Aquatic Insects
Vol. 31, No. 4, December 2009, 279–292

Taylor & Francis
Taylor & Francis Group

Two new genera of Caenidae (Insecta: Ephemeroptera) from Guinea, West Africa

Peter Malzacher*

Ludwigsburg, Germany

(*Received 4 February 2009; final version received 28 April 2009*)

Larvae of two new genera of Caenidae are described from the River Niandan, Guinea. Their position in the phylogenetic system of Caenidae is discussed. *Niandancus alienus* gen. n., sp. n. is the first known representative of the Brachycercinae in the Ethiopic region. *Aenigmocaenis morgensterni* gen. n., sp. n. could represent the sister group to all other Caenidae, as the most important larval synapomorphy of the family, a band or row of microtrichia on the ventral side of the operculate gill, is lacking.

Keywords: *Aenigmocaenis morgensterni* gen. n., sp. n; *Niandancus alienus* gen. n., sp. n; larva; Brachycercinae; phylogeny; biogeography

Introduction

So far three genera of Caenidae are known from West Africa (Senegal, Gambia, Guinea, Mali, Côte d'Ivoire, Ghana, Togo). The genus *Caenis* (subfamily Caeninae) is distributed with six species in the region (Malzacher 1990, 1993); the genera *Afrocercus* and *Tigrocercus* (both subfamily Madecocercinae) are present with four species altogether (Malzacher and Staniczek 2006).

When Malzacher (2009b) gave an overview on the development of microtrichia on operculate gills he already mentioned the herein described genus *Aenigmocaenis* and discussed its phylogenetic position, subject to the still outstanding detailed investigation.

Malzacher and Staniczek (2006) presumed a vicarious distribution of the subfamilies Brachycercinae and Madecocercinae, the latter in the Ethiopic and Malagasy regions, the former in all other regions. With the knowledge of the herein described brachycercine genus *Niandancus* this assumption can no longer be upheld.

Materials

The investigated larvae were included in two 75% ethanol samples, which I received from Dr Michel Sartori (Lausanne). They were collected in Guinea in the late 1980s by the ORSTOM-team of Dr Jean-Marc Elouard. Type specimens are hosted in the

*Email: malzacher.lb@t-online.de

ISSN 0165-0424 print/ISSN 1744-4152 online

DOI: 10.1080/01650420903001825
http://www.informaworld.com

Musée Cantonal de Zoologie, Lausanne, except for a few paratypes of *Aenigmocaenis morgensterni* which are stored in the author's collection.

Systematic account

Aenigmocaenis gen. n.

Differential diagnosis of larva

Larvae of the genus can be characterised and distinguished from all other genera of Caenidae by the following combination of characters: thorax broadened. Head neither with ocellar tubercles nor with ridges and microscopic pits. Clypeus with anterio-lateral processes (Figures 2 and 9a). Maxillary and labial palps three-segmented. Length of maxillary palp reduced (Figure 9c). Basal segment of labial palp about as long as broad, nearly square or circular (Figure 9d). Sides of pronotum converging anteriorly. Foretibia and foretarsus without very long bristles. Femora short and broad, clearly broader than tibiae, without extended plates. Tibiae and tarsi shortened. Hind tibia with patello-tibial suture. (Figures 4 and 10c). Operculate gill ventrally without any kind of microtrichia (Figure 6). Y-shaped ridge on dorsal side of operculate gill nearly invisible in light microscope (Figures 1 and 5). Filaments of gills III–VI simple or with two branches only (one or two apical filaments with three or four branches). Lateral margin of operculate gills and abdomen without bristles. Lateral spines of abdomen lacking. Posterior part of sternum IX dorsally without shagreen field. Abdominal terga VII–IX without mediolongitudinal ridges and without bristles on the hind margin. Hind margin of sternum IX without a bipointed process.

Etymology

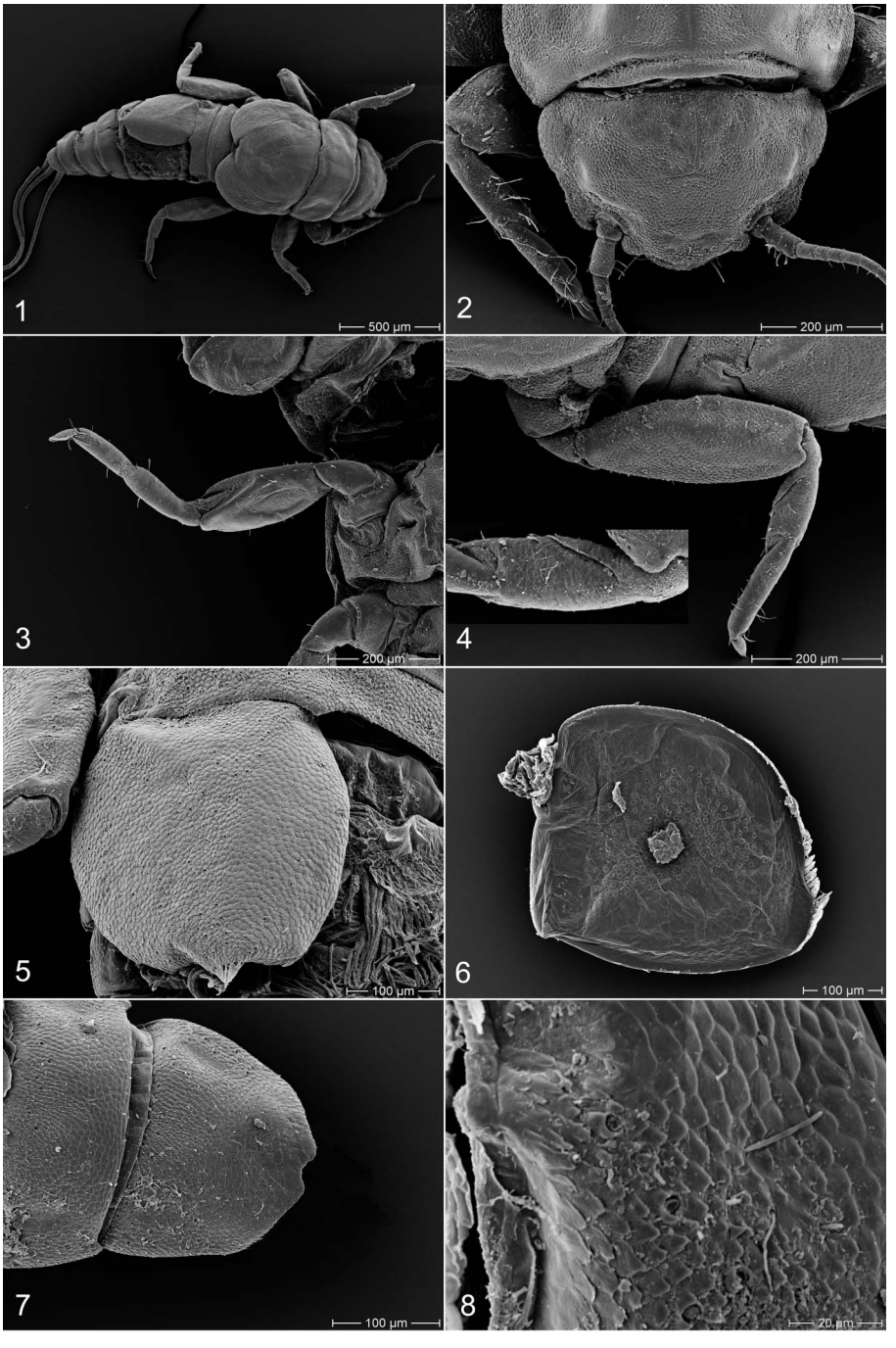
Aenigmo- refers to the rather enigmatic combination of characters and the accordingly uncertain phylogenetic position of the genus.

Aenigmocaenis morgensterni sp. n. (Figures 1–10)

Larva

Material examined. Holotype: ♂ larva, Guinea, riv. Niandan, Sassambaya, 19.04.1986. Paratypes: 2 ♂ and 14 ♀ larvae, Guinea, riv. Niandan, Sassambaya, 19.04.1986.

Measurements and colouration. Male larva (half grown): body length 1.8 mm, length of cerci 1.0 mm. Female larva (last instar): body length 2.3 mm, length of cerci 1.0 mm. *Habitus*. Body broad and robust, outline rounded, but variable depending on degree of muscle contraction (Figure 1). *Surface structure*. Body surface strongly tuberculate or sculptured with cuticular denticles and scale-like structures (Figures 2, 5 and 8) without spines or bristles. In highly magnified SEM pictures individual small bristles can be observed as well as numerous placoid sensillae (Figures 5, 7 and 8). *Colouration of cuticle*. Thorax reddish-yellowish-brown, abdomen and legs light brownish-yellow, operculate gills pale. *Epidermal pigmentation*. A transverse, dark brown dash on each side of the fore margin of pronotum. Strong dark brown spots on anterior corners of mesonotum, two more or less arcuated bands running



Figures 1–8. *Aenigmocaenis morgensterni* gen. n. sp. n.; larva. (1) Habitus, dorsal view; right operculate gill removed, (2) head and right foreleg, dorsal view; clypeal processes, (3) right mid leg, ventral view; femur with oval membrane, (4) left hind leg, dorsal view; enlarged detail: tibia with tibiopatellar suture, (5) left operculate gill, dorsal view, (6) right operculate gill, ventral view, without microtrichia, (7) abdomen, sternum IX, (8) sensillae from the basal part of sternite VI.

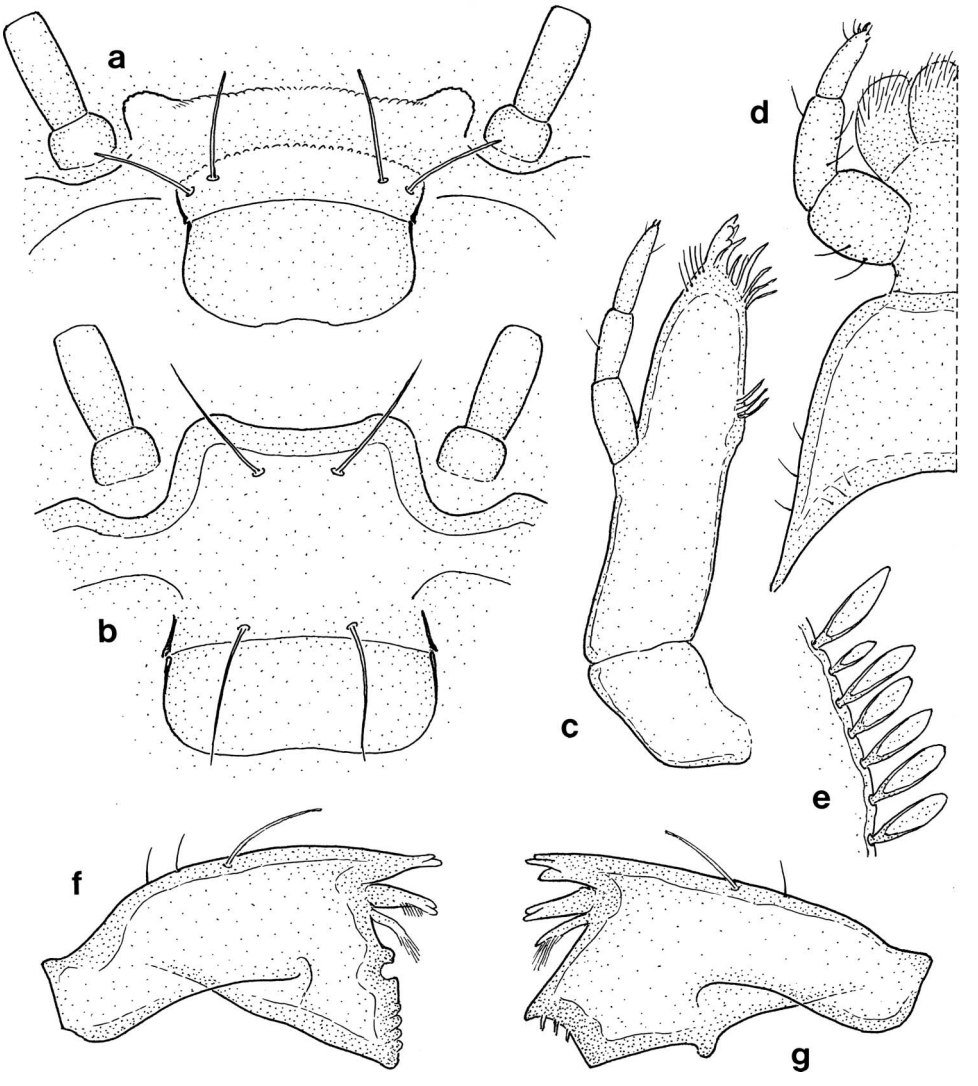


Figure 9 (a, c–g). *Aenigmocaenis morgensterni* gen. n. sp. n.; larva, (a) clypeus and labrum, frontal view; (c) maxilla; (d) labium, left half; (e) bristles on hind margin of operculate gill; (f) right mandible; (g) left mandible. (b) *Clypeocaenis afrosetosa*; larva, clypeus and labrum, frontal view.

posterio-medially, forming a trapezoid area diffusely pigmented. Abdominal sterna I, II and III with broad transverse dark-brown bands (sternum III is shining through operculate gills feigning a pigmentation of the gill base), strong transverse bands also on terga VII–IX, ventrally paler bands on hind margin of prosternum, medially on mesosternum and on posterior abdominal sterna.

Head. Genae bulged, semi-elliptical in dorsal view. Antennal bases very close to margin of head; pedicel with strong, apically rounded bristles (Figure 2). Fore margin of clypeus with anterolateral semicircular or conical protrusions close to the antennal bases. Four long and strong bristles near base of labrum (Figures 2 and 9a).

Mandibles marginally with one long and strong bristle, and another one (or two) shorter and thin bristles (Figures 9f and g); dorsal surface strongly tuberculate. Maxillary palp three-segmented but shortened, about as long as galealacinia (Figure 9c). Aboral side of postmentum laterodorsally with few thin and short bristles. Third segment of labial palp nearly as long as the second one, a little narrower; basal segment very broad, nearly square or circular (Figure 9d).

Thorax. Sides of pronotum rounded and anteriorly more or less converging (Figure 1). Coxal processes present only as inconspicuous tuberculated edges or lacking. Femora, particularly forefemora, broad. Tibiae and tarsi short and sturdy (Figures 1, 3, 4 and 10c–e). Forefemur dorsally with a diagonal row of apically broadened and rounded (but not pseudobifid), very inconspicuously pinnate bristles; length of bristles different (Figures 2, 10e and f). Mid femur dorsally with two or three similar, elongated bristles, hind femur without any bristles (Figures 10c and d). Femora ventrally with an oval membrane where thickness of chitinous layer seems reduced (Figure 3). Hind tibia with tibiopatellar suture that forms an oblique line on the lateral and median side, reaching the middle of the tibia on the ventral side (Figures 4 and 10c). Foretarsus ventrally with inner row of about five bristles, outer row lacking. Mid tarsus with inner row of about three apical bristles, outer row 0–2 bristles. Hind tarsus with inner row of 3–4 and outer row of two apically bristles. All

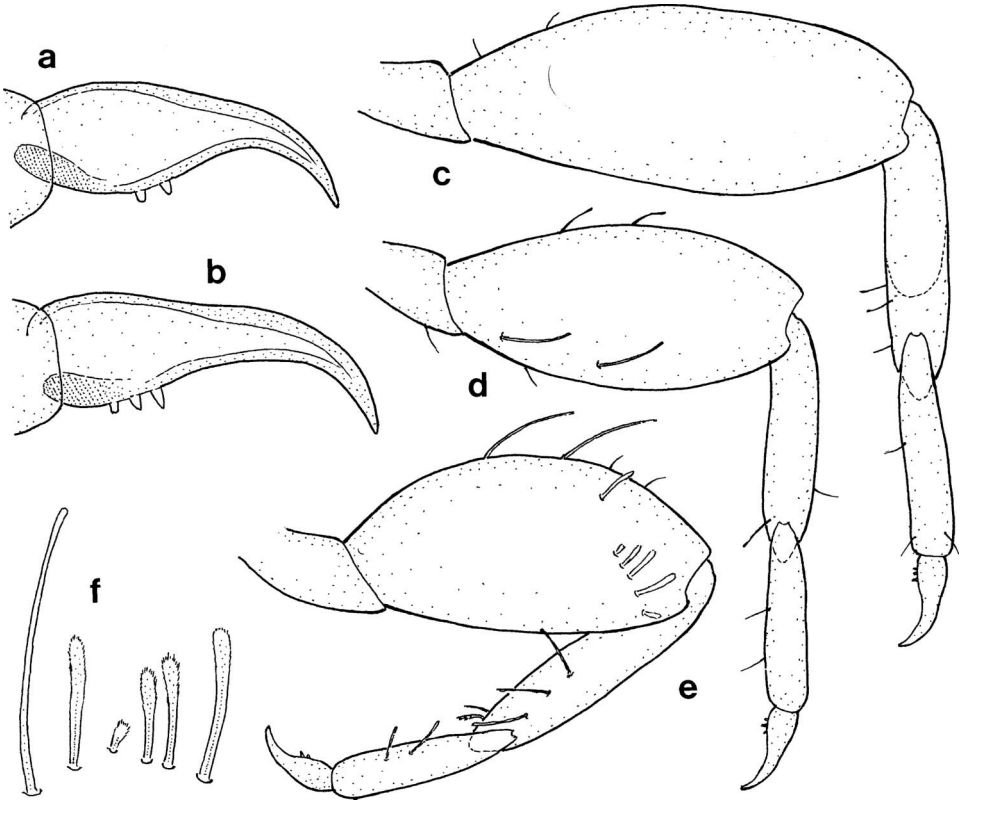


Figure 10. *Aenigmocaenis morgensterni* gen. n. sp. n.; larva. (a) claw of foreleg; (b) claw of hind leg; (c) hind leg; (d) mid leg; (e) foreleg; (f) bristles from the transverse row of foreleg.

bristles simple (Figure 3). All claws very similar, basal part stout, tip slender and strongly bowed, two or three strong denticles (Figures 10a and b). Hind claw homodont (all denticles of the same shape and size).

Abdomen. Posterolateral processes lacking, sometimes a slight curving of the hind margin feigns a small denticle (Figures 1 and 7). Posteromedian process of tergum II short, broadly triangular (Figures 1 and 5). Lateral margin of abdomen and operculate gills without bristles. Hind margin of operculate gill provided with short and broad, apically pointed bristles (Figures 6 and 9e), inner margin with few short and thin bristles. Besides a short longitudinal elevation on basolateral corner, no y-shaped ridge on dorsal side is visible under light microscope; in SEM it is indicated by differing surface structure (Figures 1 and 5). Ventral side of operculate gills without row or band of microtrichia (Figure 6). Gills III–VI relatively small, delicate, and translucent, marginal filaments simple or bifurcate, only one apical filament with three branches. The longest filament hardly reaching length of gill plate. Hind margins of all visible terga without bristles (Figure 1). Hind margin of sternum IX with a narrow and shallow indentation (Figure 7). No shagreen field on dorsal side.

Eggs (taken from a female last instar larva)

Eggs are broadly oval with two large cap-shaped epithemata. There is one, very thin and inconspicuous micropyle laying in the equatorial level. Chorionic structures cannot be observed under light microscope.

Sternum of teneral subimago (visible through cuticle of female last instar larva)
Forming a narrow isosceles triangle, coxae contiguous.

Etymology

Named in honour of the famous German poet Christian Morgenstern. Besides the fact that I admire him, his poems often are – just as the species – also from a certain mysteriousness (see Knight 2004).

***Niandancus* gen. n.**

Differential diagnosis

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

Head with very long ocellar tubercles (Figure 11a), without ridges and microscopic pits. Ocellar tubercles distally without dense long setae. Clypeus anteriorly not protruding. Labrum strongly bent posteriorly on ventral side of head (Figure 11a). Maxillary and labial palps two-segmented (Figures 11b and c), directed ventrally (Figure 11a).

Legs narrow and slender, claws elongated and very thin (Figures 11d–f). Foretibiae and tarsi without filtering setae. Femora without extended plates. Mid and hind coxae with conspicuous, spine-shaped processes (Figures 11e and f).

Operculate gill dorsally without sublateral longitudinal ridge. On the ventral side without broad field of simple microtrichia but with spines near the lateral margin and clusters of 2–5 spines on the hind margin (Figures 12d–e). Operculate gill without protruding edge at posterolateral corner; posteromedian corner produced posteriorly

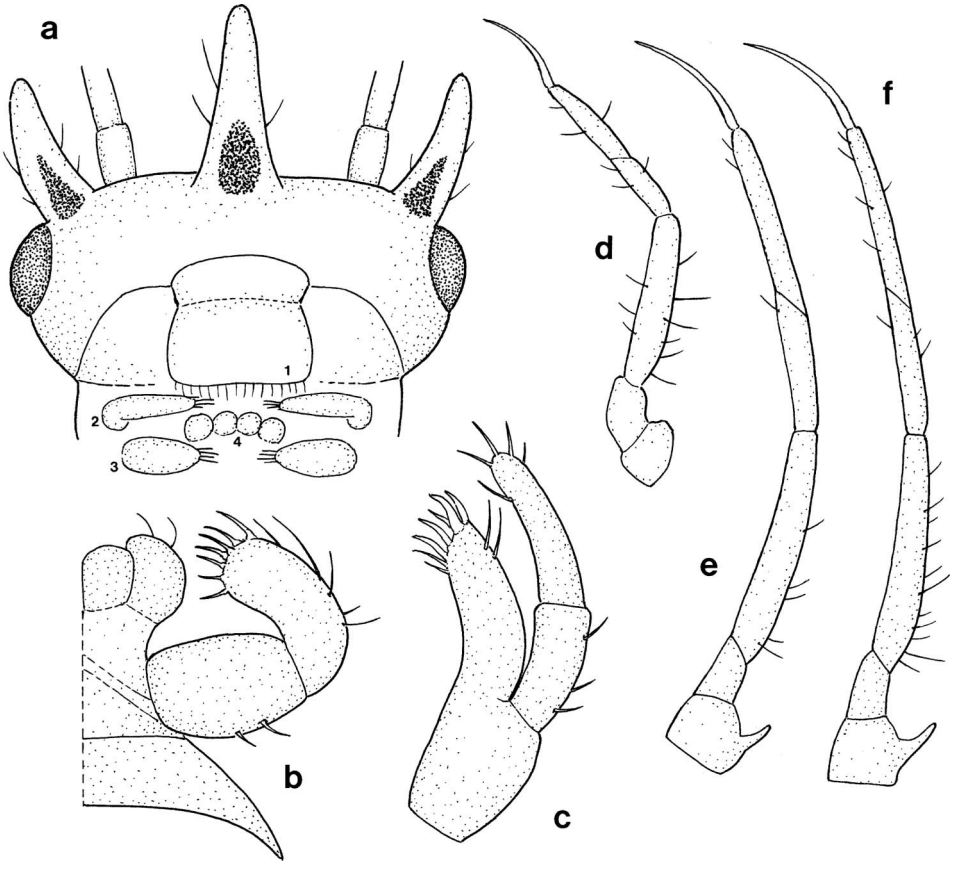


Figure 11. *Niandancus alienus* gen. n. sp. n.; larva. (a) Head, ventral view with mouthparts, 1 = labrum, 2 = maxillary palp, 3 = segment II of labial palp, 4 = glossae and paraglossae from apical; (b) labium, right half; (c) maxilla; (d) foreleg; (e) mid leg; (f) hind leg.

(Figure 12c). Lateral spines of abdomen very long, protruding laterally, slightly bent dorsally; segment VIII with a rather long spine, too and even IX with small pointed triangles (Figure 12a). Lateral spine VI not curved medially. Abdominal tergum VII with very long hair-like bristles on the hind margin. Hind margin of sternum IX without a bi-pointed process with concave margin between the points.

Etymology

Niandan is the name of the Guinean river where the larva was found.

***Niandancus alienus* sp. n.** (Figures 11–12)

Larva

Material examined. Holotype: Larva (immature), Guinea, riv. Niandan, Sassambaya, 07.04.1987.

Measurements and colouration. Immature larva, body length 1.5 mm, length of cerci 0.6 mm. Colouration of chitinous layers pale yellowish. Epidermal pigmentation: a brown blotch on the vertex. Operculate gills with a tinge of brown.

Head. Pedicel 3.5 times longer than broad and 3.5 times longer than scape, with long thin bristles. Lateral ocellar tubercles long and slightly curved; frontal ocellar tubercle very long, nearly half as long as width of head (Figure 11a) (only *Sparbarus nasutus* and *S. tubulatus* show ocellar tubercles of similar length, see Sun and McCafferty 2008). Labrum situated posteriorly on the ventral side of the head (Figure 11a). Maxillary and labial palps two-segmented (Figures 11b and c), lining up ventrally so that only the second segments are visible ventrally (Figures 11a, 2 and 3). Maxillary palp only 1.7 times length of galealacinia, slender, with few apical bristles (Figure 11c). Basal segment of labial palp clearly longer than broad; postmentum very short and broad, sickle-shaped (Figure 11b).

Thorax. Legs narrow and slender, only with few bristles. Mid and hind coxae with spine-shaped processes. Trochanteres elongated. Femora basally narrowed, slightly converging from the broadest part in the basal forth to the apex. Tibiae distinctly shorter than tarsi. Claws very long and thin (Figures 11d and f).

Abdomen. Posterolateral processes III–VIII very long and curved, protruding laterally (Figure 12e), only slightly bent dorsally. First gill very long, about as long as the second gill (Figure 12b). Operculate gill with protruding posteromedian corner. Branches of Y-shaped ridge not as strongly diverging as in most of the other Brachycercinae, not reaching the insertion of the gill (Figure 12c). Ventral side with two different kinds of

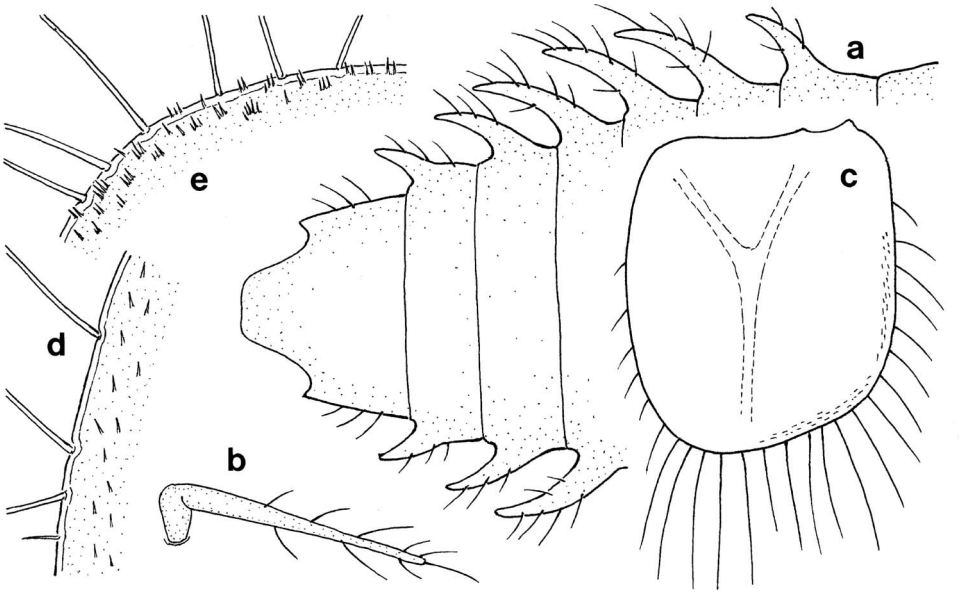


Figure 12. *Niandancus alienus* gen. n. sp. n.; larva. (a) Outline of abdomen, sterna II–IX; (b) first gill; (c) operculate gill; (d) section from lateral margin of operculate gill, ventral side, with spine-shaped microtrichia; (e) section from posterior margin of operculate gill, ventral side, with microtrichia forming clusters of spines.

microtrichia, simple spines along lateral margin (Figure 12d) and clusters, sometimes comb-like structures consisting of up to five spines, at posterior margin (Figure 12e). First gill, lateral margin of abdomen, and operculate gill only with few bristles, becoming very long at hind margin of operculate gill (Figures 12b and c). Very long and thin bristles can also be observed on hind margin of tergum VII, reaching length of two segments. Hind margin of terga VIII–X with denticles or small rectangular scales. Hind margin of sternum IX strongly bulged out (Figure 12a).

Remarks
The herein described single larval specimen, in spite of its small size, cannot represent a very early instar, as most of the diagnostic characters are already strongly differentiated. This also suggests a fairly small size of the adults of the new species, which seem to be not as large as most of the other Brachycercinae.

Etymology
This is the first species of Brachycercinae to be found in the Ethiopic region, which is reflected by the Latin *alienus*, meaning "foreign".

Discussion

Aenigmocaenis

Aenigmocaenis belongs to the Caenidae due to the medially overlapping gill covers, a larval synapomorphy of the family. On the other hand, the second larval synapomorphic character, operculate gills ventrally with sublateral microtrichia, is lacking in the new genus. Malzacher (2009b) summarises three different possibilities of interpretation:

(1) The genus does not belong to the Caenidae, then the medially overlapping gill covers would be a result of a convergent development. This is not likely, as the general morphology of this species overall resembles a Caenid larva.
(2) The genus nests within the Caeninae, but a change of ecological niche led to a total reduction of microtrichia. This is, however, debatable, because the specimens were found in a sample containing a lot of *Caenis* larvae, so it can be assumed that they all inhabit the same habitat.
(3) The lack of microtrichia on the ventral side of the gill cover represents a rather plesiomorphic character state close to the respective character state in the Neoephemeridae. In this case the new species could be considered the sister group to the remaining Caenidae.

Gattolliat and Sartori 2008 noticed that *Caenis malzacheri* under the light microscope appears to lack microtrichia on the ventral side of the operculate gill. However, in *Callistellina panda* these microtrichia also seem to be lacking but become visible under SEM. Therefore the presence or absence of microtrichia in *Caenis malzacheri* can only be decided after an investigation by SEM. Other characters such as general body shape, setation and shield-shaped microtrichia on the surface prove *Caenis malzacheri* to be a species close to the *Caenis macrura* group. A possible lack of microtrichia on the ventral side of the operculate gill therefore could not be interpreted as a synapomorphy with *Aenigmocaenis morgensterni*.

Besides lacking microtrichia on the gill cover, the larva of *Aenigmocaenis morgensterni* shows two other, most likely plesiomorphic characters that are not

shared by all other Caenidae. In *A. morgensterni* there is a tibiopatellar suture present on the hind tibia. This character is distributed in most other Ephemeroptera families, in the majority of them on middle and hind leg (Kluge 2004). This is also the case in Neoephemeridae and Ephemerellidae, the nearest relatives of the Caenidae. In all other Caenidae, however, the tibiopatellar suture is partly or totally reduced. Only few species show inconspicuous sutures or traces of it, but it is never as pronounced as in *Aenigmocaenis*. The second character concerns the shagreen field on the posterior plate of the sternum IX, which is almost present among all species of Caenidae (apart from *Aenigmocaenis*, this shagreen field on sternum IX is otherwise only lacking in *Callistellina* and *Trichocaenis*). The lack of gill cover microtrichia and shagreen field on sternum IX as well as the presence of a tibiopatellar suture thus could point to a sister group relationship of *Aenigmocaenis* to all other species of Caenidae.

In the Caenidae there is a tendency of reduction leading to different characters in the subfamilies or groups of genera that can be interpreted as apomorphies. Results of four reductions can also be observed in *Aenigmocaenis*.

(1) Reduction of maxillary palps leads to a reduced number of segments in the Brachycercinae and in two genera of the Caeninae, or to a total disappearance of the maxillary palp in the Madecocercinae (McCafferty and Wang 1995; Malzacher and Staniczek 2006). In *Aenigmocaenis* only a shortening of the palp has taken place. Parallel developments can also be observed in other families of the Pannota (McCafferty and Wang 2000).
(2) Reduction of lateral abdominal spines. In the outgroups (Neoephemeridae, Ephemerellidae s. l.) lateral spines are very common. In the Caenidae they are also present in nearly all of the species. In species of *Caenis*, however, there is a huge variability in length and shape of those spines that can be very small at times. In Brachycercinae a partial reduction has taken place: while spines of the anterior segments are highly specialised forming a gill basket, the spines on segments VII–IX are more or less reduced and often lacking (Soldán 1986; Sun and McCafferty 2008) (see also below for *Niandancus*). In all other Caenidae these spines are present except in *Aenigmocaenis*, which seems to be the only species where they are lacking. The disappearance of nearly all bristles could be connected with a general tendency to a rounding of the body. The lack of bristles can also be observed in *Callistellina* (Sun and McCafferty 2008).
(3) Reduction of filament branches on gills III–VI. In the Neoephemeridae these gills show filaments with five and more branches (Kluge 2004). Within the Caenidae, filaments with up to five branches are present in the Brachycercinae, a great number of *Caenis* species, and even the madecocercine *Afrocercus*. So a significant reduction of this number can be regarded as an apomorphy. It is realised in the *Clypeocaenis* group (Malzacher 2009b) where nearly all filaments are two-branched or simple (Malzacher 2009a) and in *Madecocercus* with only short and simple filaments (Kluge 2004; Malzacher and Staniczek 2006). The gills of *Aenigmocaenis* are shaped like in species of the *Clypeocaenis* group.
(4) No ridges on dorsal side of operculate gill. Kluge (2004) interpreted those ridges as a synapomorphy of the Caenoidea. Their length is diminished in some *Potamanthellus* species (Neoephemeridae) and in few Caeninae of the

genera *Tasmanocoenis* and *Wundacaenis* (Suter 1993, 1999). In *Caenis vanuatensis* the shortened ridges are present only in the anterior part of the gill and their posterior ends are clearly separated from each other (Malzacher and Staniczek 2007). With regard to its presence in the outgroup Neoephemeridae, a reduction of the dorsal ridge on the gill cover therefore can be regarded as an apomorphic development within the Caenidae.

Apart from these reductional characters there are other derived characters in the new genus. The most important is the narrow and triangular shape of the imaginal sternum, which could be observed through the cuticle of a female last instar larva. This character would indicate that *Aenigmocaenis* is placed within the Caeninae. This is also supported by the above listed apomorphic reductions.

The simple egg structure of *A. morgensterni* can be interpreted as plesiomorphic character present also in other Caeninae. The eggs of other subfamilies show very differentiated apomorphic structures (Malzacher and Staniczek 2006), although in two species of the Brachycercinae simple chorionic structures are present (Sun and McCafferty 2008).

Anterolateral protrusions and long and strong bristles of the clypeus could even suggest a phylogenetic position of *Aenigmocaenis* close to the *Clypeocaenis* group (compare Figures 9a and b), which could also be indicated by the reduction of gill filament branches. Depending on the weighting and assessment of the individual above mentioned characters, different phylogenetic assignments of the genus seem to be possible. A definite decision on the phylogenetic position of *Aenigmocaenis* is therefore difficult to be made and should only be undertaken by including molecular analyses.

Niandancus

Niandancus shows all the larval synapomorphies of the subfamily Brachycercinae, namely the head with ocellar tubercles, lateral spines of abdomen bent dorsally, two-segmented labial palps, and narrow and slender legs, with the length of forelegs diminished. Except for the lateral spines on the abdomen, all these characters are highly developed in *Niandancus*. Ocellar tubercles are the longest and most voluminous of all species of the subfamily and comparable only with two species of *Sparbarus nasutus* and *S. tubulatus* (formerly *Brachycercus*, see Sun and McCafferty 2008). Additionally, the legs of *Niandancus* are more elongated as in nearly all Brachycercinae, particularly the length and slenderness of the claws exceed all other species (Soldán 1986; Sun and McCafferty 2008).

Shape and arrangement of lateral abdominal processes, however, represent an early stage of evolutionary development. The very long and laterally protruding processes are only slightly bent dorsally. There is no reduction of spines on posterior segments (only in segment I they are completely lacking) and no abrupt diminishing of the length of segments VI–VII (VIII) as is the case in most Brachycercinae. This combination of characters is very similar to the one in *Caenoculis acutalis* (Zhou, Sun, McCafferty 2003) that was recently assigned to the Brachycercinae (Sun and McCafferty 2008). *Insulibrachys needhami* also shows a similar arrangement, although the spines are shorter and broader (Soldán 1986). Finally, in an undescribed genus from Thailand and West Africa, this combination of characters is also present, except that the very long spines are only spread laterally and not bent

dorsally at all. Other characters of this undescribed genus are Caeninae-like. In the case of *Caenoculis acutalis* the arrangement of abdominal spines could be regarded an initial stage of the development of the brachycercine gill basket, which is a little more advanced in *Niandancus and Insulibrachys*.

Incidentally, in *Caenoculis acutalis* there are coxal processes on the hind legs but they are smaller than those that could be found on middle and hind leg of *Niandancus*. These structures cannot be found in Brachycercinae, but they are common in the Caeninae.

The structure and arrangement of microtrichia on the ventral sides of the operculate gills are also unique in *Niandancus*. Sublateral bands of simple spines are present in most Brachycercinae. In a few species of Brachycercinae, the formation of clusters of 2–3 spines has taken place (e.g. in *Brachycercus gilliesi*, Malzacher, unpublished). In *Caenoculis acutalis* scale-like microtrichia of about five spines form a broad and very dense band on the lateral and posterior margin of the operculate gill. In *Niandancus*, however, there are simple spines on the lateral margin and clusters of two to five spines on the hind margin of the operculum. These results once more support the assumption that different evolutionary stages of microtrichia occur in all subfamilies of the Caenidae and are the result of parallel development (Malzacher and Staniczek 2006). The posteromedian corners of the operculate gills are clearly protruding in *Niandancus*. In the Brachycercinae such a shape of the operculate gill can only be found in *Cercobrachys petersorum* and, a little weakened, in *Susperatus* ssp. In *Brachycercus* the posterolateral corners are protruding and in all other species a protrusion of the one or the other hind corners cannot be observed (Sun and McCafferty 2008).

The mouthparts of *Niandancus*, besides their shifted posterior position, show shapes which cannot be found in any other Brachycercinae (see Sun and McCafferty 2008), e.g. the broadly rounded labial palp without any trace of a tip, the elongated and narrow galealacinia with a straight median margin, and the shortened maxillary palp. It is noticeable that in Brachycercinae the rounded labial palp can be observed in *Insulibrachys*. However, the phylogenetic assessment of these characters is difficult.

According to the present knowledge, *Niandancus* can be best regarded as a basal taxon of Brachycercinae. *Niandancus* has retained a plesiomorphic arrangement of the long and only slightly bent lateral abdominal spines, which are more or less developed to a bent gill basket in the remaining Brachycercinae, but have ocellar tubercles and long, slender legs and claws as synapomorphic characters of Brachycercinae. The latter two characters are even more developed than in the remaining Brachycercinae. Only *Caenoculis acutalis* with its plesiomorphic, three-segmented palps may have a more basal position to the remaining Brachycercinae. In *Caenoculis bishopi* and *C. nhahoensis*, besides the three-segmented palps, some other Caeninae-like plesiomorphies can be observed: habitus *Caenis*-like; legs not slender, femora broadened; forelegs not shortened. This would mean that *Caenoculis acutalis* is closer to the base of Brachycercinae than these species. Incidentally, neither Soldán (1986) nor Sun and McCafferty (2008) mentioned shape and arrangement of the microtrichia on the ventral side of the operculate gills in these two genera, which should be clarified before a final phylogenetical assignment can be made. These differences in my opinion demand the erection of a separate genus for *Caenoculis acutalis*. After having a look at the paratype of *Caenoculis dangi*, deposited in the Museum of Linz, Austria, I can

confirm the opinion of Sun and McCafferty (2008) that this species does not share any apomorphies with the Brachycercinae. There is a regular row of microtrichia on the ventral side of the operculate gill. This character is present only in the Caeninae.

The presence of *Niandancus* in Guinea is the first record of Brachycercinae in the Ethiopic region, which refutes the presumption of a vicarious distribution of the subfamilies Madecocercinae in the Ethiopic and Malagasy regions and Brachycercinae in all other regions (Malzacher and Staniczek 2006). With the discovery of the putative most basal brachycercine genus in Africa it becomes likely that the Brachycercinae once also were distributed in western Gondwana.

The similarity of some characters in *Niandancus* and *Insulibrachys*, particularly the plesiomorphic state of the gill basket, could support this biogeography. This is also supported by the fact that Cuba and Guinea, where they occur today, have been situated rather close to each other before the separation of the South American and African continental plates.

Acknowledgements

My special thanks go to Michel Sartori, Musée Cantonal de Zoologie, Lausanne, for leaving me the material for investigation. I also thank N. Kluge, St. Petersburg State University, for valuable information. Thanks also to Arnold Staniczek and Susanne Leidenroth, Staatliches Museum für Naturkunde, Stuttgart, for help and making the SEMs.

References

Gattolliat, J.-L., and Sartori, M. (2008), 'Order Ephemeroptera', *Arthropod fauna of the UAE*, 1, 47–83.

Kluge, N.J. (2004), *The Phylogenetic System of Ephemeroptera*, Dordrecht: Kluwer.

Knight, M. (2004), 'The knee', in *Christian Morgenstern Sechssprachig*, ed. M. Hansen, Stuttgart: Verlag Freies Geistesleben und Urachhaus, pp. 96–98.

Malzacher, P. (1990), 'Caenidae der äthiopischen Region (Insecta: Ephemeroptera). Teil 1. Beschreibung neuer Arten', *Stuttgarter Beiträge zur Naturkunde, Serie A*, 454, 1–28.

Malzacher, P. (1993), 'Caenidae der äthiopischen Region (Insecta: Ephemeroptera). Teil 2. Systematische Zusammenstellung aller bisher bekannten Arten', *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 66, 379–416.

Malzacher, P. (2009a), 'New larvae of Caeninae from Madagascar (Ephemeroptera: Caenidae)', *Stuttgarter Beiträge zur Naturkunde A, Neue Serie*, 2, 177–194.

Malzacher, P. (2009b), 'Comparative morphology of gill cover microtrichia in the Caenidae (Insecta: Ephemeroptera)', in *International Perspectives in Mayfly and Stonefly Research. Proceedings of the 12th International Conference on Ephemeroptera and the 16th International Symposium on Plecoptera, Stuttgart 2008*, ed. A.H. Staniczek, *Aquatic Insects*, 31 (Suppl. 1), 31, 485–494.

Malzacher, P., and Staniczek, A.H. (2006), 'Revision of the Madecocercinae (Ephemeroptera: Caenidae)', *Aquatic Insects*, 28, 165–193.

Malzacher, P., and Staniczek, A.H. (2007), '*Caenis vanuatensis*, a new species of mayflies (Ephemeroptera: Caenidae) from Vanuatu', *Aquatic Insects*, 29, 285–295.

McCafferty, W.P., and Wang, T.-Q. (1995), 'A new genus and species of Tricorythidae (Ephemerptera: Pannota) from Madagascar', *Annales de Limnologie*, 31, 179–183.

McCafferty, W.P., and Wang, T.-Q. (2000), 'Phylogenetic Systematics of the major lineages of pannote mayflies (Ephemeroptera: Pannota)', *Transactions of the American Entomological Society*, 126, 9–121.

Soldán, T. (1986), 'A revision of the Caenidae with ocellar tubercles in the nymphal stage (Ephemeroptera)', *Acta Universitatis Carolinae, Biologica*, 1982–1984, 289–362.

Sun, L., and McCafferty, W.P. (2008a), '*Callistina panda*, a striking new genus and species of Caeninae (Insecta: Ephemeroptera: Caenidae) from Madagascar', *Bulletin de la Société d'Histoire naturelle de Toulouse*, 137, 7–15.

Sun, L., and McCafferty, W.P. (2008b), 'Cladistics, classification and identification of the brachycercine mayflies (Insecta: Ephemeroptera: Caenidae)', *Zootaxa*, 1801, 1–239.
Suter, P.J. (1993), '*Wundacaenis*, a New Genus of Caenidae (Insecta: Ephemeroptera)', *Invertebrate Taxonomy*, 7, 787–803.
Suter, P.J. (1999), 'Illustrated Key to the Australian Caenidae Nymphs (Ephemeroptera: Caenidae)', *Cooperative Research Centre for Freshwater Ecology, Albury, Identification Guide No*, 23, 1–36.
Zhou, C.-F., Sun, L., and McCafferty, W.P. (2003), 'A new species of *Caenoculis* Soldán from China (Ephemeroptera: Caenidae)', *Pan-Pacific Entomologist*, 79, 185–191.