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Revision of the Madecocercinae (Ephemeroptera: Caenidae)

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Abstract
The new genus *Tigrocercus* with the species *Tigrocercus contractus* from West Africa (Guinea, Mali and Togo) is described as well as three new species of the genus *Afrocercus* Malzacher, 1987: *Afrocercus sartorii* from Côte d'Ivoire, and from Guinea both *Afrocercus inflatus* and *Afrocercus guinensis*. A herein described larva from the type locality of *Afrocercus guinensis* most probably belongs to this species. Both genera are related to *Madecocercus* Malzacher, 1995. The larva of *Madecocercus tauroides* is described, together with the imago of a new species *Madecocercus bibulus*. The diagnoses of the genera of Madecocercinae are corrected and extended, and a new synapomorphy for the Madecocercinae is assessed. The phylogenetic relationships of the subfamilies of Caenidae are discussed.

Keywords: Brachycercinae, Africa, Madagascar, new species, new genus, phylogeny

Introduction

The Caenidae were divided into the subfamilies Caeninae and Brachycercinae by Malzacher (1987). In 1997 he confirmed this phylogeny by giving a number of synapomorphies for the subfamilies. The Brachycercinae comprised the genera *Brachycercus*, *Cercobrachys*, *Insulibrachys*, *Afrocercus* and *Madecocercus*. Distributed in Africa and Madagascar, *Afrocercus* and *Madecocercus* were represented by *Afrocercus forcipatus* Malzacher, 1987, and *Madecocercus tauroides* Malzacher, 1995, both only known from a few imaginal specimens. McCafferty and Wang (1995) described *Provonshaka thomasorum* in the Tricorythidae solely based on larval material. When Elouard and Sartori (2001) reared a female imago of *Madecocercus* from a *Provonshaka* nymph the genera were synonymised. Consequently the genus *Provonshaka* was removed from the Tricorythidae and is now regarded as junior synonym of *Madecocercus* (Elouard & Sartori 2001).

McCafferty and Wang (2000) separated *Afrocercus* and *Madecocercus* from the Brachycercinae. Based on two larval characters, namely the loss of the maxillary palp and the posteriorly expanded forefemora, they established the new subfamily Madecocercinae.

The new African and Malagasy material presented in this study expands our knowledge of the Madecocercinae and of the genera of Caenidae in general. The new genus *Tigrocercus* is preliminary placed in the Madecocercinae. The availability of new characters leads to an improved phylogeny of Caenidae.

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Material, methods, and terminology

Recently we received material of West African and Malagasy Caenidae from Dr. Michel Sartori, Lausanne. It was collected in Guinea, Côte d'Ivoire, Mali, and Togo from 1985 to 1988, and in Madagascar in the 1990s by the ORSTOM-team of Dr. Jean-Marc Elouard. It contained the new genus *Tigrocercus* and new species of the genera *Afrocercus* and *Madecocercus*.

The holotypes and paratypes of the new species described herein are deposited in the Musée Zoologique, Lausanne, Switzerland. Additional paratypes are deposited in the State Museum of Natural History, Stuttgart, Germany.

Genitalia and eggs 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/Pd layer, and examined with an ISI-SS40 scanning electron microscope at 10 kV. Digital photographs were directly acquired by using DISS 5 (point electronic).

Terminology used for the genitalia follows Malzacher (1991).

The numbering in the figures of the genitalia is as follows: 1. forceps, 2. penis, 3. styliger plate, 4. styliger sclerite, 5. apophyses of the styliger sclerite, 6. central sclerite, 7. lateral sclerite, 8. basolateral sclerite.

General remarks on pigmentation

Pigments deposited in the epidermis are blackish brown in general. Strong pigmentations are black, in lower densities they appear blackish brown, brown or grey. Densities are often variable in different individuals or populations.

Systematic account

Tigrocercus Malzacher, gen. n.

Type-species: *Tigrocercus contractus* sp. n.

Distribution. At present this genus is recorded from Guinea, Mali, and Togo. It is likely that this genus is distributed throughout West Africa.

Differential diagnosis. The genus can be distinguished from all other genera of Caenidae by the following combination of characters:

Imago. (1) Pedicel 2.0–2.25 times longer than broad; 2.5 times length of scape (♂) (Figure 1f). (2) Antennal flagellum basally not dilated (♂) (Figure 1f). (3) Coxae widely separated; prosternum broad, more or less semicircular (♂ ♀) (Figure 1e). (4) Segments 2–5 of foretarsus subequal in length (♂). (5) Foreleg 1.5–1.8 times length of hind leg (♂). (6) Trochanter of foreleg elongated; forefemur long and narrow, 3.0–3.3 times length of trochanter (♂, 3.3–3.6 in the ♀) (Figure 7d). (7) Distance from tip of wing to cross vein R1–R2 about 1.1–1.2 times distance from cross vein R1–R2 to middle of costal brace (♂ ♀). (8) Metanotum flat, without transverse ridge; with membranous hind margin (♂ ♀). (9) Abdomen with long lateral filaments on the segments IV–IX, those on V–VIII about 1.5 times the length of the segment (♂ ♀) (Figure 1g). (10) Segment IX with posterolateral processes (♂ ♀) (Figure 1a). (11) Segment IX and styliger clearly broader than long (♂) (Figure 1a). (12) Lateral sclerite at base weakly sclerotised (♂) (Figure 1a–c). (13) Forceps muscle strongly developed forming a functional unit with lateral sclerites and forceps (♂). (14) Styliger sclerite large, weakly sclerotised, with 2 long bent apophyses approaching the bases of forceps (♂) (Figure 1a–c). (15) Forceps long and sickle shaped, basally broadened, apically with a long ridge (♂) (Figure 1d). (16) Forceps articulated laterally to lateral sclerites (♂) (Figure 1a–c). (17) Terminal filum 1.1–1.2 times length of cerci (♂).

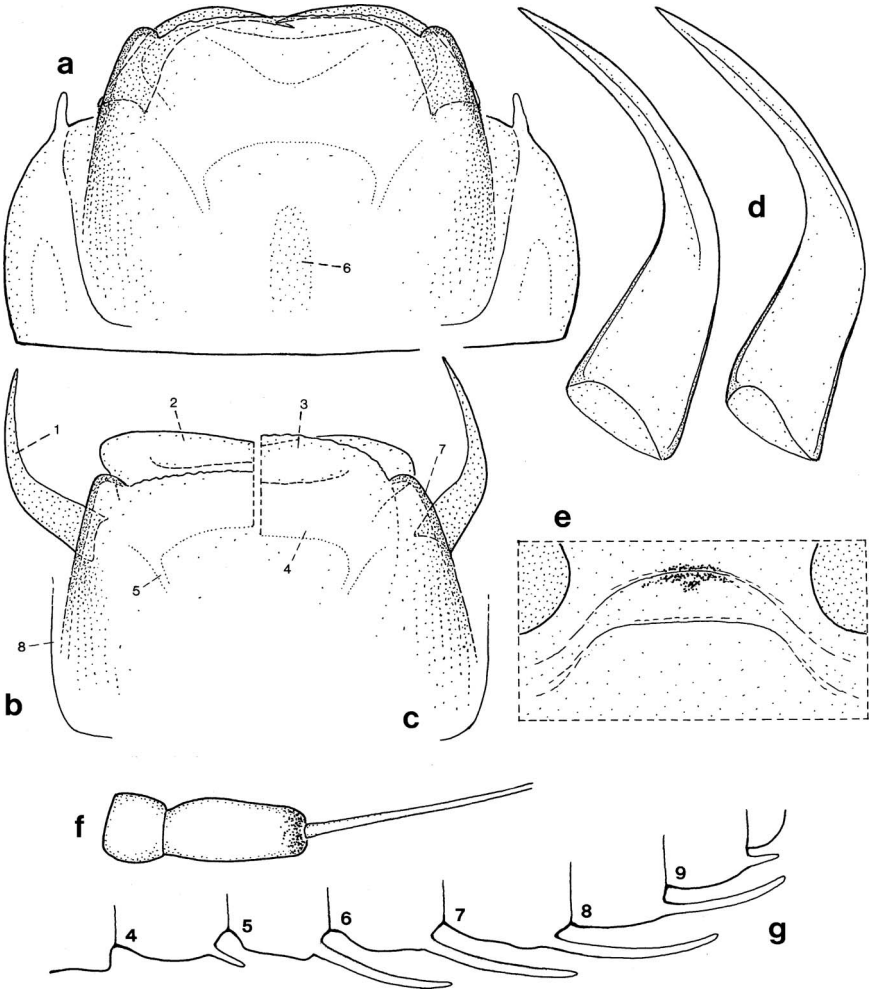

Figure 1. *Tigrocercus contractus* gen n. sp. n.; male. (a–c) genitalia: 1 = forceps, 2 = penis, 3 = styliger plate, 4 = styliger sclerite, 5 = apophyses of styliger sclerite, 6 = central sclerite, 7 = lateral sclerite, 8 = basolateral sclerite; (d) forceps, different shapes; (e) prosternum; (f) antenna: scape, pedicel and base of flagellum; (g) lateral outline of abdomen with filaments.

Egg. (18) Eggs without epithemata and threads (Figure 14b). (19) Chorion of eggs with longitudinal rows of scale like structures (Figure 14b, and c).

Etymology. *Tigro-* refers to the shape of the forceps that closely resembles the mandible of a tiger beetle. The suffix *–cercus* is commonly used in the Caenidae.

Tigrocercus contractus Malzacher sp. n.

Material

Holotype ♂ (micro-slide): Guinea, riv. Koumba, nr. Sita, 26.01.1987. - Paratypes: 2 ♂: Guinea, riv. Koumba, nr. Sita, 26.01.1987. - Additional material: 5 ♂: Mali, riv. Faleme, 18.01.1986. – 1 ♂, 13 ♀: Togo, riv. Mono, Landa, 01.12.1985.

Male imago

Body length 3.1 – 3.7 mm; wing length 3.3 – 3.5 mm; length of foreleg 2.2 – 2.5 mm. Ratio of forefemur : foretibia = 0.58 – 0.69; ratio of foretibia : foretarsus = 1.18 – 1.26; ratio of foreleg : hind leg = 1.58 – 1.73; ratio of first segment of foretarsus : 2nd : 3rd : 4th : 5th = 1 : 1.8 – 2.3 : 1.8 – 2.1 : 1.7 – 2.3 : 1.8 – 2.4. Ratio of body length: length of cercus: length of terminal filum = 1 : 2.6 : 2.9.

Colouration of chitinous layers: Mesothorax strongly yellowish-brown; head, prothorax and tergum X lighter yellowish brown. Other parts yellowish-white.

Epidermal pigmentation: Frons and vertex, pronotum and prealar bridge rather strongly pigmented, scutellum and metanotum a little lighter. Abdominal terga with transverse bands, rather strong on tergum I and II; the latter with median black spot; bands on other terga lighter and more or less interrupted medially. Pedicels and segments of foretarsi with rings of pigments. A transverse dash on the fore margin of prosternum.

Base of antennal flagellum not dilated (Figure 1f). Prosternum as in Figure 1e. Sparsely structured, transverse fold sometimes nearly invisible. Lateral filaments of abdominal segments V – VIII very long (Figure 1g).

Genitalia and sternum IX as in Figure 1a – c. Penis lobes voluminous and rounded, often totally covered by the styliger and the contracted forceps. Styliger sclerite and central sclerite often scarcely visible. Forceps as in Figure 1d.

For other details see the generic diagnosis.

Female imago

Body length: 4.5 – 6.0 mm; wing length: 4.0 – 4.5 mm.

Colouration of chitinous layers as in male but with mesothorax dark yellowish-brown with blackish-brown sutures.

Epidermal pigmentation a little stronger than in male, abdominal terga nearly entirely pigmented.

Prosternum with broadly rounded fore margin, median transverse fold often lacking. Lateral filaments of abdominal segments V – VIII rather longer than in males.

Eggs

Shaped like a fir cone (Figure 14b), often covered by a membrane (Figure 14a). Chorion consisting of six longitudinal rows of scale-like structures. Lateroapical parts of each scale somewhat protruding, overlapping the laterobasal parts of scales of adjoining rows (Figure 14b, and c). Each scale with central circular area of elongated pores.

Larva. Unknown.

Etymology. The species name refers to the contracted forceps.

Afrocercus Malzacher, 1987

Type species: *Afrocercus forcipatus* Malzacher, 1987.

Distribution. Uganda, Guinea, Côte d'Ivoire.

The genus *Afrocercus* was first described from a single male from Uganda. With the knowledge of three new species from West Africa and the probable larva, it is now possible to give a new diagnosis.

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

Imago. (1) Pedicel 1.3–1.6 times longer than broad; 2.0 times length of scape (♂) (Figure 7f). (2) Antennal flagellum basally dilated (♂) (Figure 7f). (3) Coxae widely separated; prosternum broad, more or less rectangular (♂ ♀). (4) Segment 2 of foretarsus strongly elongated, nearly as long as segments 3–5 together (♂). (5) Foreleg at least twice as long as hind leg (♂). (6) Trochanter of foreleg elongated; forefemur broad and relatively short, 2.2–2.3 times length of trochanter (♂, 2.5–2.7 in ♀) (Figure 7a, and b). (7) Distance from tip of wing to cross vein R1–R2 about 1.4–1.7 times distance cross vein R1–R2 to middle of costal brace (♂ ♀). (8) Metanotum flat, without transverse ridge; with posteromedian flat, tongue-shaped process (♂ ♀) (Figure 6e). (9) Abdomen with short or very short lateral filaments on segments IV–VII (♂ ♀). (10) Segment IX without posterolateral processes (♂ ♀) (Figures 2a, and c, 7a, and b). (11) Segment IX and styliger of approximately equal length and width (♂) (Figures 2a, and c, 6a, and b). (12) Lateral sclerite broadened at base (♂) (Figures 2a, and c, 6a, and b). (13) Forceps muscle strongly developed forming a functional unit together with lateral sclerites and forceps (♂). (14) Styliger sclerite small, often weakly sclerotised and nearly invisible (Figure 6a, and b), sometimes with short paramedial apophyses (♂) (Figure 2a, and c). (15) Forceps short, apically rounded or inwardly curved, with blunt point, with more or less blurred ridges (♂) (Figures 2b, and d, 6c). (16) Forceps

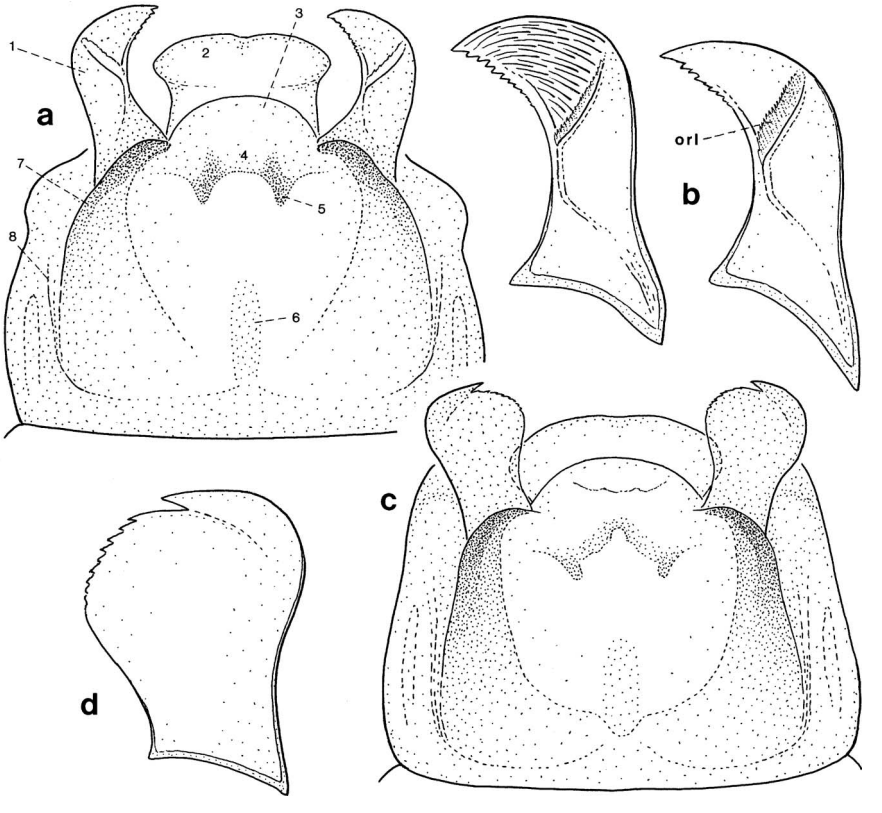

Figure 2. *Afrocercus guinensis* sp. n.; male (a and b). a. genitalia: 1 = forceps, 2 = penis, 3 = styliger plate, 4 = styliger sclerite, 5 = apophyses of styliger sclerite, 6 = central sclerite, 7 = lateral sclerite, 8 = basolateral sclerite; (b) forceps, different shapes: orl = oblique ridge with lamella. *Afrocercus inflatus* sp. n.; male (c and d). (c) genitalia; (d) forceps.

articulated lateroapically to lateral sclerites (♂) (Figures 2a, and c, 6a, and b). (17) Terminal filum 1.5 – 1.8 length of cerci (♂).

Egg. (18) Eggs without epithemata, with short, smooth, apically hooked threads and a dense band of longer threads around equator (Figure 14f). (19) Chorion of eggs with longitudinal rows of circular or oval fields with more or less elevated margins with two opposing threads (Figure 14d, and e).

Larva (presumed). (20) Body short and broad (Figure 3). (21) Head without ocellar tubercles. (22) Labial palp three-segmented (Figure 4b). (23) Maxilla without palp, cardo fused with stipes (Figure 4a). (24) Margins of legs, second gills and abdomen fringed with long setae (Figure 3). (25) Femora short and broad, without extended plates (Figure 3). (26) Second gills medially overlapping (Figure 3). (27) Second gill ventrally with lateral field of small spine-shaped microtrichia (Figure 4d), without band of scales. (28) Gills 3 – 6 with branched filaments, filaments of gill 6 in apical half only (Figure 5b, and c). (29) Abdominal segments IV-VII with long pointed posterolateral projections not bent dorsally (Figure 5a). (30) Dorsal surface densely covered with robust tubercles (Figure 5d).

Afrocercus guinensis Malzacher sp. n.

Material

Holotype. ♂ (micro-slide): Guinea, riv. Milo, Boussoule, 18.03.1987. - Paratypes. 3 ♂, 42 ♂ SI, 1 ♀: Guinea, riv. Milo, Boussoule, 18.03.1987. - Additional material: 5 ♂, ca. 150 ♂ SI, 1 ♀: Guinea, riv. Milo, Boussoule, 19.04.1986, – 5 ♂, 40 ♂ SI, 16 ♀ (I and SI): Guinea, riv. Niandan, Sassambaya, 15.05.1986, 19.03.1987, 27.11.1987, 12.04.1988. One subadult larva: Guinea, riv. Niandan, Sassambaya, 19.04.1986.

Distribution. Guinea.

Male imago

Body length 1.8 – 2.5 mm; wing length 2.0-2.4 mm; length of foreleg 1.5 – 1.9 mm. Ratio of forefemur : foretibia = 0.42 – 0.50; ratio of foretibia : foretarsus = 0.96 – 1.01; ratio of foreleg : hind leg = 2.22 – 2.50; ratio of first segment of the foretarsus : 2nd : 3rd : 4th : 5th = 1 : 4.1 – 4.4 : 2.1 – 2.6 : 1.5 – 2.2 : 1.6 – 2.0. Ratio of body length : length of cercus : length of terminal filum = 1 : 2.2 – 2.5 : 3.4 – 3.8.

Colouration of chitinous layers. Mesothorax yellowish brown. Other parts paler, yellowish white.

Epidermal pigmentation. Weakly pigmented. Hind margin of prothorax with laterally broadened blackish streak, with more or less visible lateral pigmentation. Abdominal terga I – VII with broad transverse bands, most pronounced on tergum I and II, but here with median interruptions. Terga VIII – X pale. Foretibiae and tarsi pigmented.

Body short and broad. Antennal flagellum basally dilated; dilated part two times as long as pedicel (Figure 7f). Forefemur very broad, about two times as long as the elongated trochanter (Figure 7a). Prosternum, metanotum and lateral filaments on abdominal segments as in generic diagnosis.

Genitalia as in Figure 2a. Penis with short rounded or weakly pointed lobes and transverse bulge ventrally. Lateral sclerites apically sclerotised and yellowish brown. Styliger sclerite with two short slightly yellowish brown apophyses forming semicircular margin between them. Forceps as in Figure 2b and Figure 15a, slightly bent backwards as seen in lateral view

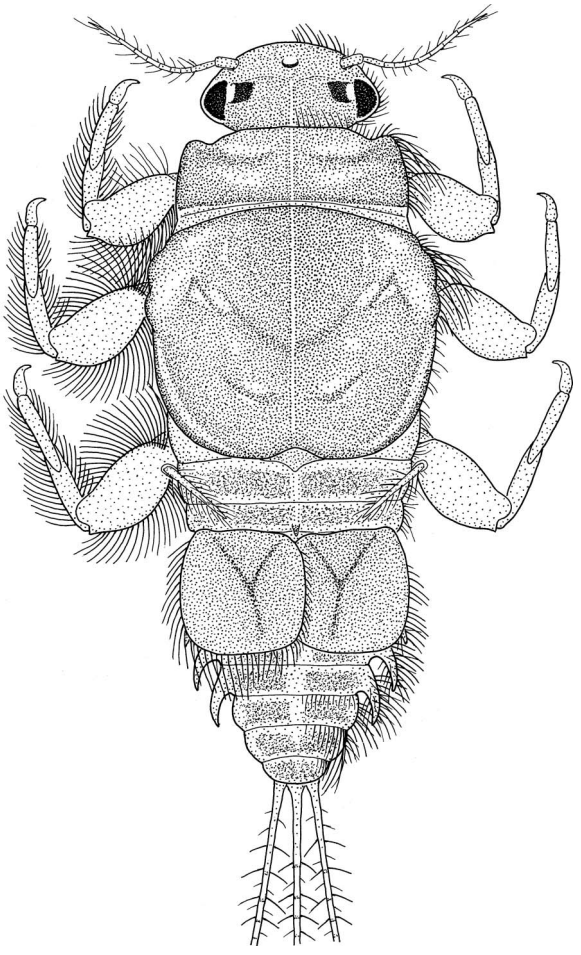

Figure 3. *Afrocercus guinensis* sp. n.; larva, habitus; right half with setae on body outline; left half with setae on legs and second gill.

(Figure 7g, and h). Ventral surface of forceps with ridges, subapical ridge with an obliquely arranged lamella, distal surface covered with trichomes (Figure 2b, left and Figure 15a). Forceps essentially colourless except for brownish ridges.

Note. The impression that there are more trichomes in Figure 2b compared to Figure 15a is due to the fact that in the light optical picture trichomes from the dorsal side are shining through.

Female imago

Body length: 2.5 – 3.0 mm; wing length: 2.8 – 3.0 mm.

Colouration of chitinous layers as in males.

Epidermal pigmentation significantly stronger than in males. Pronotum extensively pigmented. Mesonotum with dark sutures; metanotum with curved transverse band and tongue-shaped process with conspicuous black mark (as in Figure 6e). Abdominal terga VIII – X with grey shadings.

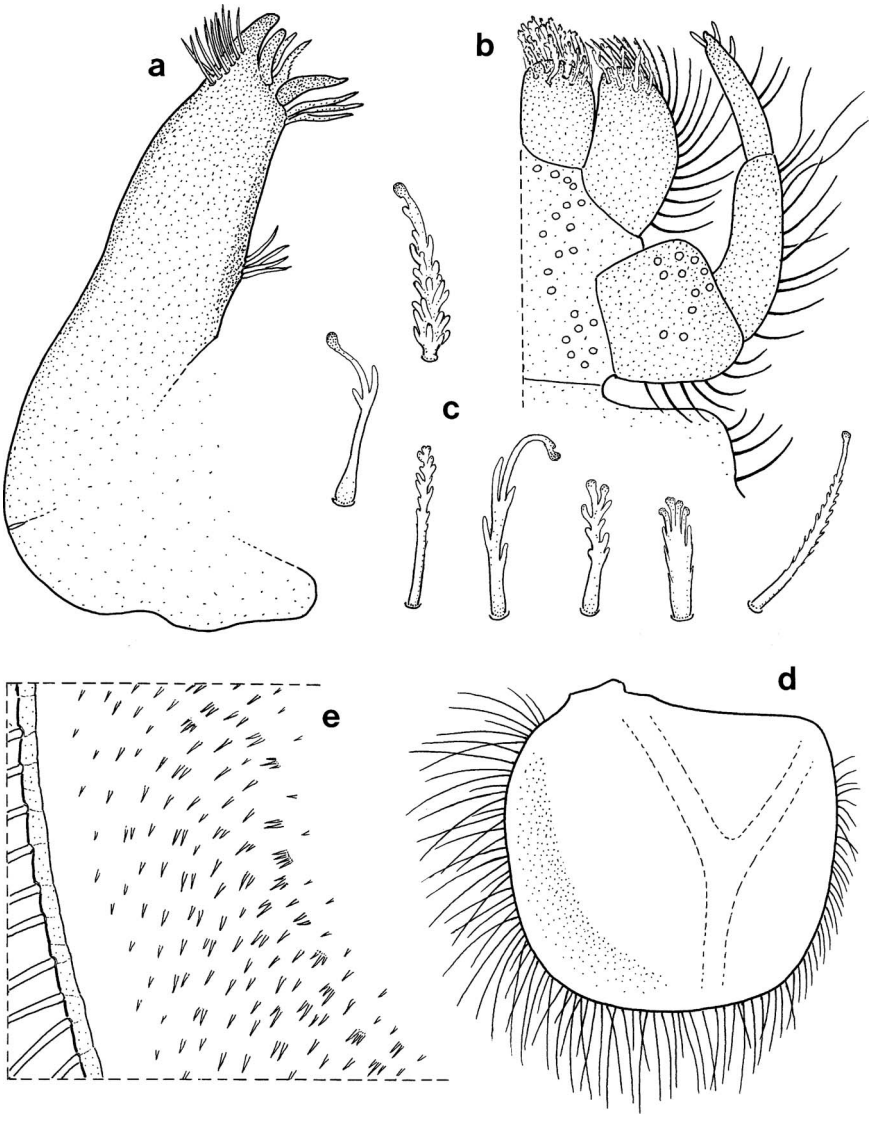

Figure 4. *Afrocercus guinensis* sp. n.; larva, mouthparts (a – c). (a) maxilla, galealacinia; (b) labium, right half; (c) irregular setae on apical region of glossae and paraglossae, different forms – second gill (d – e). (d) general view; (e) ventral side, sector of marginal field (pointed field in d) with single and clustered spine-shaped microtrichia.

Antennal flagellum basally somewhat dilated but narrower than in male. Relative length of antennae shorter than in male (compare Figure 7e, and f).

Larva

Note. A sample from Sassambaya, riv. Niandan contains one female Caenid larva that definitely does not belong to the genus *Caenis* but shows similarity to the larva of *Madecocercus*. We presume that it is the larva of *Afrocercus guinensis* because many specimens of this species are recorded from that locality.

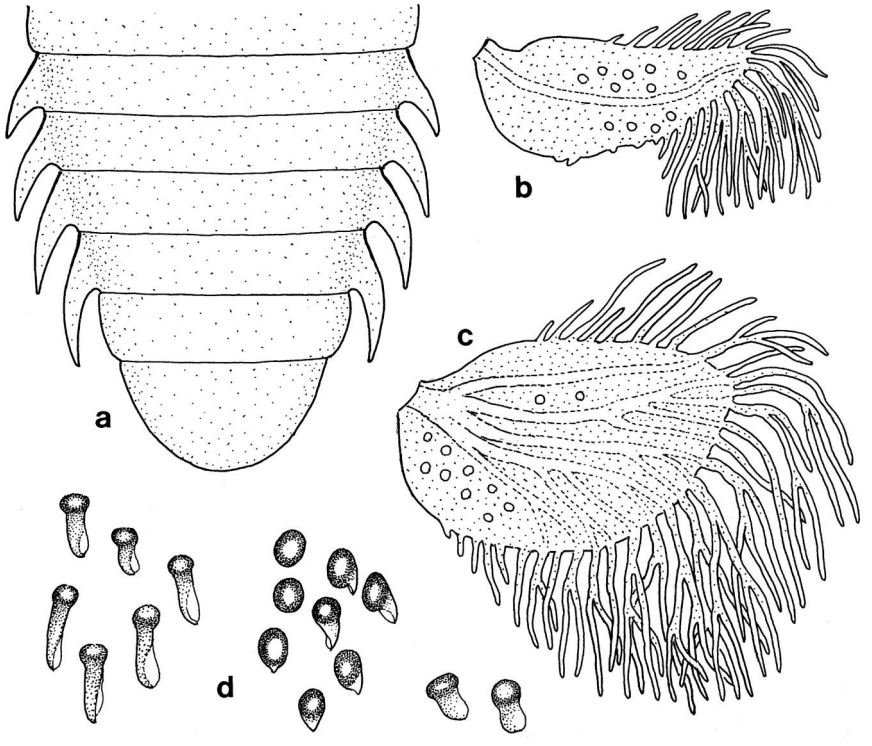

Figure 5. *Afrocercus guinensis* sp. n.; larva. (a) outline of the abdomen, sterna III-IX; (b) gill 6; (c) gill 4; (d) robust tubercles on dorsal surface of second gill (left), metanotum (middle), and forefemur (right).

Body short and broad, with head regularly oval, pronotum broadly rectangular and mesonotum a little broader than long (Figure 3). Length (immature) 2.8 mm.

Colouration of chitinous layers. Head, thorax and second gills evenly medium brown. Other parts a little lighter.

Epidermal pigmentation. Sparse on pronotum, second gills and abdominal terga.

Dorsal surface of body, legs and gills II densely covered with robust dark brown tubercles usually with short apical, laterally compressed spines (Figure 5d). Ocelli conspicuously flat. Basal segment of three-segmented labial palp of square shape, twice as broad as second segment (Figure 4b). Apical setae of glossae and paraglossae irregular, of unusual shape, with tongue-shaped projections (Figure 4c shows different forms). Claws without denticles, strongly bent. Tarsi articulated dorsally to the tibiae. Femora ventrally with clearly bordered oval field where thickness of the chitinous layer seems reduced.

Margins of gills 3 – 6 with branched filaments, filaments fewer on gill 6. The overlapping gill covers and the pattern of the filaments on the successive gills are a main diagnostic character to differentiate *Afrocercus* larvae from *Madecocercus* larvae.

For other details see the generic diagnosis (numbers 20 – 30).

Eggs

As in the generic diagnosis (18 and 19). If threads of equatorial band unrolled, ridges corresponding to circular fields visible; each ridge with a pair of long threads reaching about half to three quarters the circumference of the equator (Figure 14d, and e).

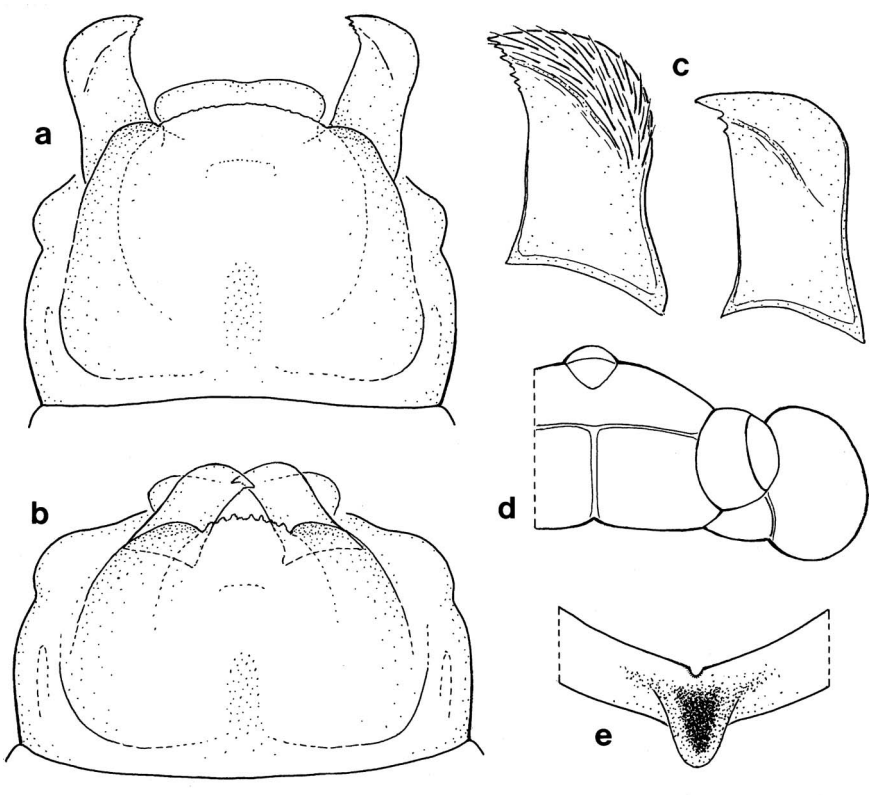

Figure 6. *Afrocercus sartorii* sp. n.; male a and b. genitalia; (b) with contracted forceps muscles; (c) forceps, different shapes; (d) head, right half; (e) median part of metanotum; with tongue-shaped process.

Etymology. The species name refers to its presently known distribution.

Afrocercus sartorii Malzacher sp. n.

Material

Holotype ♂ (micro-slide): Côte d'Ivoire, riv. Maraoué, 17.06.1976. - Paratypes: 1 ♂, 3 ♀: Côte d'Ivoire, riv. Maraoué, 17.06.1976.

Distribution. Côte d'Ivoire

Male imago

Body length 1.8 – 2.0 mm; wing length 1.9 mm; length of foreleg 1.3 mm. Ratio of forefemur: foretibia = 0.48 – 0.53; ratio of foretibia: foretarsus = 0.81 – 1.0; ratio of foreleg: hind leg = 2.03 – 2.11; ratio of first segment of the foretarsus : 2nd : 3rd : 4th : 5th = 1 : 4.0 – 4.2 : 2.5 – 2.6 : 2.0 – 2.3 : 1.8 – 1.9. Ratio of body length : length of cercus : length of terminal filum = 1 : 2.4 : 4.4.

Colouration of chitinous layers. Mesothorax yellowish brown; other parts yellowish white.

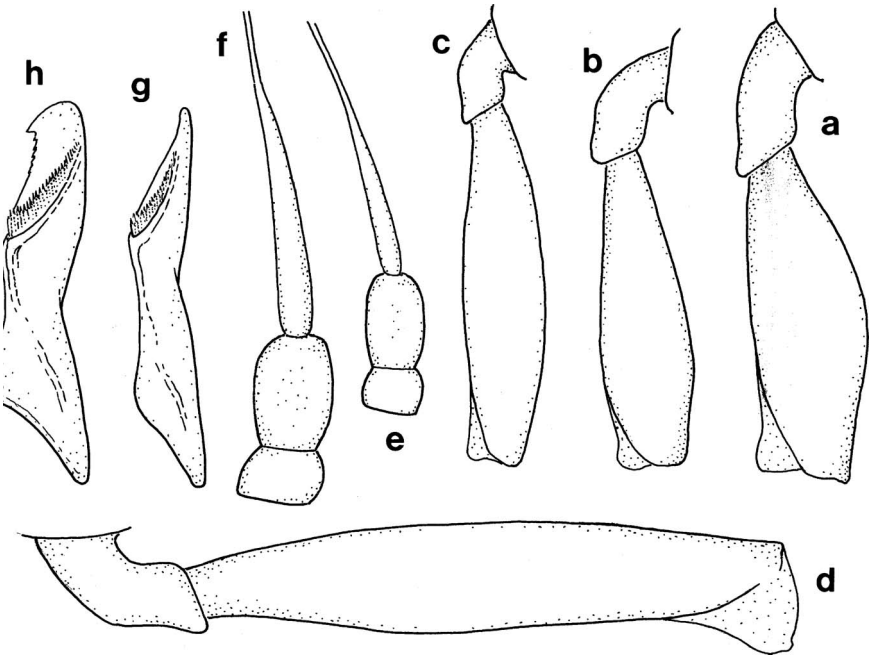

Figure 7. *Afrocercus guinensis* sp. n.; (a, e–h). (a) femur and trochanter of foreleg; (e) and (f) antennae: scape, pedicel and base of flagellum; (e) female; (f) male; (g) and (h) forceps; (g) lateral view; (h) paralateral view. Femur and trochanter of foreleg. (b–d). (b) *Afrocercus sartorii* sp. n.; (c) *Caenis gilliesi*; (d) *Tigrocercus contractus* sp. n.

Epidermal pigmentation. Generally weakly pigmented. A transverse band on venter of head. Margins of prothorax with blackish streaks. Median mesonotal suture edged with grey. Metanotum slightly pigmented, tongue-shaped process with a deep black mark (Figure 6e). Abdominal terga I–VII with broad transverse bands, most pronounced on terga I and II, with median interruptions and paratergal marks. Terga VIII–X pale.

Body short and broad. Antennal flagellum basally dilated; dilated part about one and a half times length of pedicel. Forefemur a little narrower than in *Afrocercus guinensis*, about 2.3 times length of elongated trochanter (Figure 7b). Prosternum, metanotum and lateral filaments as in generic diagnosis.

Genitalia as in Figure 6a, and b. Penis with short rounded lobes. Styliger nearly colourless and sparsely structured, sclerites hardly perceivable. Forceps as in Figure 3c with a ventral subapical oblique ridge separating apical part which is covered by strong trichomes (Figure 6c, left).

Female imago

Body length 2.5–2.8 mm; wing length 2.5–2.7 mm.

Colouration of chitinous layers as in males.

Epidermal pigmentation significantly stronger than in males. Pronotum extensively pigmented. Mesonotum with dark sutures, slightly pigmented also between them. Conspicuous black mark covering nearly totally tongue-shaped process of metanotum. Abdominal terga VIII–X with grey shading.

Larva. Unknown.

Eggs

As in generic diagnosis (numbers 18–19). Chorionic fields a little denser than in *A. guinensis* (Figure 14f).

Etymology. The species name was given in honour of Dr. Michel Sartori, Lausanne, who kindly made this material available to us.

Afrocercus inflatus Malzacher sp. n.

Material

Holotype ♂ SI. (micro-slide): Guinea, riv. Tomine (Rio Corubal), Telimélé, 27.01.1986.

Distribution. Guinea.

Male

Body length 2.3 mm; wing length 2.3–2.4 mm.

Colouration of chitinous layers. Mesothorax yellowish brown. Other parts yellowish white.

Epidermal pigmentation quite strong. Frons and vertex pale. Foretibia strongly pigmented. Margins of prothorax broadly blackish, with a median transverse streak. Mesonotal sutures strongly edged with grey. Further pigmentation on scutellum, prealar bridge tongue-shaped process of metanotum and anterior to hind coxae. Wing base, subcosta and radius greyish. Abdominal terga I–VII with broad transverse bands, most pronounced on tergum I, pigments more densely at hind margins. All paraterga and tergum VIII only with traces of pigments. Terga IX and X pale.

Body short and broad. Antennal flagellum basally dilated; dilated part about one and a half length of pedicel. Forefemur as in *Afrocercus guinensis*, about two and a half times the length of elongated trochanter. Prosternum, metanotum and lateral filaments as in generic diagnosis.

Genitalia as in Figure 2c. Penis lobes more voluminous than in other species. Anterior margin of styliger sclerite with deep rounded indentation. Forceps as in Figure 2d. Tip of forceps bent medially. Medial margin of forceps strongly rounded.

Female and larva. Unknown.

Etymology. The species name refers to the inflated apical part of the forceps.

Madecocercus Malzacher, 1995

Provonshaka McCafferty & Wang, 1995
Type species: *Madecocercus tauroides* Malzacher, 1995

Distribution. Madagascar.

With the discovery of a new species, the diagnosis of *Madecocercus* is revised as follows:

Differential diagnosis

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

Imago. (1) Proportions of pedicel and scape variable: length of pedicel 1.5 – 2.7 times length of the scape (♂). (2) [Antennal flagellum basally dilated (*M. bibulus*) or not dilated (*M. tauroides*)] (♂) (Figure 8d). (3) Coxae widely separated; prosternum broad, anterior posterior border rounded (♂ ♀). (4) Second segment of foretarsus strongly elongated, nearly as long as segments 3 – 5 together (♂). (5) Foreleg at least twice as long as hind leg, often clearly longer (♂). (6) Trochanter of foreleg elongated. (7) Distance from tip of the wing to cross vein R1 – R2 about 1.3 – 1.5 times the distance from cross vein R1-R2 to middle of costal brace (♂ ♀). (8) Metanotum flat, without transverse ridge; with short and broad posteromedian process (♂ ♀). (9) Abdomen with lateral filaments of medium length [on segments IV – VII in *M. bibulus* and V – VIII in *M. tauroides*] (♂ ♀). (10) Abdominal segment IX without posterolateral processes (♂ ♀) (Figure 8a). (11) Abdominal segment IX and styliger more or less of square shape (♂) (Figure 8a). (12) Lateral sclerite of styliger tape-shaped, not clearly broadened at base (♂) (Figure 8a). (13) Forceps muscles

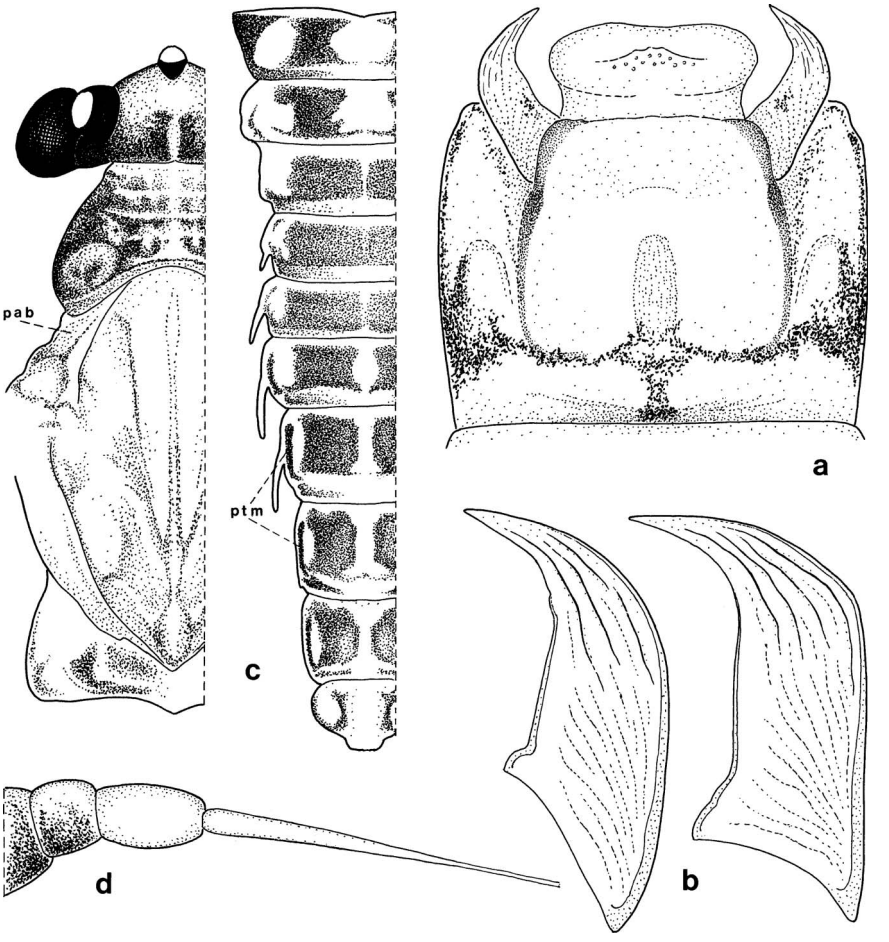

Figure 8. *Madecocercus bibulus* sp. n.; male. (a) genitalia: 1 = forceps, 2 = penis, 3 = styliger plate, 4 = styliger sclerite, 5 = apophyses of styliger sclerite, 6 = central sclerite, 7 = lateral sclerite, 8 = basolateral sclerite; (b) forceps; (c) pattern of epidermal pigmentation; left half of body: pab = prealar bridge, ptm = paratergal marks; (d) antenna: scape, pedicel and base of flagellum.

strongly developed forming a functional unit with lateral sclerites and forceps (♂). (14) Styliger sclerite of medium size, with paramedian apophyses of differing length (*M. tauroides*) or weakly sclerotised and more or less invisible (*M. bibulus*) (Figure 8a) (♂). (15) Forceps of medium length (variable), pointed, with ridges (♂) (Figure 8b). (16) Forceps articulated laterotherminally to lateral sclerites (♂) (Figure 8a). (17) Terminal filum about 1.2 times the length of cerci (♂).

Egg. (18) Eggs without epithemata, regularly scattered with barbed and apically hooked threads. (Figure 15b). (19) Chorion of eggs with longitudinal rows of circular or square fields; two threads leading in opposite directions from each of these fields (Figure 15b – d).

Larva. (20) Body short, broad and flattened. (21) Head without ocellar tubercles. (22) Labial palp three-segmented. (23) Maxilla with rudimentary palp (Figure 10a, and b) or palp lacking, cardo and stipes not fused to each other. (24) Margins of legs, second gills and abdomen fringed with long setae. (25) Femora short and broad, with posteriorly extended plates. (26) Second gills not completely overlapping medially. (27) Second gill ventrally with band of scale-shaped microtrichia (Figure 10c, and d). (28) Gills 3 – 6 with short or very short simple marginal filaments. (29) Posterolateral projections on abdominal segments II and V – VIII, not bent dorsally. (30) Dorsal surface densely covered with robust tubercles (Figure 11d, and e).

For characters (20), (21), (24), (25), (26) see Figure 1 in McCafferty and Wang (1995) and Elouard and Sartori (2001); (22), (23), (29) see Figures 2, 3, 9 and 10 in McCafferty and Wang (1995); (27), (28) see Figures 85A, C and D in Kluge (2004).

***Madecocercus bibulus* Malzacher sp. n.**

Material

Holotype ♂ (micro-slide): Madagascar, Rianila, Ambodifaha, riv. Rongaronga, 31.10.1994. - Paratypes: 8 ♂, 1 ♂ SI, 3 ♀: Madagascar, Rianila, Ambodyfaho, riv. Rongaronga, 31.10.1994. – Further material: 21 ♂, 1 ♀: Rianila, Andasibe, small rivers, 24.10. 1994. – 2 ♂, 33 ♂ SI, 1 ♀: Manampatrana, Mahafasa, 13.06. 1995. – 1 ♂, 3 ♂ SI, 2 ♀: Matitanan, Ankarimbelo, 20.06. 1995.

Distribution. Madagascar.

Male imago

Body length 3.1 – 4.4 mm; wing length 3.1 – 4.4 mm; length of foreleg 2.6 – 2.9 mm. Ratio of forefemur : foretibia = 0.36 – 0.40; ratio of foretibia : foretarsus = 1.24 – 1.45; ratio of foreleg : hind leg = 2.19 – 2.34; ratio of first segment of the foretarsus : 2nd : 3rd : 4th : 5th = 1 : 3.2 – 3.6 : 1.6 – 2.5 : 1.4 – 2.0 : 1.5 – 1.8. Ratio of body length : length of cercus : length of terminal filum = 1 : 3.1 : 4.0.

Colouration of chitinous layers: Mesothorax yellowish brown. Other parts yellowish white.

Epidermal pigmentation: Colouring pattern of dorsal surface as in Figure 8c. Dark brown pigmentation on pleura and coxae, especially at sutures and margins of coxal hollows, also on margins of femora. Femora, middle and hind tibiae with long thin dashes on outer surface, dashes darker apically, sometimes forming transverse bands. Foretibiae regularly and strongly pigmented. Abdominal sterna sometimes with basomedial marks that can be enlarged on IX as in Figure 8a.

Antennal flagellum basally dilated; dilated part up to two times the length of pedicel (Figure 8d). Forefemur a little narrower than in *Madecocercus tauroides*, ratio length : breadth = 4.2 (3.5 in *M. tauroides*). Abdomen with lateral filaments of medium length on segments IV – VII (Figure 8c).

Genitalia as in Figure 8a. Penis with short rounded lobes. Styliger nearly colourless except for brown lateral sclerites; styliger sclerite hardly perceivable; lateral sclerites narrow and tapering basally. Forceps as in Figure 8b, with 2 – 4 ridges running towards tip in apical half and with some less conspicuous ridges in basal part.

Note. The rather high variability of the forceps shape is shown in Figure 9 top. The forceps of *M. tauroides* (Figure 9 down) shows a similar variability. For other diagnostic characters of this species see Malzacher (1995, p. 2).

Female imago

Body length 4.4 – 5.5 mm; wing length 3.9 – 4.9 mm.

Colouration of chitinous layers and epidermal pigmentation as in males.

Eggs

As in generic diagnosis (18 and 19). Chorionic fields large and square-shaped with two transverse ridges connecting bases of threads. Surface of chorion with scattered small round knobs (Figure 15b – d).

Larva. Unknown.

Etymology. The ORSTOM team who had found this species preliminarily attributed it to an undescribed genus they called *Bibicercus* (this genus name however never had been

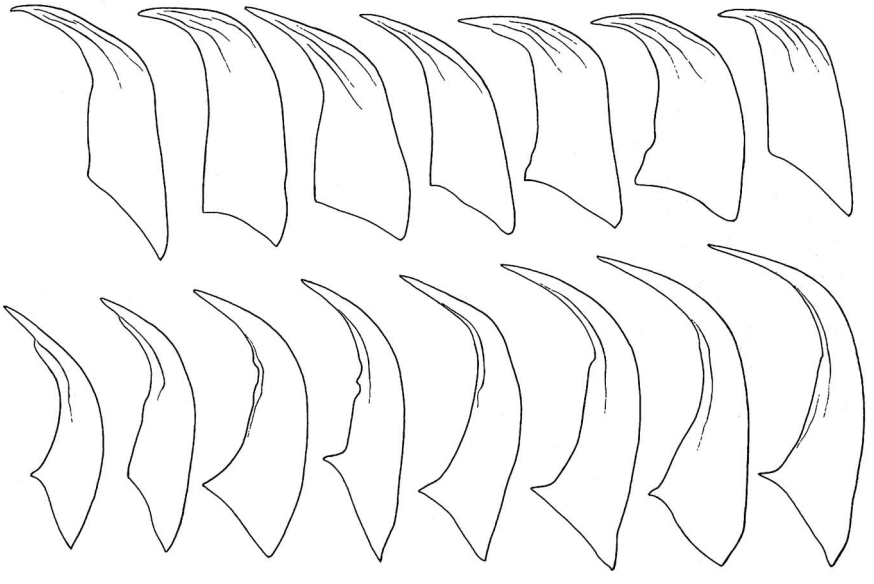

Figure 9. Variability of forceps shape. (top) *Madecocercus bibulus*. (down) *Madecocercus forcipatus*.

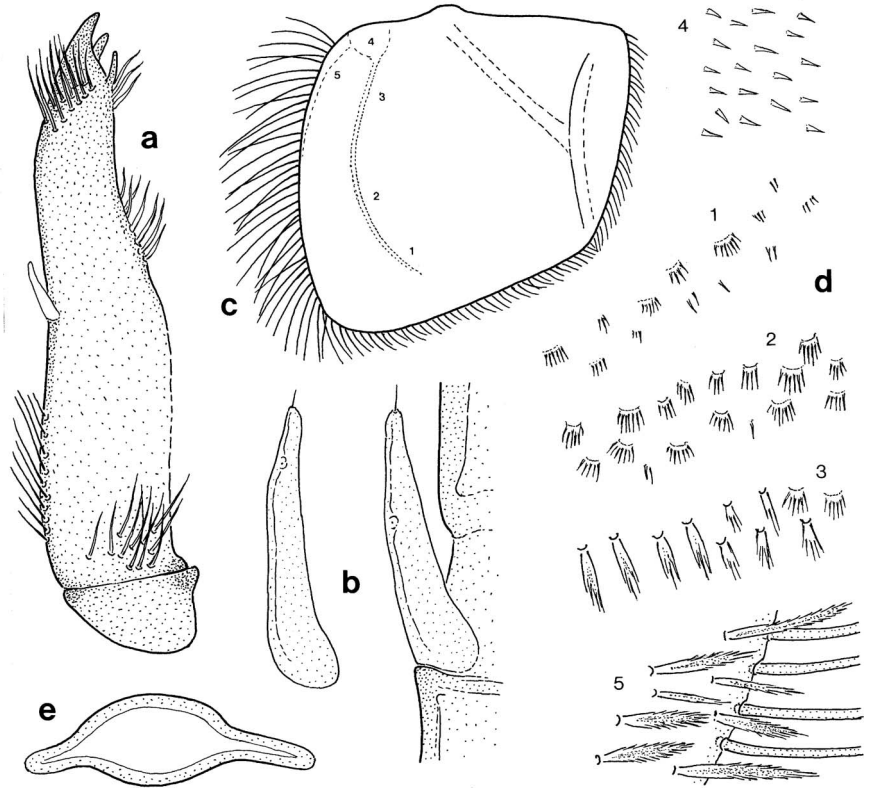

Figure 10. *Madecocercus tauroides*; larva. (a) maxilla with rudimentary palp; (b) palps of maxilla; (c) second gill; (d) microtrichia from different areas of ventral side of gill 2 (numbers in Figure 10c); (e) femur, transverse section.

published). After we realised that this species belongs to *Madecocercus*, we referred in its species name to the prefix of the preliminary genus name of the ORSTOM team.

Note. McCafferty and Wang (1995) described a new Malagasy genus and species *Provonshaka thomasorum* from larval material and placed it in the Tricorythidae. When Elouard and Sartori (2001) reared a female imago of *Madecocercus tauroides* from a *Provonshaka* nymph the genera were synonymised. Consequently the genus *Provonshaka* was removed from the Tricorythidae and is now regarded a junior synonym of *Madecocercus* (Elouard & Sartori 2001). For the present study we have re-investigated an incomplete paratype of *Provonshaka thomasorum* McCafferty and Wang (1995) and also some of the material from Elouard and Sartori (2001). Our own examination of the available material confirms the synonymy of both genera. Our comparison of the nymphal and subimaginal forcipes also confirms that the larval material of Eloard and Sartori (2001) is conspecific with *Madecocercus tauroides*.

However, the limited material available from McCafferty and Wang (1995) does not allow an unambiguous assignment of the specimen to either *M. tauroides* or *M. bibulus*. It may also be possible that *Provonshaka thomasorum* represents a third species of *Madecocercus*. A future re-examination of the larval holotype of *Provonshaka thomasorum* will have to clarify its

taxonomic status. So we give here only a new description of the larva of *Madecocercus tauroides* based on the material from Elouard and Sartori (2001).

Madecocercus tauroides Malzacher, 1995

Larva

Material

2 larvae, 1 nymphal exuvia: Madagascar, Antongombato, riv. Makis, 29.03.1994, 2.04.1994, 3.04.1994. – 1 nymphal exuvia: Namorona, riv. Namorona, Ambiabe, 22.04.1994. – 4 larvae: Betsibika, Plantario BLANC, 8.11. 1995. – 1 larva: Mananjari, riv. Vintanona, Andranomaitso, 12.11.1996. – 1 larva: Sakanila, riv. Lakato, 17.10.98.

Body length. Male: 4.5 mm, female: 6.5 mm. Body broad and flattened, with head oval, pronotum broadly rectangular and mesonotum a little broader than long, outline fringed with long setae (Elouard & Sartori 2001, Figure 1).

Colouration of chitinous layers. Yellowish brown.

Epidermal pigmentation. Dorsum shaded with grey. Pronotum and mesonotum with dark grey pattern of spots and lines, on pronotum sometimes like a mask. Femora with longitudinal pale dashes, here margins stronger grey.

Dorsal surface of body, legs and gills II densely covered with robust tubercles (microtrichia?) often hand-shaped with finger-like processes (variability see Figure 11e). In exposed areas (as hind margins and median ridges of abdominal terga VII – X, lateral margins of VIII and IX or margins of femora and gill) the tubercles are more or less elongated and cone-shaped (Figure 11d). Basal segment of three-segmented labial palp more or less circular,

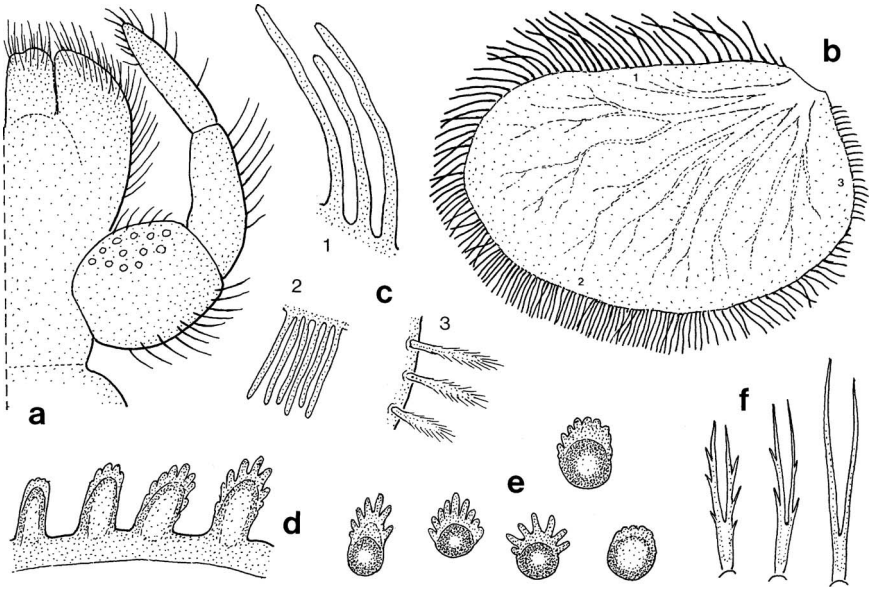

Figure 11. *Madecocercus tauroides*; larva. (a) labium, right half; (b) gill 4; (c) filaments from margins of gill 4 (numbers in Figure 11b); (d) cone-shaped tubercles from posterior margin of abdominal tergum VIII; (e) different shapes of tubercles from the body surface; (f) bifurcate setae from abdominal sterna.

twice as broad as second segment and three times as broad as third segment (Figure 11a). Claws without denticles, strongly bent. Tarsi articulated dorsally to the tibiae. Femora with flattened posteriorly extending plates, ventrally with clearly bordered oval field where thickness of the chitinous layer seems reduced.

Operculate gills widened laterally, articulation and y-shaped ridges located medially, median ridge close to the margin (Figure 10c). Median margins not or only basally overlapping, ventrally with a band of scale-shaped microtrichia, a small basal field with spines, and submarginal plumose setae (Figure 10c, and d). Margins of gills 3–6 with short simple filaments, basolateral with plumose setae or spines (Figure 11b, 3). In gill 3 filaments of anterior margin short, those of posterior margin longer. In gills 4 and 5 filaments of anterior margin longer than those of posterior margin (Figure 11b 1 and 2). Gill 6 forms an elongated lamella three times longer than broad, with short filaments only in its apical part. Abdominal segment II clearly broader than segments III and IV, with very short and broad posteriomedian process, segments V–VIII with lateral spines. Terga VII–IX with median ridges covered by large cone-shaped tubercles like in Figure 11d. Abdominal sterna densely covered with long deeply bifurcated setae (Figure 11f).

For other details see the generic diagnosis.

Key to the subfamilies of Caenidae and to the genera and species of Madecocercinae Imagines

1. Prosternum narrow, forming a triangle or trapezoid with sclerotised margins. Coxae contiguous. ..... Caeninae
– Prosternum broad. Coxae widely separated (Figure 1e)..... **2**
2. Forceps grooved. Eggs with longitudinal grooves and polar caps .... Brachycercinae s. str.
– Forceps with ridges (Figures 1d, 2b, 8b, 9). Eggs without longitudinal grooves and polar caps. Chorion with longitudinal rows of scales, circular or square fields, often with filaments (Figures 14a–f and 15b–d) ..... Madecocercinae **3**
3. Abdominal-segments IV–IX with lateral filaments, very long on V–VIII (Figure 1g). Foreleg of the male 1.5–1.8 times length of hind leg. Segments of the male foretarsus subequal in length. Sternum IX of male and styliger clearly broader than long (Figure 1a). Forceps long and sickle shaped with a long ridge (Figure 1d), articulated laterally to the lateral sclerites (Figure 1a–c). Eggs fir cone-shaped, without threads (Figure 14a–c) ..... ***Tigrocercus contractus***
– At most 4 abdominal segments with lateral filaments. Foreleg at least twice as long as the hind leg. Second segment of the male foretarsus nearly as long as the segments 3–5 together, first segment very short. Abdominal segment IX without filaments or posterolateral spines. Length of sternum IX and styliger about equal to width (Figures 2a, and c, 6a, and b, 8a). Forceps articulated laterotherminally with the lateral sclerites (Figures 2a, and c, 6a, and b, 8a). Eggs with threads (Figures 14d–f and 15b–d)..... **4**
4. Small species; ♂ body length 1.8–2.5 mm, ♀ 2.5-3.0 mm; ♂ wing length 1.9–2.4 mm, ♀ 2.5–3.0 mm. Abdomen with short or very short lateral filaments on the segments IV-VII. Forceps short, apically rounded or inwardly curved, with blunt point (Figures 2b, and d, 6c). Eggs with a dense belt of long, smooth and apically hooked threads around the equator; the remaining surface with longitudinal rows of more or less elevated circular or oval fields, each with two short threads (Figure 14d–f) ..... *Afrocercus* **5**

– ♂ body length more than 3.0 mm, ♀ more than 4.5 mm; ♂ wing length more than 3.0 mm, ♀ more than 4.0 mm. Abdominal filaments of medium length or longer (Figure 8c). Forceps with a long pointed tip (Figure 9). Eggs with long barbed threads regularly covering the surface (Figure 15b–d) ..... *Madecocercus* **8**

5. Forceps with oblique denticulated lamella in the apical third (Figures 2b and 12a)..... **6**
– Forceps without lamella **7**

6. Forceps tapering to the tip; lateral margin regularly curved. Apophyses of styliger sclerite blurred or invisible (Malzacher 1987, Figures 1, 3a) ..... ***Afrocercus forcipatus***
– Forceps narrow medially; lateral margin more or less s-shaped (Figure 2b). Apophyses of styliger sclerite short and broad, brownish coloured (Figure 2a) ..... ***Afrocercus guinensis***

7. Sides of forceps parallel (Figure 6c). Genitalia weakly sclerotised; sclerites hardly visible (Figure 6a, and b)..... ***Afrocercus sartorii***
– Forceps strongly dilated apically (Figure 2d). Fore margin of styliger sclerite with indentation between the short apophyses (Figure 2c) ..... ***Afrocercus inflatus***

8. Abdominal segments V–VIII with lateral filaments. Base of antennal flagellum not dilated. Forceps sickle-shaped, more or less regularly tapering to the tip (Figure 9, bottom row). Lateral sclerite broad. Chorion-fields small and circular (see Elouard & Sartori 2001, Figures 2 and 3). ..... ***Madecocercus tauroides***
– Abdominal segments IV–VII with lateral filaments (Figure 8c). Base of antennal flagellum dilated (Figure 8d). Basal part of forceps with more or less parallel sides (Figure 9, top). Lateral sclerite narrow (Figure 8a). Chorion-fields large and square (Figure 15c, and d). ..... ***Madecocercus bibulus***

Key to the subfamilies of Caenidae and to the genera of Madecocercinae Larvae

1. Body flattened. Legs short with femora about three times as broad as tibiae. Maxillary palps rudimentary or lacking (Figures 4a, 10a, and b) ..... Madecocercinae **3**
– Body more or less cylindrical. Femora not conspicuously broadened. Maxillary palps well developed **2**

2. Head with ocellar tubercles. Legs long and narrow (spider's legs), all segments more or less of the same breadth. Lateral spines of abdomen bent dorsally, forming a "gill basket". Maxillary and labial palps two-segmented..... Brachycercinae
– Head without ocellar tubercles. Femora clearly broader than tibiae. Lateral spines of abdomen not bent dorsally. Labial palps three-segmented ..... Caeninae

3. Femora (at least fore- and middle femora) anteriorly and posteriorly strongly broadened forming extended plates (Figure 10e). Posterolateral abdominal spines on segments V–IX. Abdominal segment II clearly broader than segments III and IV. Operculate gills widened laterally from the articulation (Figures 10c and 11), posteromedially not or only basally overlapping, ventrally with a band of scale-shaped microtrichia (Figure 10c, and d). Gills 3–6 only with short simple filaments ..... *Madecocercus*
– Femora without extended plates (Figure 3). Posterolateral abdominal spines on segments IV–VII (Figure 5a). Abdominal segments III and IV nearly as broad as segment II. Operculate gills regularly shaped (like in *Caenis*), median margins entirely overlapping (Figure 3), ventrally with a lateral field of small spine-shaped microtrichia (Figure 4d, and e). Gills 3–6 with long branched filaments (Figure 5b, and c) ..... *Afrocercus*

Discussion

The higher phylogeny of the Caenidae

Malzacher (1987, 1997) suggested the subdivision of the family Caenidae into two monophyletic subfamilies Caeninae and Brachycercinae. The Brachycercinae then included the genera *Brachycercus* s.l, Kluge, 1991 (which is equivalent to *Brachycercus* and *Cercobrachys* Soldan 1986), *Insulibrachys, Afrocercus,* and *Madecocercus.* McCafferty and Wang (2000) excluded *Madecocercus* and (provisionally) *Afrocercus* from the Brachycercinae and placed them in a new subfamily Madecocercinae as adelphotaxon of the Brachycercinae.

Kluge (2004) postulated a sistergroup relationship between Brachycercinae and remaining Caenidae. The latter he split into *Madecocercus* + Caeninae. Kluge listed *Afrocercus* under Caenidae inc. sed., leaving the monophyly of the Madecocercinae as unresolved. For an overview of the hitherto proposed phylogenies with the proposed apomorphic characters (see Figure 12).

Our view of the relationships of the Caenidae and the distribution of characters is shown in Figure 13. The characters used are discussed as follows:

(1) *Prosternum with ridges forming a triangle or trapezoid, coxae contiguous.* This synapomorphic character supports the monophyly of the Caeninae s.l. (see also Malzacher 1997).

(2) *Metanotum with transverse ridge* is a further character that supports the synapomorphy of the Caeninae (see also Figure 6 in Malzacher 1987). The specific shape of this transversal ridge can be characteristic for species or species-groups. In Brachycercinae and Madecocercinae the metanotum is flat with a posteriorly more or less extended lamella. In some Caeninae similar lamellae can be found in addition to the transversal ridge (e.g. *Tasmanocoenis tillyardi*). In *Caenis robusta* and *Caenis elouardi* the metanotal ridge is reduced.

(3) *Row of scale-shaped microtrichia on the ventral side of the gill cover.* The presence of this character has been regarded as another synapomorphy of the Caeninae for a long time (Malzacher 1997). With the better knowledge of the larva of *Madecocercus tauroides* (Elouard & Sartori 2001) it became obvious that the latter species also has such a row of microtrichia on the ventral side of its gill cover (Kluge 2004). However, the presence of this row of microtrichia in *Madecocercus* was not confirmed by McCafferty and Wang (2000) who yet regard this character as an synapomorphy of the Caeninae. On the other hand, Kluge (2004) evaluates the presence of such a row of microtrichia as a synapomorphic character of *Madecocercus* + Caeninae (Figure 12b).

Our own investigation of the respective character reveals that different evolutionary stages of these structures occur in all subfamilies. This parallel development leads from evenly distributed small spines to clusters of spines and finally to scale-like microtrichia consisting of a greater number of spines (up to 30) which are totally fused in their basal part. The fused part can be represented by a narrow basal band only, but can even extend up to nearly two thirds of the entire length of scales. The different stages of this development can be seen most distinctively in the Madecocercinae: in *Afrocercus* there is a broad sublateral field of small spines (Figure 4d) evenly distributed in its lateral part, but forming clusters towards its median border. At its medial border even early stages of scale-shaped microtrichia can be observed (Figure 4e). In its apomorphic condition (as seen in *Madecocercus*, Figure 10c), all microtrichia are condensed in a narrow band whose position corresponds to the medial border of the broad field of spines in *Afrocercus*. In *Madecocercus tauroides*, there are different shapes of microtrichia present (Figure 10c, and d) in different areas of the narrow band: a basal field of evenly distributed spines (Figure 10d, 4), scale-shaped microtrichia of different shapes in the proximal and median parts of the row

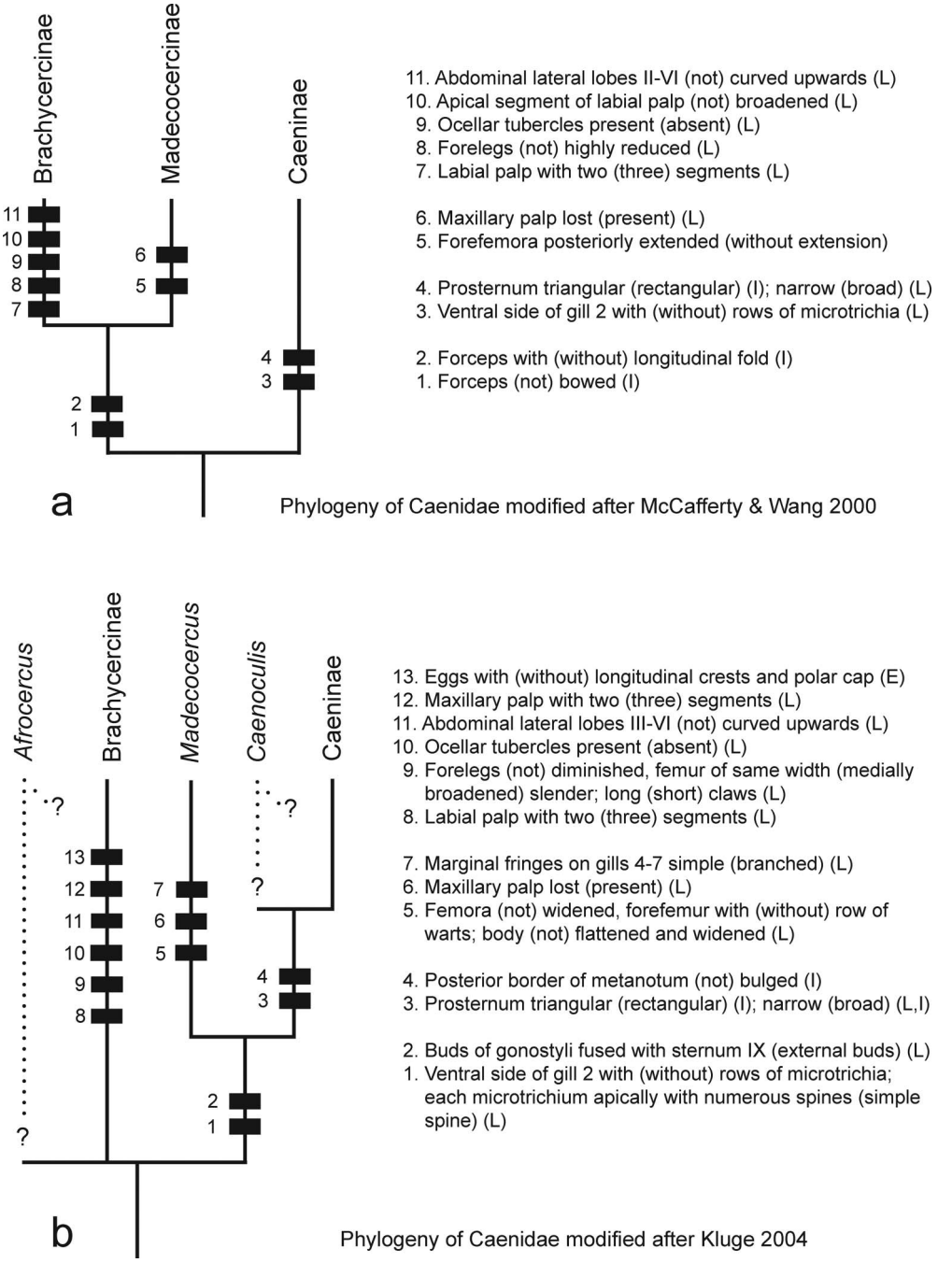

Figure 12. Phylogeny of Caenidae. (a) Modified after McCafferty & Wang 2000; (b) Modified after Kluge 2004.

(Figure 10d, 2 and 3), and even transitional stages to elongated plumose setae (Figure 10d, 3 and 5). The distal part of the band finally shows different scale-shaped microtrichia (Figure 10d, 1) like the ones in *Afrocercus*.

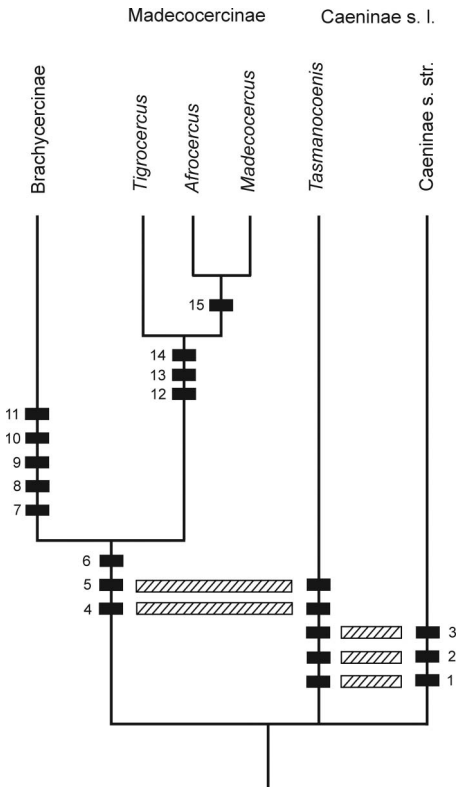

Figure 13. Distribution of characters within the subfamilies of Caenidae based on the present study. For explanation see text.

In the Brachycercinae there are sublateral bands of spines present (Kluge 2004), sometimes with basal fusions of two or three spines (e.g. in *Brachycercus gilliesi* and *B. pini*, Malzacher, unpublished). In other species of Brachycercinae a line of few small and inconspicuous spines extends close to the lateral margin (Kluge 2004).

In the Caeninae nearly all known larvae have rows of scale-shaped microtrichia. Unlike in *Madecocercus*, these rows are very regular, sometimes forming a band of compact transverse rows of 2 – 8 microtrichia (see Table 18 in Malzacher 1984). Hence we assume the presence of such a band as possible autapomorphic character of the Caeninae s.l. The presence of a sublateral broad field of microtrichia like in *Afrocercus* occurs only in *Clypeocaenis oligosetosa*. The most parsimonious explanation of this character state is a reversal of this character in *C. oligosetosa*.

(4) *Forcipes with longitudinal folds.* McCafferty and Wang 2000 did not differentiate between the grooved forcipes of the Brachycercinae and the forcipes with ridges occurring in all Madecocercinae. Kluge (2004) regards the presence of grooved forcipes as a plesiomorphic groundplan character of Caenidae. In our view the presence of grooved or ridged forcipes is clearly an apomorphy as in the outgroup Neoephemeridae there are no grooved or ridged forcipes present. The Caeninae s. str. also have a smooth forceps without grooves or ridges. In the Australian genera of Caeninae various character states are present: forcipes with a smooth surface in *Tasmanocoenis tonnoiri* (Suter 1984) and *Wundacaenis dostini* (Suter 1993), ridged forcipes in *Tasmanocoenis arcuata* and *Tasmanocoenis jillongi* (Alba-Tercedor & Suter 1990),

and grooved ones in *Tasmanocoenis tillyardi*. This species even shows an intraspecific variability of this character. There are specimens with grooved forcipes (type specimen, Malzacher 1987, Figure 3b) and other specimens that have forcipes with both grooves and ridges (Alba-Tercedor & Suter 1990, Figure 2). In all known Brachycercinae there are grooved forcipes present, whereas in the Madecocercinae only ridged forcipes occur. It is difficult to assess the polarity of this character, but in our view grooved forcipes could be interpreted as a further developmental stage of ridged forcipes. A medially extended ridge (as present in *Afrocercus*) could lead to a grooved forceps. A functional interpretation of these structures cannot be undertaken at present, but a putative function in sperm transfer or penetration should be taken into account.

The presence of ridged forcipes could be regarded as a synapomorphic groundplan character of Brachycercinae, Madecocercinae, and *Tasmanocoenis*. It is however also possible that grooved forcipes could be a parallel development in the Brachycercinae + Madecocercinae on the one hand and in the Australian Caeninae on the other hand.

(5) *Modified genitalia.* The genitalia of the Brachycercinae + Madecocercinae on the one hand and the Australian Caeninae on the other hand show a complex functional unit consisting of (a) the forceps, (b) a strong forceps muscle inserting at the inner side of the forceps base, and (c) a well developed lateral sclerite with strongly sclerotised articulation with the forceps. This allows a very strong contraction of the forceps (compare Figures 1a, b and 6a, b) not to be observed in any other mayflies. In the remaining mayflies the forceps muscle lies within the coxopodite, inserting at the whole anterior margin of the first segment of forceps (compare figures in Grandi 1960b). Although a long and strong forceps muscles as such could be interpreted as a plesiomorphic character because of its presence in the outgroup Neoephemeridae, the specific arrangement of all parts correlated with a new function has to be regarded as apomorphic within the Caenidae. It could be possible that the modified genitalia represent a synapomorphic character that unites the Brachycercinae, Madecocecinae, and the Australian genera *Tasmanocoenis* and *Wundacaenis*. The imagines of *Wundacaenis* are however little known, so we confine our conclusions largely to *Tasmanocoenis*.

(6) *Number of maxillary palp segments reduced.* In the maxillary palps of Brachycercinae + Madecocercinae a reduction in number of segments has taken place. We regard this character as apomorphic for this taxon, although it is also present in the Caeninae genera *Clypeocaenis* and *Barnardara* and in some other families (Kluge 2004). While the Brachycercinae have retained two segments, the reduction of maxillary palp segments in the Madecocercinae even went further (see 12).

(7) *Larval head with ocellar tubercles.* The specific shape and height of the ocellar tubercles can vary considerably. This character is generally regarded as apomorphic character for the Brachycercinae. Soldán (1986) mentions that the problematic genus *Caenoculis* (see below) also has small ocellar tubercles.

(8) *Lateral spines of the larval abdomen bent dorsally forming a "gill basket".* This is a characteristic feature only present in the Brachycercinae. A parallel development of this character can be observed in *Machadorythus* (McCafferty & Wang 2000).

(9) *Labial palps two-segmented.* While the reduction of the labial palp can be frequently observed in mayflies, within the Caenidae it can be assessed as an apomorphic character of the Brachycercinae.

(10) *Larval legs narrow and slender, claws elongated* (spider's legs), length of foreleg diminished. This apomorphic character of the Brachycercinae is obviously correlated to the larval habitats, namely sandy or muddy substrate. This character also occurs in the Machadorythidae.

(11) *Chorion of egg with longitudinal grooves.* The eggs of Brachycercinae have a specific surface unique within the Caenidae. The longitudinal grooves represent gaps between chorionic thickenings (Malzacher 1982).

(12) *Maxillary palp rudimentary or lacking.* McCafferty and Wang (1995) described the maxillary palp lacking in the maxilla of *Provonshaka thomasorum*. McCafferty and Wang (2000) regard a lost maxillary palp as autapomorphy of the Madecocercinae. However, when we had a look at the larva of *Madecocercus tauroides*, we noted a rudimentary maxillary palp in this species (Figure 10a, and b). On the other hand, in the larva of *Afrocercus guinensis* there is definitely no maxillary palp present (Figure 4a). As a consequence, a rudimentary maxillary palp has to be assumed in the groundplan of the Madecocercinae. A similar reduction of the maxillary palp can be observed in the Ephemerellinae and other Pannota (McCafferty & Wang 2000).

(13) *Femora widened, at least three times wider than tibiae, margins densely fringed with long setae.* This character can be assessed as synapomorphic character of the Madecocercinae. While in *Afrocercus* the femora are simply widened, the femora of *Madecocercus* are additionally flattened to form posterolateral plates (Figure 10e). The outer margins of these plates are each equipped with a row of long setae. These structures form – together with the larval body in general – a concave surface that enables the larva to adhere to the ground. A similar adhesive function is developed in certain flattened Heptageniidae, e.g. in *Rhithrogena*.

(14) *Chorion of eggs with longitudinal rows of structures* (scales, circular or oval fields with elevated margins, rectangular fields with ridges). This is a new synapomorphy of the Madecocercinae as their eggs were previously unknown (see Figures 14a – f and 15b – d).

(15) *Chorionic fields each with two lateral filaments* running in opposite direction along the surface of the egg (see Figures 14d – f and 15b – d). This character is a synapomorphy of *Afrocercus* + *Madecocercus*.

As eggs, larvae and females of *Afrocercus* were unknown until now, Kluge (2004) could not confirm the close relationship between the genera of Madecocercinae. In his phylogeny of the Caenidae he assumed a sistergroup relationship between *Madecocercus* and Caeninae s.l. based on two putative synapomorphies, namely the fusion of gonostyli buds with sternum IX in the last larval instars, and the development of rows of microtrichia on the ventral side of gill 2. The discovery of eggs, larvae and females of *Afrocercus*, together with the discovery of *Tigrocercus*, revealed new synapomorphies for the Madecocercinae (see 6 – 8 above). Additionally, the gill morphology of *Afrocercus* suggests that the development of microtrichia rows is a parallelism that evolved twice within the Madecocercinae and Caeninae (see 3 above).

In the male larvae of Brachycercinae the buds of the forcipes bulge the outline of the abdominal sternum IX. Kluge regards this as a plesiomorphic character with reference to the bulged forceps buds in the Neoephemeridae. Kluge (2004) considered the loss of those bulges as synapomorphic for Caeninae and *Madecocercus*. Our own observations do not confirm this character distribution: in most of the Caeninae the forceps buds are not completely fused with sternum IX but only diminished. In most of the *Caenis* species gradual bulges can be seen and there is definitely a sexual dimorphism in the shape of sternum IX visible (see Malzacher 1992, Figures 5a – d, 6a – d and g). It may be well possible that the extent of bulging is correlated with the shape of the forcipes and of sternum IX: we observed a voluminous bulging only in species with straight forcipes. In these species the apices of the forcipes are not bent inwards but reach the margin of sternum IX at an acute angle.

McCafferty and Wang (2001) assumed bowed forcipes as synapomorphic for the Brachycercinae + Madecocercinae. However, bowed and straight forcipes can be observed

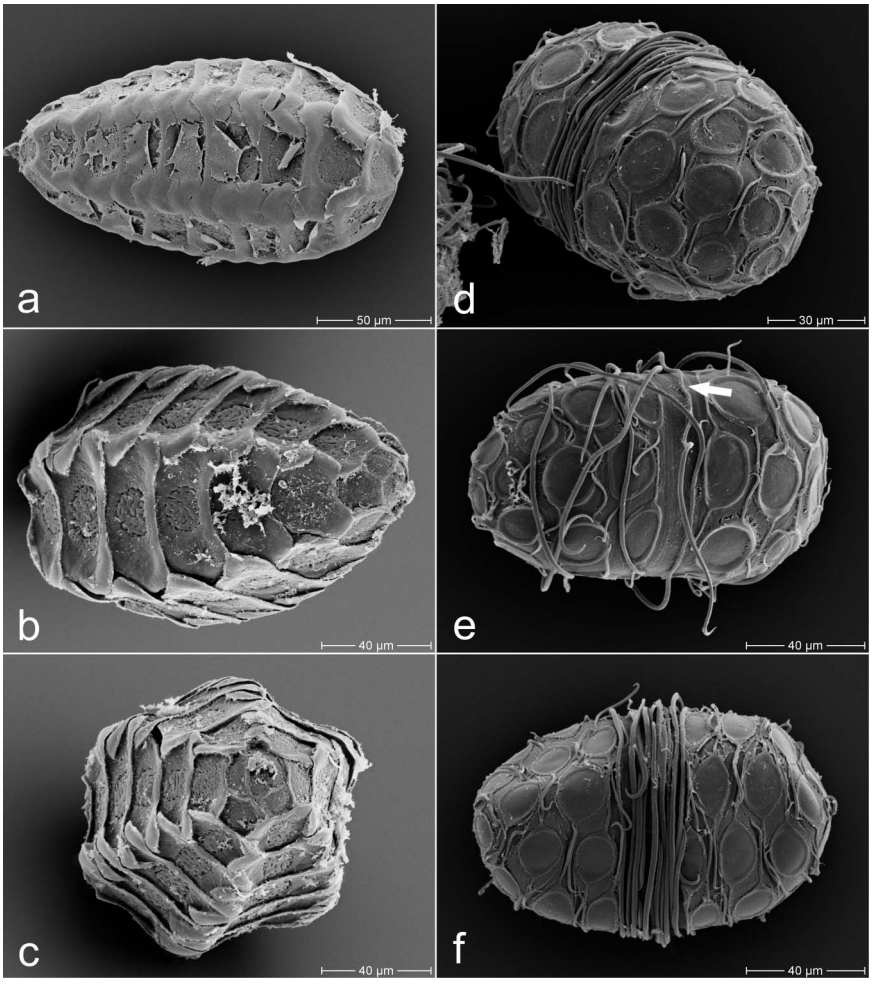

Figure 14. SEM photos of eggs. (a – c) *Tigrocercus contractus* gen n. sp. n. (a) lateral view showing thin membrane that extensively covers the chorionic structures; (b) latero-polar view, chorionic structures visible; (c) polar view; (d) and (e) *Afrocercus guinensis* sp. n. (d) latero-polar view; (e) lateral view, with unrolled equatorial threads; arrow: ridges from which the threads lead (see text); (f) *Afrocercus sartorii* sp. n., lateral view.

in all subfamilies of Caenidae. In the Madecocercinae, *Afrocercus* has short and more or less straight forcipes. In *Tigrocercus contractus* and in *Madecocercus tauroides* the forcipes are strongly bowed, and in *Madecocercus bibulus* even transitions between bowed and straight forcipes can be observed (compare Figures 1d, 2b, and d, 6c, 8b, 9).

The evolution of the genitalia within the Caenidae

The tendency to an extensive reduction of length and segment numbers of the forceps can be observed in a few families of Ephemeroptera, e.g. Polymitarcyidae, Euthyplociidae, and Neoephemeridae, the latter with different stages of reduction in some species of *Potamanthellus* (Bae & McCafferty 1998, Figures 24, 22, 23). In the Caenidae this development is most advanced leading to genitalia with a one segmented, short and

apically rounded forceps that lost its former function. This development is also correlated with reduced forceps muscles. However, within the Caenidae an enormous number of different forcipes with new shapes, arrangements and functions have been realised (Malzacher 1991). A unique character of the highly autapomorphic genitalia of Caenidae is represented by a styliger that shifted anteriorly and fused with sternum IX (Malzacher 1997). Additionally, new sclerotised structures such as the lateral sclerite and the basolateral sclerite are developed. The above mentioned type of genitalia, especially the short and rounded forceps, is similar to the genitalia of the *Caenis elouardi*- and the *Caenis reissi*-group. These closely related groups are distributed in West Africa and the eastern Amazon region indicating that they have been separated by continental shifting (Malzacher 1991).

There is the question if the reduced type of genitalia has to be assumed at the base of the Caenidae itself or rather at the base of the subfamily Caeninae. Regarding the outgroup Neoephemeridae, that is equipped with a long forceps muscle and with a multisegmented forceps, a long forceps muscle could also be assumed at the base of the Caenidae. Therefore the long and strong forceps muscles of the Brachycercinae could be interpreted as a plesiomorphic character. Consequently the strong reduction of the forceps would be a derived character evolved within the Caeninae.

However, as explained above, the forceps muscles in the Brachycercinae +Madecocercinae have got a completely new function and a different insertion at the forceps base (see character 5), The totally new structure leads to the assumption that the reduction of the forceps and its muscles already occurred at the very base of the Caenidae. However, this implies the reactivation of a genital system with the above mentioned functional unit.

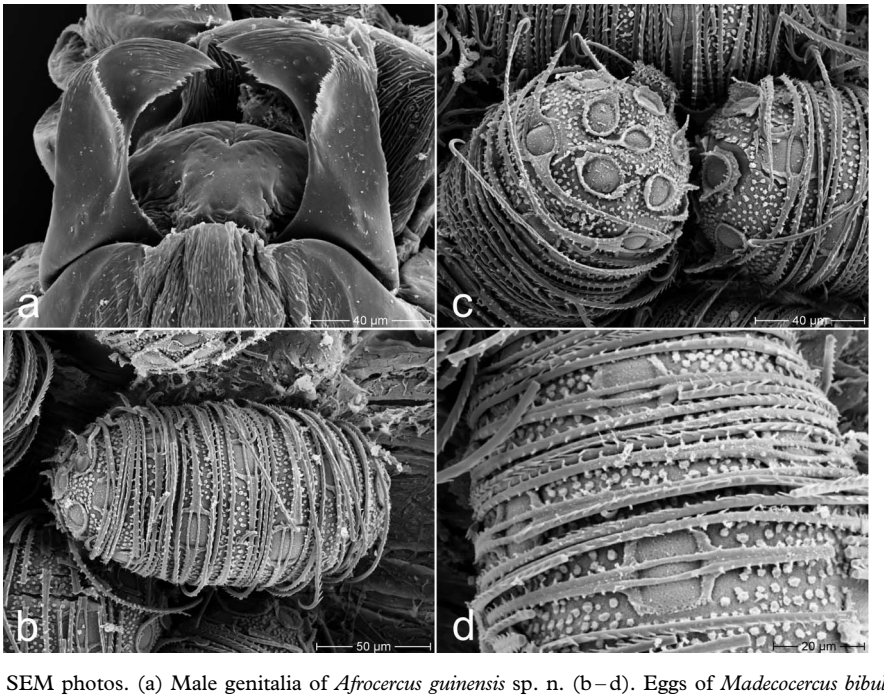

Figure 15. SEM photos. (a) Male genitalia of *Afrocercus guinensis* sp. n. (b–d). Eggs of *Madecocercus bibulus* sp. n.; (b) lateral view; (c) polar view; (d) detail of threads and square fields and knobbed structure of chorion surface.

Remarks on taxonomy and phylogenetic relationships within the Madecocercinae

Apart from the very distinctive characters of the egg structure the adults of the three genera differ mainly in size, shape of the body, proportions of the male forelegs and the male genitalia. It is difficult to assess the polarisation of these characters. In *Tigrocercus*, which seems to be most plesiomorphic, segments 2–5 of the male foretarsus have nearly the same length. This is rather similar to the foretarsi in most of the Caeninae with forelegs of medium length as well as in the outgroup Neoephemeridae. So the relative length of the tarsomeres to each other could be plesiomorphic in this case. This character state is also widely distributed in other Ephemeroptera, e.g. in *Ephemerella*, *Ephemera*, *Choroterpes*, *Thraulus,* and *Rhithrogena* (comparative figures e.g. in Grandi 1960a and in Ulmer 1939). All other Brachycercinae and Madecocercinae have got very thin and elongated male foretarsi. They are made up of a very short first segment, a very long second segment, and also segments 3–5 are elongated but with decreasing length. This configuration is clearly a synapomorphic character. Only in one species, *Brachycercus japonicus*, all segments are of the same length though slender and elongated (Tojo 2001, Figure 12). All other genera with identical proportion of the tarsus, e.g. *Campsoneuriella*, *Afronurus* (Ulmer 1939), *Epeorus* and *Siphlonurus*, are only distantly related to the Caenidae.

Afrocercus and *Madecocercus* seem to be sister groups. In contrary to the large overlapping chorionic scales in *Tigrocercus,* eggs with rows of circular or oval fields and long threads in *Afrocercus* + *Madecocercus* can be interpreted as a synapomorphy. This particular type of threads (Figures 14d–f and 15b–d) cannot be found elsewhere within the Pannota.

Besides the shape of forceps and some larval characters (compare the genus-diagnoses) a terminal filum that reaches at least one and a half the length of the cerci is autapomorphic for *Afrocercus*. In all other Brachycercinae + Madecocercinae, terminal filum and cerci are more or less equal in length.

There are two rather conspicuous differences between the two known species of *Madecocercus* that at first gave grounds to presume two different genera: the base of the antennal flagellum is dilated in *M. bibulus* but not dilated in *M. tauroides*. Lateral filaments occur on the abdominal segments IV–VII in *M. bibulus,* but on V–VIII in *M. tauroides*. However, distinctive characters like these often occur within the same genus. In *Caenis* and *Brasilocaenis,* related species sometimes show different shapes of the base of the antennal bristle. These structures may be sense organs with a specific function during mating flight (Malzacher 1986, Figure 12). The genus *Brachycercus* includes a number of different arrangements of lateral filaments. In *B. harrisella* lateral filaments are present in the abdominal segments III-VIII, in *B. japonicus* III–VII (Tojo 2001), in *B. capnicus* III–VI (Zhou et al. 2004), in *B. etowah* and *B. minutus* IV–VI (own observation). But there are also some larval characters that can be interpreted as synapomorphies of *Madecocercus*: gill II irregular with enlarged lateral part; gills III–VI with reduced simple filaments; femora with posteriorly extended plates. Therefore there is no reason to split *Madecocercus* into two genera. There is also no sound argument to split *M. tauroides* into several species. The variable shape and length of the forcipes present in different populations of *M. tauroides* obviously reflect continuous transitions (Figure 9 down) and do not justify the establishment of different species.

Biogeography of the Brachycercinae and Madecocercinae

The separation of Brachycercinae and Madecocercinae (McCafferty & Wang 2000) is also supported by their geographical distribution: the Brachycercinae show a holarctic, neotropic

and orientalic distribution, whereas the genera of the Madecocercinae occur vicarious in the Ethiopic and Malagasy regions.

The problematic genera Caenoculis and Tigrocercus

There are some imaginal records of an undescribed species from Thailand (coll. J. Peters). Its genitalia and eggs show similarities to the ones of *Tigrocercus*. Thus there is a legitimate reason to assume that this genus could be also distributed in the eastern Oriental region. Peters (in litt.) presumes that the undescribed specimens could be the unknown imago of the enigmatic Caenid genus *Caenoculis*, whose position in the phylogenetic system of Caenidae is unresolved. At present it is impossible to clarify this issue without having reared imagines of *Caenoculis*. Furthermore the larva of *Tigrocercus* is yet unknown. Therefore the assignment of this genus to the Madecocercinae remains preliminary, although shape of forceps and egg structure point to an inclusion of *Tigrocercus* within the Madecocercinae.

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