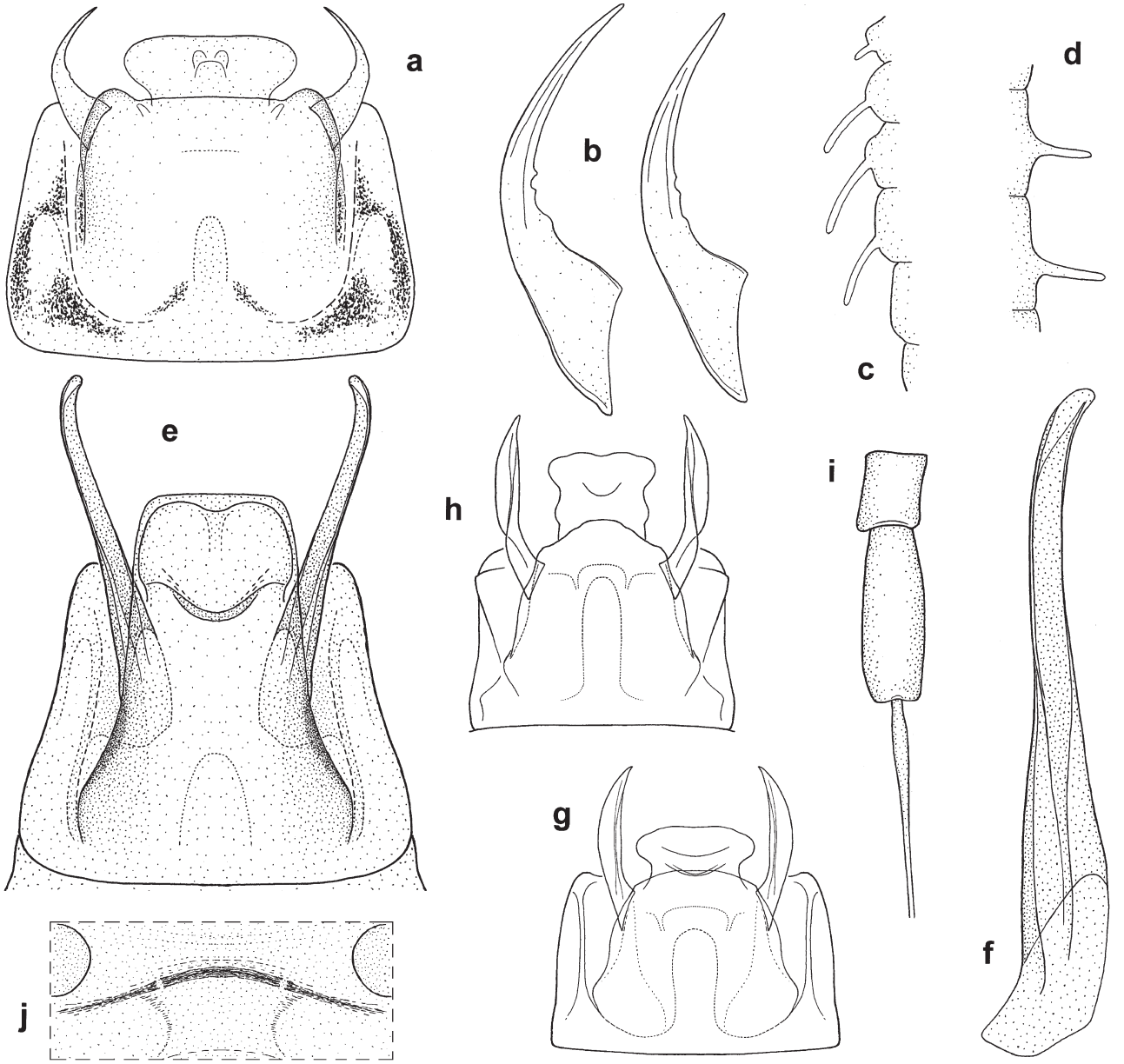


Fig. 10. *Tigrocercus nastassjae* n. sp., ♂ (a–d), *Oriobrachys* sp., ♂ (e–f, i–j), *Brachycercus harrisella* (g) and *Cercobrachys etowah* (h). – **a**, **e**, **g**, **h**. Genitalia. **b**, **f**. Forcipes. **c**. Lateral outline of abdomen with filaments. **d**. Abdominal terga I and II with finger-like processes, lateral view. **i**. Antennal scape, pedicel and base of flagellum. **j**. Prosternum.

on ventral side of operculate gill represented only by a few inconspicuous spines immediately on the posterior lateral margin. [All characters, except the last one, from Sun & McCafferty 2008.]

Remarks

The material contains one larva that shows the generic characters of *Oriobrachys* as described by Sun & McCafferty (2008). About 6 km from the locality where this larva was collected, four Brachycercinae male subimagines were found. The two localities are located in the immediate mouth region of two tributaries of the Seturan River, so it is likely that larva and imagines belong to the same species. The larva cannot be assigned clearly to *Oriobrachys mahakam* Sun & McCafferty 2008, so I describe it here as *Oriobrachys* sp. and only tentatively link it to the males.

Oriobrachys sp.
(Figs. 10e, f, i, j, 11, 12e, f, 49)

Material examined

B1313PLM, Seturan, Seturan River, tributary, 116°30'38"E, 3°00'05"N, 17.IV.2001, P. Derleth & M. Sartori, 1 ♂ SI. Same locality, 20.IV.2001, 3 ♂♂ SI. – B0821, Seturan, Seturan River, Temalat, 116°33'29"E, 2°59'29"N, 21.VI.2000, P. Derleth & J.-L. Gattolliat, 1 larva.

Description

Male imago

Measurements and colouration

Body length 2.5–3.3 mm; wing length 2.0–2.2 mm. – Ratios of fore legs etc. cannot be given because only subimagines are available whose fore legs are not finally developed.

Colouration of cuticle: Meso- and metanotum brown; head and pronotum yellowish-brown; abdomen yellowish-white.

Epidermal pigmentation: Pigmentation of dorsal and lateral side as in Fig. 49. Characteristic strong pattern of metanotum and abdominal terga. Ventral side with grey pigments on base of mouthparts rudiments, transverse prosternal ridge, anterior field of mesosternum, metasternum, and anterior abdominal sterna.

Morphology

Head: Rectangular (Fig. 49). Pedicel 2.3 times as long as scape, 3.5–3.7 times as long as wide. Base of antennal flagellum weakly dilated (Fig. 10i).

Thorax: Sides of pronotum parallel, anteriorly more or less bulging out (Fig. 49). Prosternum with a transverse ridge divided by two incisions in a median and two lateral segments (Fig. 10j). Mesonotum broad, scutellum posteriorly rounded.

Abdomen: Very short lateral filaments on segments III–VI. Without finger-like process on tergum II.

Genitalia and sternum IX as in Fig. 10e. Penis club-shaped with broad shaft (in contrary to the other genital structures the subimaginal penis often does not show its

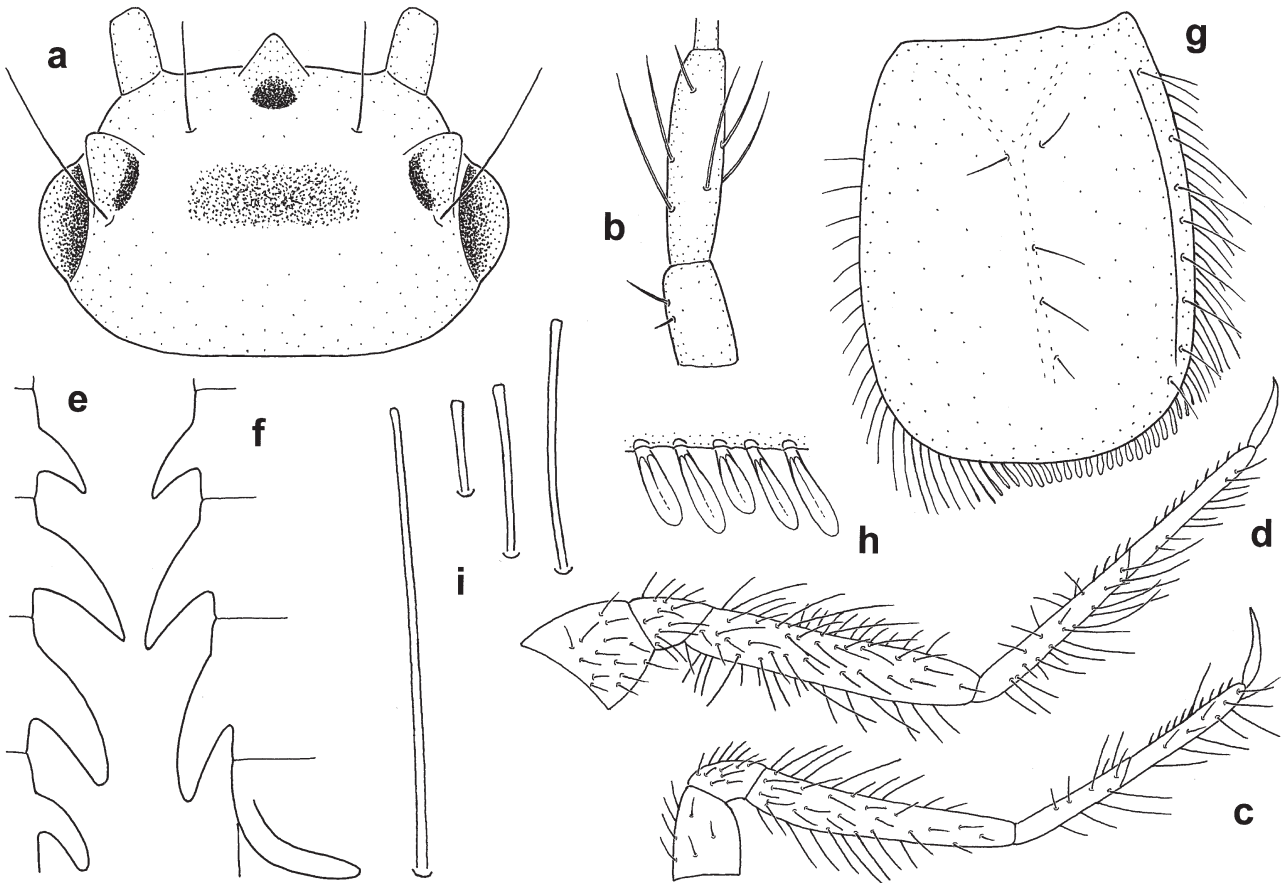


Fig. 11. *Oriobrachys* sp., larva. – **a**. Head, dorsal view. **b**. Antennal scape and pedicel. **c**. Fore leg. **d**. Hind leg. **e**. Abdomen with postero-lateral processes, lateral view. **f**. Abdomen with postero-lateral processes, dorsal view. **g**. Operculate gill. **h**. Bristles from hind margin of operculate gill. **i**. Bristles from legs and other parts of the body.

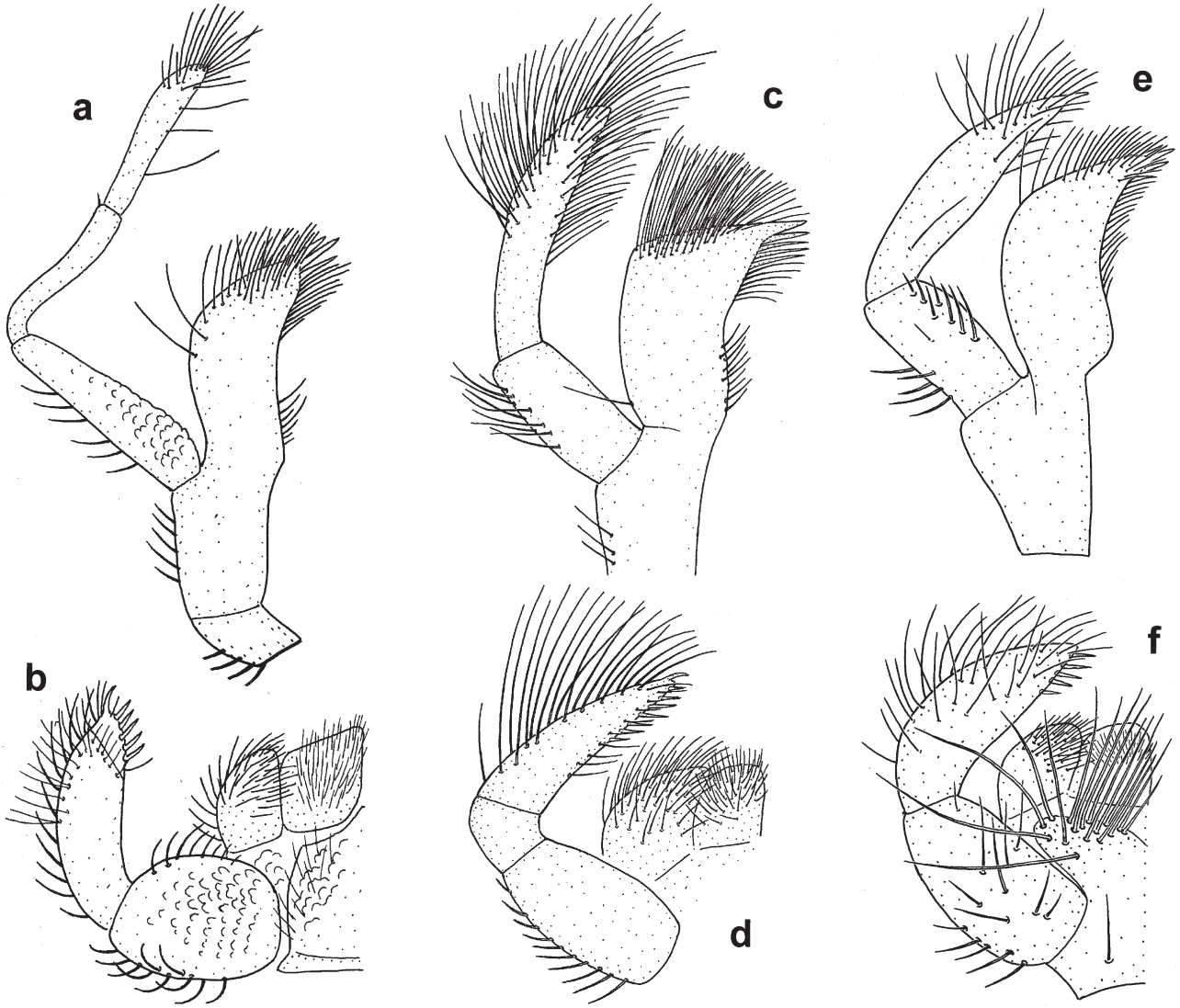


Fig. 12. *Kalimaenis sibylliana* n. sp. (a, b), *Clypeocaenis soldani* n. sp. (c, d) and *Oriobrachys* sp. (e, f), larva. – **a**, **c**, **e**. Maxilla. **b**, **d**, **f**. Labium.

final shape). Styliger sclerite with convex medial part of anterior margin and without apophyses. Because of the very elongated styliger plate, the anatomical details, particularly the styliger sclerite, are difficult to interpret. A medial strongly curved transverse structure could be the anterior or the posterior margin of the latter. Lateral and basolateral sclerites slightly bent and basally connected. Forcipes very long, narrow and tubular with the apex bent medially and rounded (Fig. 10f); the strongly broadened base covered by the lateral parts of the styliger plate. A strongly developed forceps muscle inserts at the inner side of the forceps base.

Female imago unknown.

Larva

Measurements and colouration

Female larva with small wing pads, body length 4.0 mm, length of cerci 1.0 mm.

Colouration and pigmentation: Apart from a transverse blackish band between the ocelli the pigmentation is not preserved (soft parts in beginning decomposition).

Morphology

Head (Fig. 11a): Ocellar tubercles shortly triangular, frontal tubercle pointed and slightly broader than long, the lateral ones apically broadly rounded; a very long bristle at base of lateral ocellus and a shorter one between lat-

eral and frontal ocellus. Pedicel about twice as long as scape, 3.5–3.7 times as long as wide; with about 10 bristles clearly longer than half the length of pedicel (Fig. 11b). Labrum nearly rectangular, with long apical bristles. Mandibles with a dorso-lateral row of long bristles. Maxilla and labium as in Figs. 12e, f. Prementum clearly outlined and slightly raised above level of glossae and paraglossae; antero-lateral part with very long and strong bristles, the longest as long as segment II of labial palp. Segment II of labial palp about as long as segment I, with inner margin slightly convex, apically narrowed, bluntly pointed and with about 11 very strong spines, 4–5 of them in an oblique row on dorsal side.

Thorax: Sides of pronotum with angled protrusion in anterior part. Proportions and setation of legs as in Figs. 11c, d. Tips of most bristles bluntly rounded, often slightly broadened (Fig. 11i) (those bristles can be found all over the body, in moderate length, particularly on the ventral side, together with very long pointed ones). Anterior bristles on mid and hind tarsi long and thin, slightly stronger and shorter on fore tarsi. Coxal processes not present.

Abdomen: Tergum II without a postero-medial process. Segments II–VI (Figs. 11e, f) with postero-lateral processes; process of segment II short, of segment VI long, tongue-shaped and strongly bent medially, nearly parallel on posterior margin of tergum VI; all processes with long, strong and blunt bristles. Lateral margins of segments VII–IX with a few short and blunt bristles. Gill I about two-thirds length of operculate gill. Operculate gill (Fig. 11g) with a sublateral ridge, area laterally from the ridge extending ventrally; ridge with 7–8 very long and pointed bristles. Lateral margin of gill with similar, slightly shorter bristles, changing to blunt bristles on posterior-lateral corner and short broadly spatulate ones on hind margin (Fig. 11h); on the inner hind corner the bristles are longer and thinner again. Y-shaped ridge hardly ascertainable.

4 New tribe Clypeocaenini

The description of the new Caeninae genus *Kalimaenis* is used as an opportunity to discuss the system of the subfamily Caeninae particularly the group of *Clypeocaenis*-like genera. McCafferty & Wang (2000) separated the genera *Clypeocaenis*, *Barnardara* and *Amercaenis* due to the synapomorphic character "fore legs and maxillary palps with filtering setae" as "clear monophyletic lineage" from the other Caeninae. The relationship among the three genera was not discussed. Kluge (2004) regards *Amercaenis* as sister group of the two other genera because of two synapomorphic characters of the latter: two-segmented maxillary palp and differentiated arrangement of filtering setae. Since 2004 three new Caeninae genera have been described namely *Callistellina* (Sun & McCafferty 2001, sub. *Callistina*), *Trichocaenis* (Malzacher 2009a) and the herein described *Kalimaenis* n. gen. Based on the synapomorphies discussed below, all these genera together

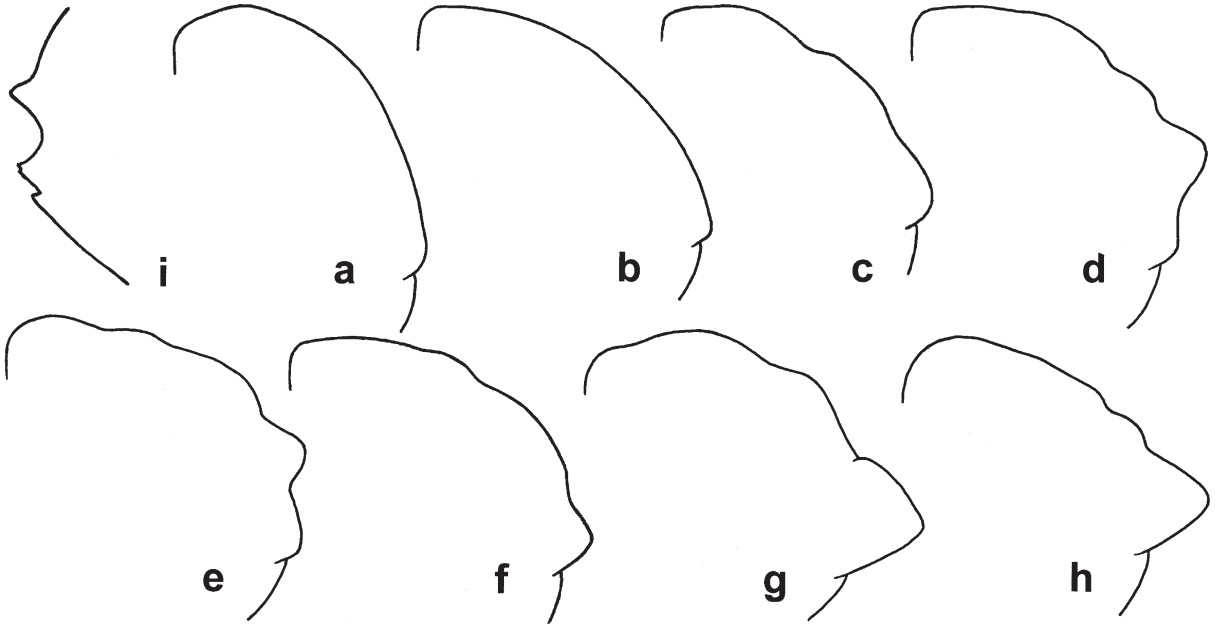
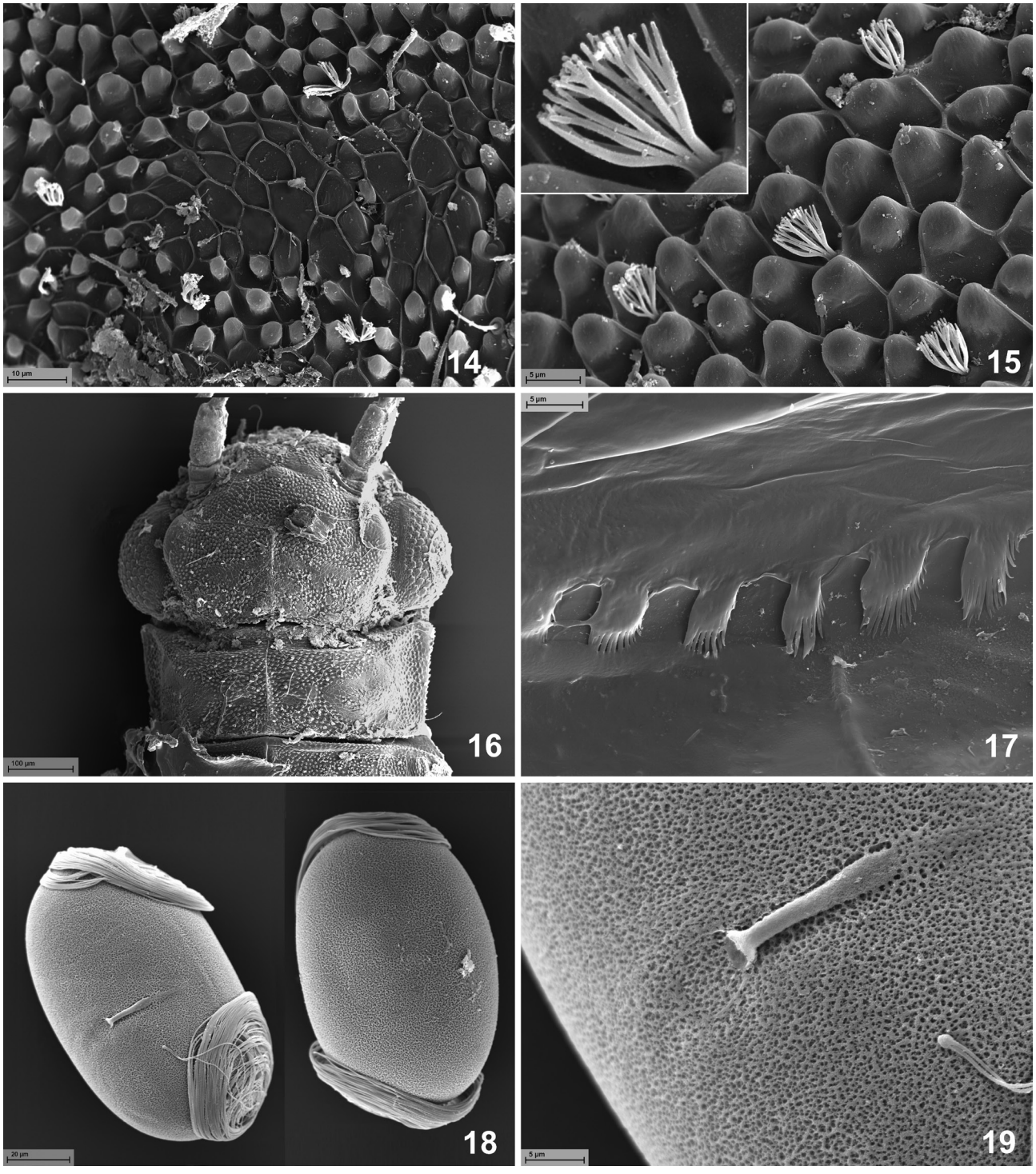


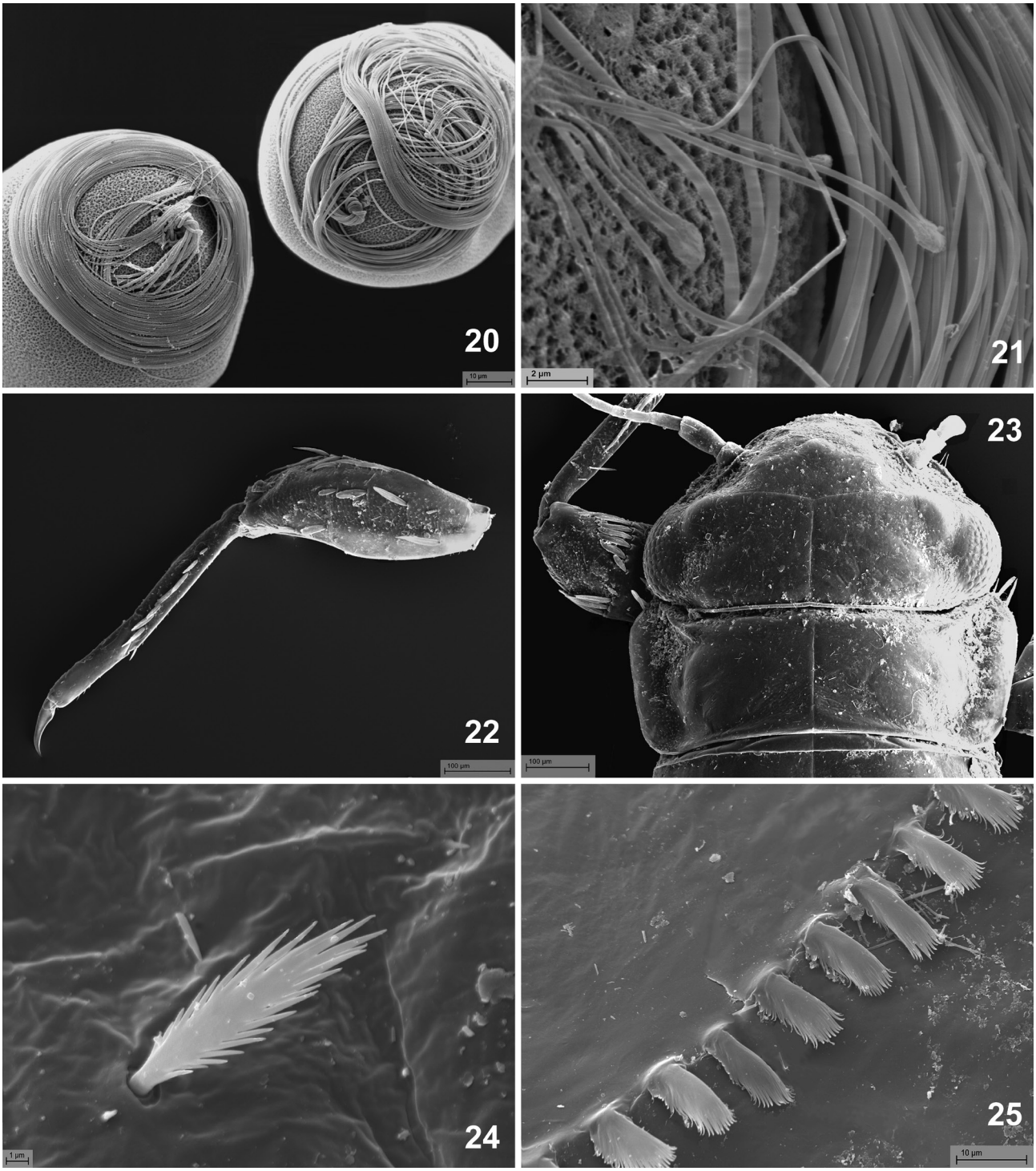
Fig. 13. *Caenis lactea* (a), *Caenis bidigitata* n. sp. (b), *Trichocaenis inexperta* (c), *Barnardara demoori* (d), *Kalimaenis sibylliana* (e), *Amercaenis ridens* (f), *Clypeocaenis afrosetosa* (g), *Clypeocaenis soldani* (h), *Tigrocercus nastassjae* (i). – **a**–**h**. Outlines of larval head, lateral view (body axis horizontal). **i**. Outline of imaginal prosternum, lateral view.

can be regarded as a monophyletic tribe of the subfamily Caeninae that has to be named Clypeocaenini, opposite to the tribe Caenini with the genera *Caenis*, *Afrocaenis*, *Brasilocaenis* and *Caenopsella*. A third tribe could be the Tasmanocoenini but its position within the phylogenetical system is still unclear.



Figs. 14–19. *Caenis fregatula* n. sp. (14–17) and *C. bidigitata* n. sp. (18–19). – **14**. Head, details of surface. **15**. Pronotal surface, details, with hand-shaped microtrichia (small frame: in high magnification). **16**. Head and pronotum. **17**. Operculate gill, microtrichia from ventral side. **18**. Egg. **19**. Egg, micropyle.

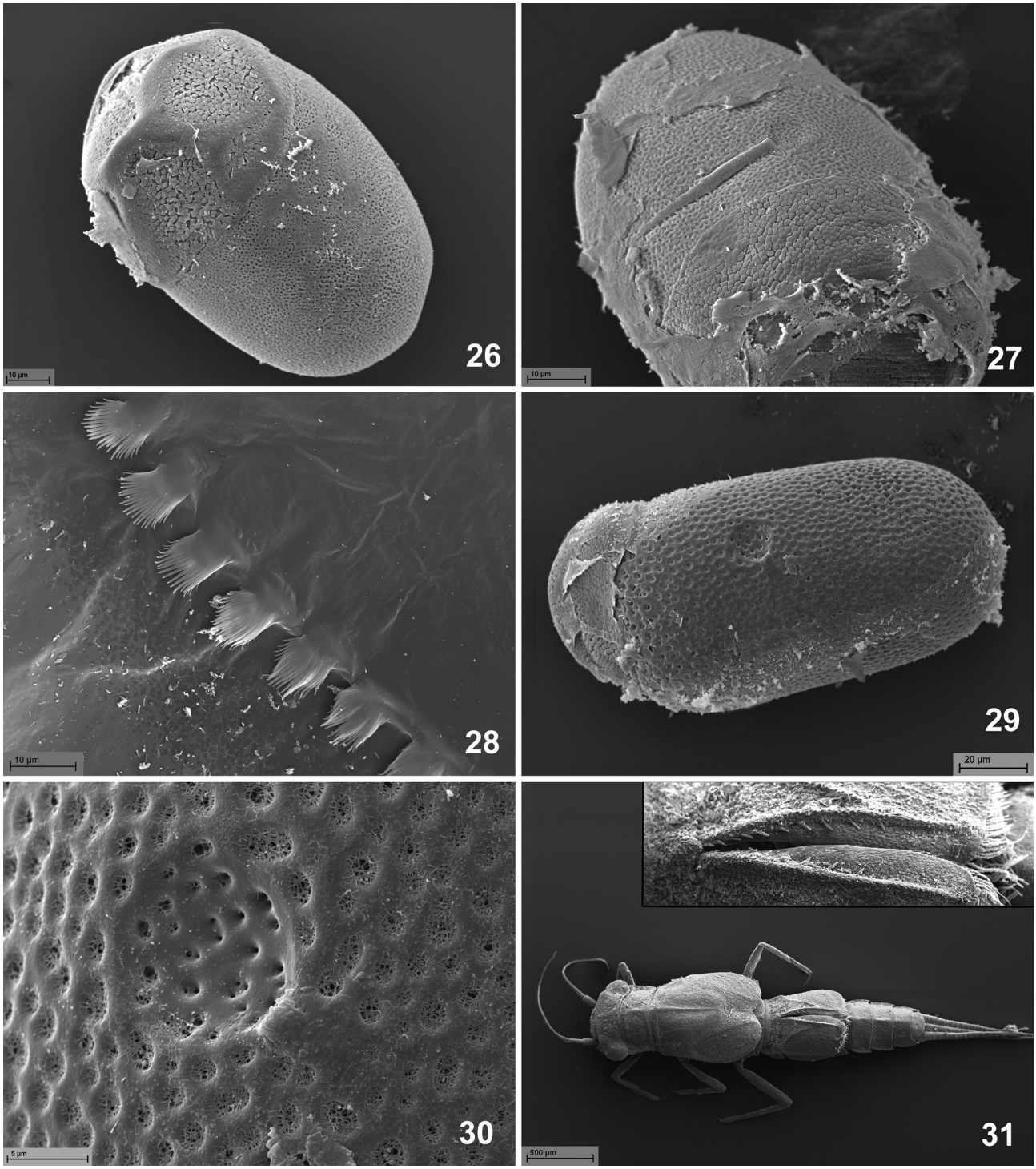
The herein suggested phylogeny of the Clypeocaenini genera (Fig. 50, Tab. 2) is discussed exclusively by using larval characters, since the adult stages (only known in one species of *Clypeocaenis* and in species of *Amercaenis* and *Kalimaenis*) are very *Caenis*-like without clear distinguishing characters.



Figs. 20–25. *Caenis bidigitata* n. sp., egg (20–21), larva (22–25) – **20**. Epithemata. **21**. Epithema, threads with terminal knobs. **22**. Mid leg, dorsal view. **23**. Head and pronotum. **24**. Operculate gill, frayed bristle from ventral side. **25**. Operculate gill, microtrichia from ventral side.

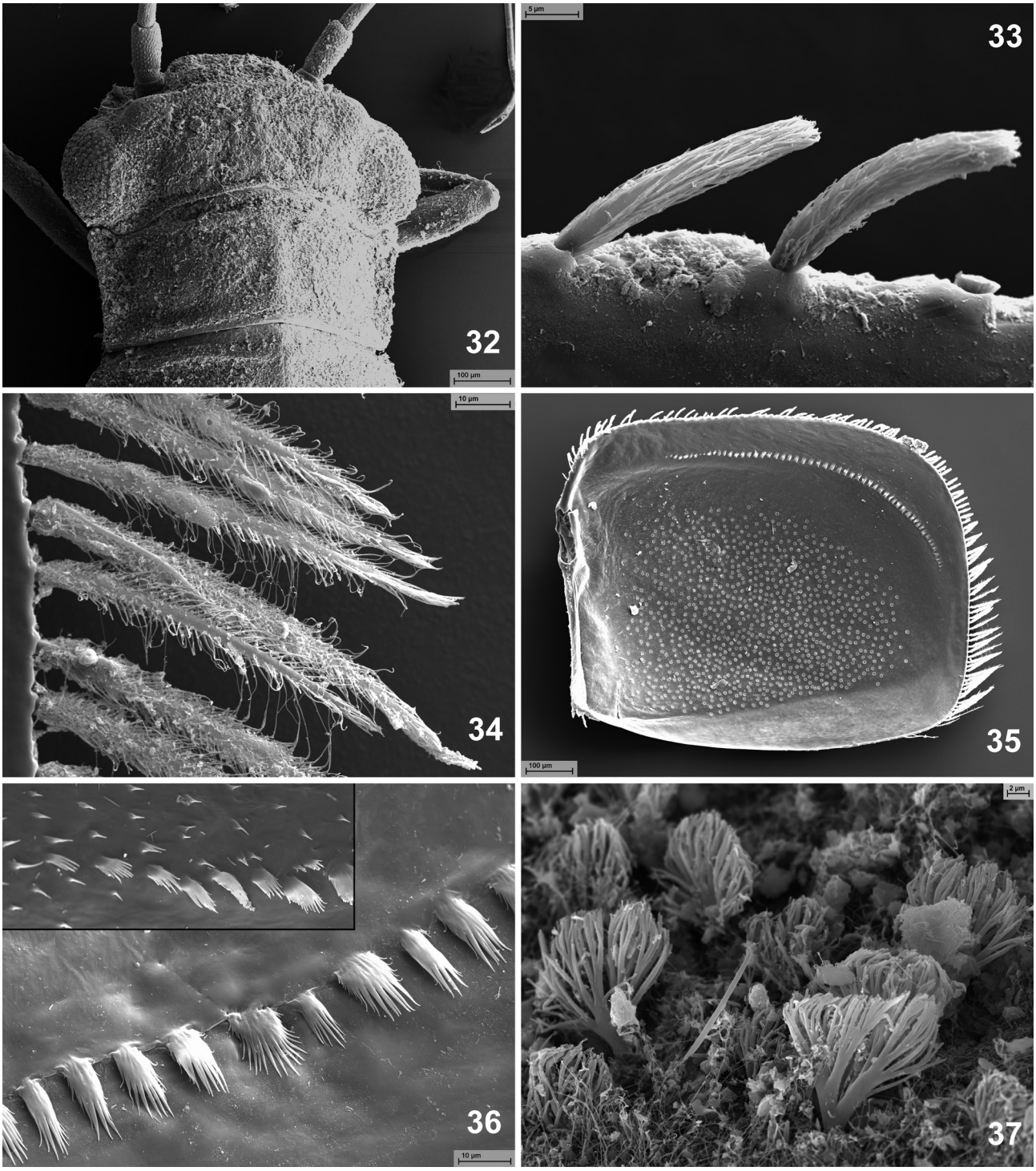
The new tribe Clypeocaenini (separated from the Caenini and Tasmanocoenini in bifurcation A) shows two synapomorphies:

(1) Gill III (first of the four respiratory gills) possesses at last 8 filaments with three or more branches, in most cases only one or two, in contrary to 15–25 in the Caenini and Tasmanocoenini. In the outgroup Neoephemeridae there are numerous filaments with 5 and more branches so that a reduction of these structures can be regarded as apomomorphic.



Figs. 26–31. *Caenis abdita* n. sp. (26–28), *Kalimaenis sibylliana* n. sp. (29–31). – **26**. Egg. **27**. Egg, micropyle. **28**. Operculate gill, microtrichia from ventral side. **29**. Egg. **30**. Egg, micropyle. **31**. Larva; keeled medial ridge on operculate gill in small frame.

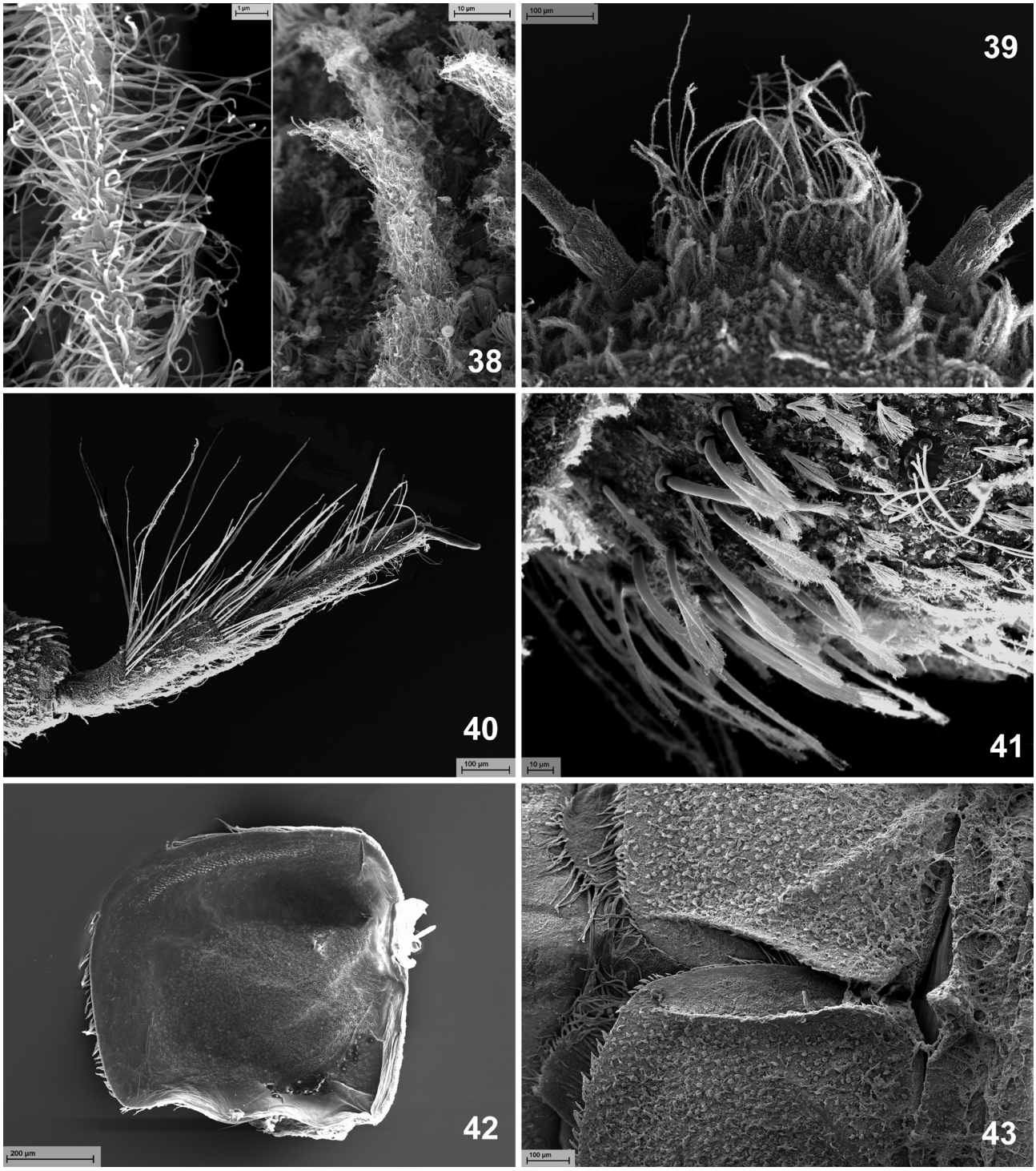
(2) Outline of head, seen in lateral view, with bulges, clypeus more or less protruding (Figs. 13c–h). In the Caenini as well as in outgroups Neoephemeridae (*Potamanthellus*) and Ephemerellidae (*Ephemerella*) the outline of the head, in lateral view, is evenly bowed (Figs. 13a, b).



Figs. 32–37. Larvae of *Kalimaenis sibylliana* n. sp. (32–36) and *Clypeocaenis soldani* n. sp. (37). – **32**. Head and pronotum. **33**. Operculate gill, bristles from lateral margin. **34**. Operculate gill, bristles from hind margin. **35**. Operculate gill, ventral view. **36**. Operculate gill, microtrichia from ventral side, sector from the row; basal part of the row in small frame. **37**. Multibranched hand-shaped bristles from body surface.

In the sister group, represented by the tribes Caenini and Tasmanocoenini, there are also two synapomorphies:

(3) Row of microtrichia on ventral side of gill II reaches hind margin of the gill (Caenini, see MALZACHER 2009b: figs. 17, 20, 23 and Tasmanocoenini, see SUTER 1984: fig. 6; ALBA-TERCEDOR & SUTER 1990: fig. 19; SUTER 1993: figs. 16, 41, 68; SUTER 1999: fig. 95).



Figs. 38–43. *Clypeocaenis soldani* n. sp., larva. – **38**. Body surface, sausage-shaped bristles (right), sector of a bristle from clypeus (left). **39**. Clypeus protrusion. **40**. Fore tibia and tarsus with filtering setae. **41**. Bristles from transverse row on fore femur. **42**. Operculate gill, ventral view. **43**. Operculate gill with keeled ridges, dorsal view.

(4) Gill II (operculate gill) with regular row of complex, very similar scale-shaped microtrichia. The plesiomorphic character state shows very different developmental stages (MALZACHER 2009b: figs. 3, 4, 5, 8, 10, 12).

Fig. 44. *Clypeocaenis soldani* n. sp., larva, operculate gill, microtrichia from ventral side.

Within Clypeocaenini the bifurcation B separates the *Amercaenis* group with the genera *Amercaenis* and *Kalimaenis* from the genera *Clypeocaenis*, *Barnardara*, *Callistellina* and *Trichocaenis* that share two apomorphies:

(5) In gill III nearly all filaments (up to 45) have one or two branches. Only one or two apical filaments show three or more branches. In the *Amercaenis* group there are 7–8 filaments with up to 5 branches and only about 20 reduced ones.

(6) Mesonotum broadened and outline of body more or less evenly curved.

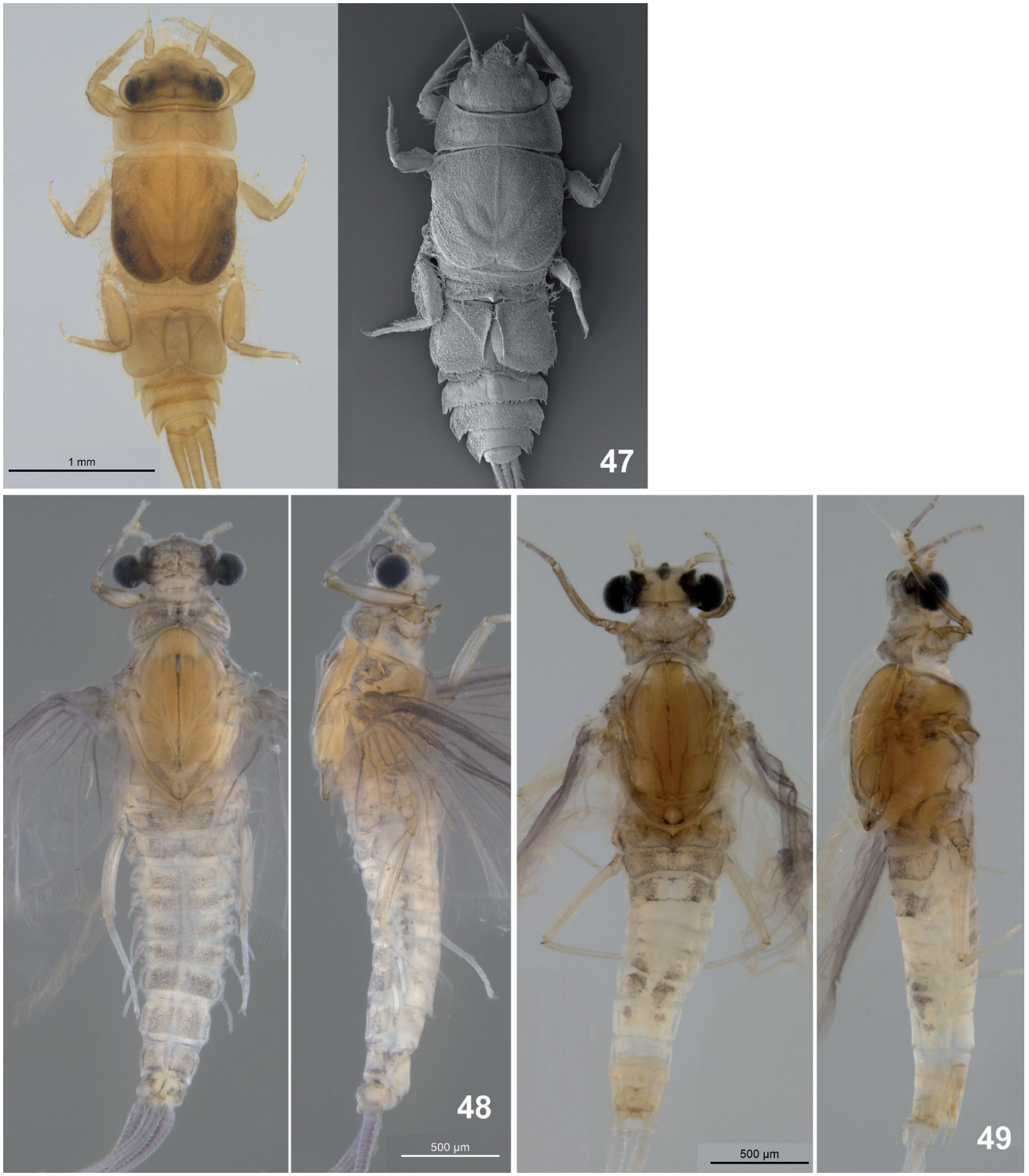
As already supposed by KLUGE (2004), *Amercaenis*, now the *Amercaenis* group, does not seem to be defined by unique apomorphic characters. Within this group the genus *Kalimaenis* shows three apomorphic characters:

(8) Legs long and slender (Figs. 8b–d), particularly in the females, with narrow femora more or less parallel-

Figs. 45–46. *Caenis* spp. – **45**. *C. sebastiani* n. sp., ♂, dorsal view (left), lateral view (right). **46**. *C. abdita* n. sp., larva, dorsal view.

sided. This shape shows a certain similarity to legs of Brachycercinae. The fore legs of *Kalimaenis* are reduced in length just like in the latter subfamily.

(9) Maxillary palps strongly elongated and narrowed with a conical segment I and S-shaped coiled segments II and III (Fig. 12a). As far as I know this shape is unique in



Figs. 47–49. Caenidae spp. – **47**. *Clypeocaenis soldani* n. sp., larva, light microscope (left), SEM (right). **48**. *Tigrocercus nastassjae* n. sp., ♂, dorsal view (left), lateral view (right). **49**. *Oriobrachys* sp., ♂, dorsal view (left), lateral view (right).

the Caenidae or even in the Pannota, where a tendency of reduction can be observed in all families. Only in *Tricorythus* a long and slender maxillary palp can be observed, but it shows only two segments (McCafferty & Wang 2000: fig. 85).

(10) Hind claws with about 7 groups of micro-denticles fused together to larger denticles (Figs. 8e, f). In the Caeninae homodont and heterodont hind claws can be found. The former show a number of denticles equal in size, whereas the latter have an additional row of more or less fused microdenticles (e. g. Malzacher 2009b: figs. 1p, 2h, 3g), a state that is apomorphic in some Caenini but can not be found in the Clypeocaenini. Groups of fused microdenticles are unique in *Kalimaenis*.

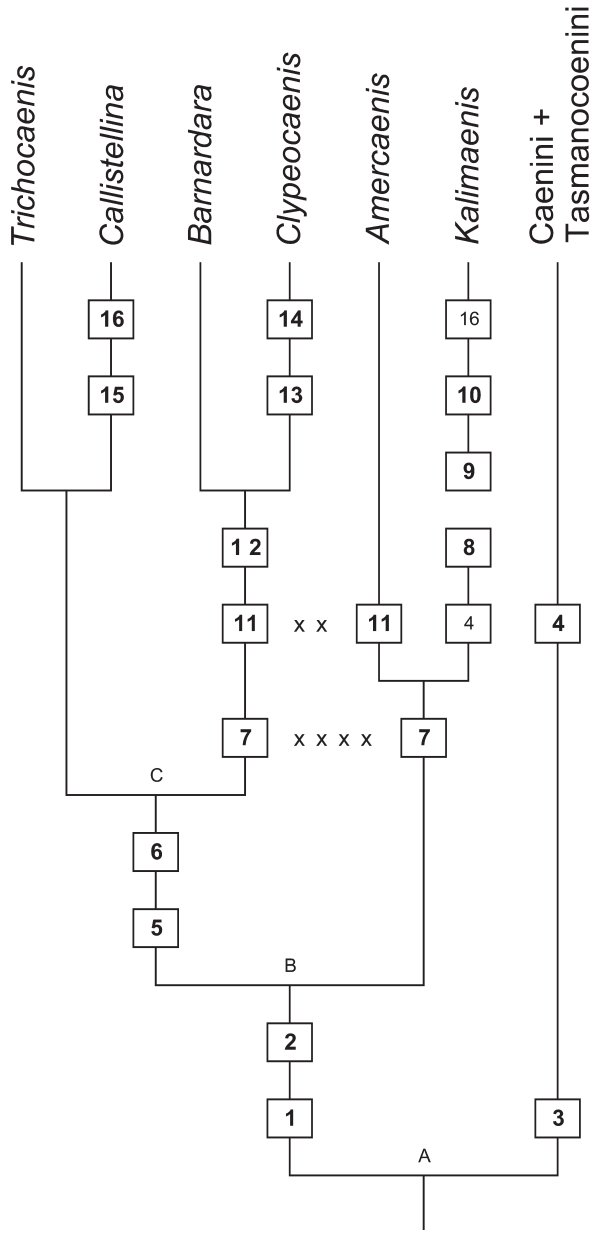


Fig. 50. Phylogeny of the tribe Clypeocaenini. – For explanation see discussion (section 5).

The remaining part of the phylogenetical tree comprises two groups of two genera each (separated in the bifurcation C). The genera *Clypeocaenis* and *Barnardara* share three apomorphic characters:

(7) Gill II with inner ridge keeled (Figs. 9d, 43; Provonsha & McCafferty 1995: fig. 7).

(11) Filtering setae on tibia and tarsus of fore leg (Fig. 40; Provonsha & McCafferty 1995: figs. 5, 16).

(12) Maxillary palp two-segmented (Fig. 12c). This character can also be observed as parallel developments in the Brachycercinae and some families of the Panota (see McCafferty & Wang 2000, Kluge 2004).

(7) and (11) are not unique in the *Amercaenis* group but can also be found in the *Clypeocaenis* group. That means in the two closely related lineages there is theoretically a possibility for another phylogenetical interpretation.

The genus *Clypeocaenis* shows two apomorphies which are further developments from (11) and (2) (partly):

(13) Filtering setae are arranged in rows (Fig. 40). A few setae also often present on inner margin of femur and in a basket-like arrangement on mandible (Provonsha & McCafferty 1995: figs. 13, 16).

(14) Clypeus strongly protruding and with long setae (Fig. 39).

The *Trichocaenis/Callistellina* group is not defined by apomorphies. Within this group *Callistellina* is separated by two apomorphic characters:

(15) Head with microscopic pits each with a hand-shaped microtrichium (Sun & McCafferty 2001: figs. 9, 10; Malzacher 2009b: fig. 10).

(16) Thoracic notae with ridges or bulges (Sun & McCafferty 2001: fig. 1). A single medial longitudinal ridge is also visible in *Kalimaenis*, Fig. 32.

5 Discussion

Caenis, species with tarsal projections

Males of all herein described species of *Caenis* are characterized by fore tarsi with apical projections on segments II–IV which have strong small spines (Figs. 1f, 4f). In the *Caenis cibaria* group from Africa the males possess tarsomeres that are apically slightly broadened and equipped with strong spines: only a few very short spines in *Caenis nigricola* (Malzacher 2011: fig. 6i) or a large number of longer spines, e. g. in *Caenis gilliesi* (Malzacher 1990: fig. 6a), a shaping that can also be observed in the Indian *Caenis picea*. Some other species from Asia (unde-

scribed) show transitional stages between these two forms: a species from Thailand with stronger apical broadenings, maybe identical with *Caenis nigropunctata* sensu ULMER (1939), and two other species from this country and from India with short processes. Whereas in all these cases the tarsal segments are equipped with processes on both sides, in Borneo the development has moved to forms with two processes on the one hand and one apico-median process on segments II and III on the other hand (segment IV has two processes in all cases). The latter character state seems to be the apomorphic one.

Within this apomorphic species group the different genital structures of *Caenis fregatula* (Figs. 3a, b) and the epithemata of the *Caenis bidigitata* eggs are conspicuous. The latter represent the so-called coiled-rope-type namely the *C. perpusilla* subtype, that is realized in *Caenis kohli* from West Africa and *Caenis perpusilla* from India and Sri Lanka (MALZACHER 2011: figs. 13, 34, 35). In contrary to these two species the epithemata of *Caenis bidigitata* show tiny end knobs. From each knob 1–4 threads are leading off (like otherwise in the *C. robusta* subtype only, compare discussion in MALZACHER 2011).

In the diagnoses of the *Caenis* species, characters which are common in the genus are listed first, followed by those which distinguish especially the here described species; e. g. the character "forceps with a tuft of long spines", which is widely distributed in the genus, is mentioned in the first part of the diagnosis and then the character "forceps with very thin spines" in the second part. In about half of all described *Caenis* species the larval stages are unknown. For that reason alone it seems difficult to use larval characters for a distinction "from all other species". In addition most of the diagnostic characters are widely distributed within the genus – often with numerous intermediate stages between the extremes – without implying hints about a phylogenetic system. One can even say they give the impression of an indiscriminate distribution. So in a diagnosis all characters mentioned in the description should be listed. As a compensation, the most important characters of the herein described *Caenis* species are compiled in Tab. 1.

Kalimaenis

This genus has two characters in common with the Brachycercinae, the presence of a forceps muscle and fore legs clearly reduced in length. The former can be regarded as a plesiomorphy although its appearance in combination with other structures forming a functional unit (present in Brachycercinae, Madecocercinae and Tasmanocoenini) seems to me to be apomorphic. Shortened fore leg is a derived state but not synapomorphic. In *Kalimaenis* the fore legs reach 0.76 of the length of the hind legs. In the Brachycercinae this value varies between 0.79 and 0.55 (taken from the figures in SUN & MCCAFFERTY 2008). Peculiarly the longest fore legs can be found in *Oriobrachys*.

Clypeocaenis

Clypeocaenis soldani is characterized by a flat, very broad body and strong setation. Bristles have more or less long branches (Fig. 38, left) or are sausage-shaped (Fig. 38, right). As far as I know, such bristles cannot be found in other species of the genus (see, however, *Caenis abdita*). The clypeus protrusion has up to 30 strong bristles; in *Clypeocaenis multisetosa* from India only 10–15 bristles can be observed (SOLDÁN 1978). About 4 bristles can be found in *Clypeocaenis oligosetosa* from Vietnam (SOLDÁN 1983). The remaining species *C. bisetosa* from Iran and India (SOLDÁN 1978), *C. afrosetosa* widely distributed in West Africa (SOLDÁN 1983), *C. femorisetosa* from Sri Lanka (SOLDÁN & LANDA 1991), and *C. umgeni* from South Africa (PROVONSHA & MCCAFFERTY 1995) only have two bristles. It can be deduced from the distribution that an apomorphic multiplication of clypeal bristles took place in the Eastern Orientalis. On the other hand the character state of microtrichia on the ventral side of the operculate gill is plesiomorphic in the eastern species *Clypeocaenis oligosetosa* and *C. soldani*, in contrary to *C. afrosetosa* (compare figs. 4 and 10 in MALZACHER 2009b). The state of this character in the other species is unknown.

Bristles with a large number of long and ultrathin branches can be found in *Clypeocaenis soldani*, *Caenis abdita* and in a specialized form in *Kalimaenis sibylliana*. This can only be interpreted as parallel development, but I do not have an explanation why all these forms occur in Borneo.

Tigrocercus

Some time ago JAN PETERS (Tallahassee), sent me two males and a female from Thailand. The males are very similar to the one described herein and the female shows eggs with the characteristic chorion structure of the eggs of the West African *Tigrocercus contractus* (MALZACHER & STANICZEK 2006: figs. 14a–c,) the only so far known species of the genus. This also supports the affiliation of the oriental species to this genus. There are some differences between *Tigrocercus nastassjae* and the specimens from Thailand that justify the description of a species of its own (in preparation). The diagnostic characters of all three species are listed in Tab. 3.

Oriobrachys

The herein described larva shows some differences to the larva of *Oriobrachys mahakam*, e. g. in shape and setation of maxilla and labium (compare Figs. 12e, f with SUN & MCCAFFERTY 2008: figs. 277, 278). Therefore it canot be excluded, that this larva represents a new species. Be

Tab. 1. Most important differential diagnostic characters of *Caenis* spp.

	Character	*C. sebastiani* n. sp.	*C. fregatula* n. sp.	*C. bidigitata* n. sp.	*C. abdita* n. sp.
1	Surface structur	honeycomb, netmeshes, often with denticles	strongly granulated, abdominal netmeshes + denticles	smooth	coarsely granulated, abdominal netmeshes + denticles
2	Surface setation		branched microtrichia		long bristles + hairs
3	Genae	slightly bulging	slightly bulging	not bulging	not bulging
4	Ratio length segment II : III of labial palp	2.0	1.8	2.3	1.7
5	Mandibular bristles	laterally, long and bent	dorsally, a few very thin	dorsal field, long bent	dorsally, a few very thin
6	Sides of pronotum	straight, slightly diverging, denticulate	diverging, slightly convex, denticulate	straight to convex, diverging, smooth	straight, parallel, ± denticulate
7	Fore femur, transverse row of bristles	straight, ± 10 bristles	irregular, ± 5 bristles	regular, 8–10 bristles	regular, ± 5 bristles
8	Shape of bristles of transverse row	large, spatulate	spatulate	very long, broad, spatulate	narrow, blunt
9	Setation of mid and hind femur	spatulate bristles	long, spatulate-pointed bristles	large, spatulate, longer and broader bristles	long bristles and sensitive hairs
10	Claws, shape and denticulation	slender without denticles	moderately bent	slender without denticles	tips bent without denticles
11	Coxal processes	inconspicuous	inconspicuous	inconspicuous	inconspicuous
12	Abdomen, lateral processes	short	short	short	short
13	Abdomen, lateral setation	long, pointed, shorter on segments VII–IX	long, pointed, shorter on segments VII–IX	long, pointed, short on segments VIII–IX	long, pointed, also on segments VIII–IX
14	Tergum II, postero-median process	short, broadly triangular	long, cone-shaped	very short, triangular	very short, broad, triangular
15	Gill II, row of ventral microtrichia	ending middle of hind margin	ending middle of hind margin	ending middle of hind margin	ending closer to lateral margin
16	Shape of microtrichia	circular to square-shaped	circular to square-shaped	± elongate	circular to square-shaped
17	Gill II, dorsal bristles, number and structure	± 6, along medial ridge	± 6, along medial ridge, strong denticles	6–8, broad spatulate, marking medial ridge	± 6, long, strong and pointed
18	Gill II, marginal setation	bristles on hind margin long and hairlike, laterally shorter, ± blunt	bristles short and spatulate on postero-lateral margin, long and thin on hind margin, moderate on lateral margins	bristles on hind margin hairlike, basally broad, laterally moderate, blunt	bristles very long on hind margin, of very different length on lateral margins
19	Gill II Y-shaped ridges	posteriorly reduced	well-developed, ± keeled	strongly reduced	well-developed
20	Setation on hind margin of terga VII–X	as usual	tergum VIII with bristles and denticles	as usual, bristles like that on hind margin of operculate gill	denticles and 4 long bristles on segment IX, very long denticles on segment X
21	Sternite IX, shape of hind margin	cut or slightly indented	flatly rounded	broadly rounded, slightly indented	only slightly protruding medially, ± angled
22	Sternite IX, bristles on hind margin	short thin, ± bifurcate	a few very short bifurcate	bifurcate, frayed	long, simple-bent medially
23	Sternite IX, dorsal shagreen field	± 3 submarginal rows	1–2 short submarginal rows	4–5 irregular rows	lacking?
24	Additional peculiar characters	labial palp segments I + II with ± 15 strong bristles	–	gill II ventrally with broad frayed bristles	larva entirely covered with mud, hold by very fine threads

Tab. 2. Differential diagnostic characters of the subfamily Caeninae, particularly the tribe Clypeocaenini.

	Character	Apomorphic state	Plesiomorphic state
1	Gill III	at last 8 filaments with 3 or more branches	more than 15, up to 25 filaments
2	Outline of head, lateral view	with bulges, clypeus ± protruding	evenly bowed
3	Gill II, ventral row of microtrichia	reaching hind margin of gill	not reaching hind margin
4	Gill II	with regular row of complex, scale-shaped microtrichia	with bands or irregular rows of spines, clusters of spines, or simple scales
5	Gill III	nearly all filaments 1- or 2-branched, only 1–3 filaments with 3 or more branches	more than 15 filaments with 3 or more branches
6	Mesonotum	broadened, outline of body evenly curved	not broadened, outline ± irregular
7	Operculate gill	inner ridge keeled	not keeled
8	Legs	long and slender, femora narrowed, with parallel sides	all parts shorter, femora broad
9	Maxillary palp	elongated, segment 1 conical, segments 2 + 3 coiled	shorter and not coiled
10	Hindclaw	with groups of fused micro-denticles	homo- or heterodont, without groups of fused micro-denticles
11	Fore leg	with filtering setae	without filtering setae
12	Maxillary palp	two-segmented	three-segmented
13	Filtring setae on fore leg	forming regular rows	irregularly arranged
14	Clypeus	strongly protruding, with long setae	± protruding, without long setae
15	Head	with microscopic pits, each with branched microtrichium	without those structures
16	Thoracic notae	with ridges or bulges	evenly bowed

Tab. 3. Differential diagnostic characters of the *Tigrocercus* spp.

Character	*Tigrocercus contractus*	*Tigrocercus nastassjae* n. sp.	*Tigrocercus* sp. (Thailand)
Base of antennal flagellum	not dilated	?	strongly dilated
Fore tarsus	segments II–V subequal in length	segments III–V subequal in length, segment I clearly longer	segments III–V subequal in length, segment I clearly longer
Abdominal terga I and II	without fingerlike processes	each with a long fingerlike process	tergum II with a fingerlike process, tergum I without
Abdominal segments	IV–IX with lateral filaments	IV–VII with lateral filaments	IV–VII with lateral filaments
Penis laterally	without tongue-shaped processes	with three small tongue-shaped processes	with three conspicuous tongue-shaped processes, the median one with large basal sclerite
Lateral sclerites	anteriorly diverging, basally not sclerotized and keeled	parallel, moderately sclerotized, with weakly S-shaped keels	parallel, strongly sclerotized, with S-shaped keels
Forceps	in its basal half moderately broadened, inner margin smooth	in its basal fourth strongly broadened, inner margin irregularly denticulated	in its basal third moderately broadened, inner margin smooth

that as it may, if the assumption in the remarks to *Oriobrachys* (see above) is correct – last doubts can only be dispelled by rearing males from larvae – the male genitalia of this genus are highly apomorphic compared to those of all other Brachycercinae genera which are rather similar to each other. The elongated and medially narrowed styliger and the very long, thin and apically rounded forcipes are unique within the Brachycercinae (compare Figs. 10e, h and g; *Cercobrachys etowah* is – according to Sun & McCafferty 2008 – closer related to *Oriobrachys* than to *Brachycercus harrisella*). On the other hand the larva of *Oriobrachys* is very similar to those of the other genera of the tribes Latineosini, to which *Oriobrachys* is assigned, and Cercobrachini. Both tribes share a synapomorphic character, namely the lateral process of abdominal segment VI long tongue-shaped and strongly bent medially (Sun & McCafferty 2008). *Oriobrachys* however is the only genus that shows the apomorphy of an operculate gill with a long sublateral ridge (Sun & McCafferty 2008). Larval and imaginal apomorphies together indicate the possibility of an own tribe opposite to the adelphotaxon Latineosini + Cercobrachini.

In more than half of the species of Brachycercinae the males are unknown. So it is not surprising that in the two monographies of the subfamily (Soldán 1986, Sun & McCafferty 2008) genital structures are hardly considered in view of phylogenetic relationships. Perhaps the knowledge of these unknown males would show the phylogenetic position of *Oriobrachys* with its striking genitalia in a different light.

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