GENITAL-MORPHOLOGICAL FEATURES IN THE CAENIDAE

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ABSTRACT

The general structure of Caenidae genitalia is described. An overview of types and shapes of different parts, especially the forceps, is given as well as remarks on their diagnostic value. Some conclusions concerning the origin and the development of the family are drawn and given for discussion.

INTRODUCTION

Thirty years have passed since THEW revised the family Caenidae. His revision was mainly based on the morphology of the genitalia. For that he had to refer to many descriptions of other authors that often were inexact or even wrong as we know today.

In the following survey of the structures of the male genitalia and its importance for taxonomy and classification I'll go into misinterpretations by Thew (1960) from case to case.

DISCUSSION

Fig. 1a shows the different parts of the genitalia from the ventral side. The penis (1) is a fused structure, consisting of the paired penes which are separated in primitive Ephemeroptera. Its two lobes are laterally more or less protruding. A ventral penis-fold covers a hollow in which the vasa deferentia are terminating. Parts of the ventral, dorsal and distal surfaces can be sclerotized and coloured brownish to dark-brown.Size, shape and structure of those sclerites can be specific for some species. There are many different penis-shapes, from very short and broad ones to caudally prolonged and club-shaped forms. The individual shape however can be very variable depending on the contraction of the penis-muscles.

Thew was wrong when he considered a penis with very large lobes such as in *Caenis scotti* as a primitive stage consisting of two separated penes. He furthermore considered *Caenis macrura* to be an intermediate stage because of a median incision in a figure of Kimmins (1942). Later Kimmins himself realized this incision was an artefact.

The caudal part of the styliger (2) is a flattened duplicature covering the base of the penis.Its structure can be taken from a longitudinal section (fig.1b). The ventral layer is very thin and transparent and the dorsal layer however is more or less sclerotized, often brown, forming the styliger-sclerite (3) as already described by Grandi (1960). At its anterior margin two apophyses can be seen. Their size, shape and position are important diagnostic characters. The sclerotized lateral margins of the styliger that I call lateral-sclerites (4) are sometimes prolonged forwards, bent to the middle and ending near the central-sclerite (5). The basolateral-sclerites (6) are two further chitinous structures that run from the base of the central-sclerite towards the backcorners of the segment. These sclerites are sometimes very thin and nearly invisible.

The unsegmented dorsoventrally flattened forceps (7) have many diagnostic features such as dimensions and proportions, shape, colouring, structure of the surface, location and type of articulation with the styliger. Finally the structures of the forceps' apex are of great importance, not only for diagnosis but also as indications of phyletic relationships (see below).

The figures 2-6 show different phenotypes of the genitalia. Fig. 2 shows both a representative of the subfamily Caeninae (*Caenis luctuosa*, a) and of the Brachycercinea (*Brachycercus harrisella*, b). Some differences between the subfamilies are visible that indicate possibly a different manner of functioning. In the Caeninae the styliger-sclerite is well developed and forms a cross brace between the forceps base. It's involved in the forceps articulations. The lateral-sclerite is slim and has no connexion with the basolateral-sclerite. In the Brachycercinae the two large lateral-sclerites form two longitudinal axis. They spread out to the base closely adjacent to the baso-lateral-sclerites. An articulation with the sparsely developed styliger-sclerite is not visible. The apophyses of the latter are closer to the middle than in the Caeninae.

Some African species such as *Caenis cibaria* (fig. 3a) and *Caenis pallida* (fig. 3b) have long forceps clearly exceeding the penis in length which is not usual in most of the other *Caenis*-species. An example of different individual penis-shapes can be seen in *Caenis cibaria*. Very simple and more or less unsclerotized forms can be found in Africa like *Caenis elouardi* (fig. 4a) and *Caenis ghibana* (fig. 4c) or in the eastern part of South America like *Caenis quatipuruica* (fig. 4b).

The species of the genus *Brasilocaenis* have highly specialized genitalia (fig. 5). The styliger is prolonged backwards and shows a tendency to converging margins, to be shown with the example of *Brasilocaenis septentrionalis* (a), *Brasilocaenis renata* (b) and *Brasilocaenis puthzi* (c). Forceps and styliger margins are connected the most closely, as well as lateral- and basolateral-sclerites which orientate themselves parallel to the longitudinal axis.

Fig. 6b shows an extreme form in the Brachycercinae, *Afrocercus forcipatus*, with characters of this subfamily such as strongly sclerotized and basally widened lateral-sclerites, a reduced styliger-sclerite and furrowed forceps.

Regarding this the genitalia of the genus *Tasmanocoenis* (fig. 6a) show different transitional stages from Brachycercinae-like forms to Caeninae-like genitalia, that will be shown below with the example of the forceps.

The different forms of the forceps can be divided into 5 groups. Besides the tufted and the grooved forms they are not identical with the groups established by Thew.

1. group: grooved forceps, to be found in the Brachycercinae and in *Tasmanocoenis* (fig. 7). *Brachycercus harrisella* (a) shows a deep straight groove limited by two ridges. In *Cercobrachys etowah* (b) the basal part of the median ridge is overlapping the lateral one so that the forceps seem to be destorted. This may be a generic character of *Cercobrachys*. The modified forceps of *Afrocercus forcipatus* (c) shows only a small ridge in the apical part and a lamella-like duplicature in the middle. In *Tasmanocoenis tillyardi* (d), the most Brachycercinae-like species of the genus, the median ridge is only visible in the basal part. It runs apically below the lateral ridge. The figure is taken from a Partype from Tasmania. In the continental form, which seems to me to be a separate species, ridges appear only in the apical half (see: SUTER 1986, fig. 30 c). They do not form a deep groove. In *Tasmanocoenis jillongi* (e, figured after HARKER) there is only a small ridge in the apical part and in *Tasmanocoenis tonnoiri* (f) ridges and grooves are lacking. This is the Caeninae-like type that leads us to:

2. group: forceps with straight, strongly sclerotized and pointed apex (but without grooves). This forceps- type can be found all over the Holarctic and in the Neotropics. Some Palaearctic species have bowed forceps like *Caenis rivulorum* (a) reminding a little of the *Tasmanocoenis*-species and those with a more or less triangular shape (b-d). North American species of this group often show very long and slender forceps such as *Caenis simulans* (e) and *Caenis jocosa* (f). In the tropical region of Middle America and central South America those forms are not to be found but in Paraguay there are similar species e.g. *Caenis pseudamica* (g) and *Caenis burmeisteri* (h). A species with a forceps shape as in *Caenis burmeisteri* could be the ancestor of two Amazonian groups: the *Caenis fittkaui*-group show abruptly narrowed apexes (fig. 9a,b). This feature is as well indicated in *Caenis burmeisteri* as the prolonged forceps-base of the *Brasilocaenis* species. In these species there are some differences in the kind of articulation of the forceps. In *Brasilocaenis irmleri* (c) the styliger and the forceps are meshed by longitudinal chitinous lamellae. In *Brasilocaenis puthzi* (d) the basal part, and in *Brasilocaenis septentrionalis* the whole forceps except the apex, are fused with the styliger. In all species the apex shows a specific shape.

3. group: Forceps apex with a number of small bristles, bent inwards (fig. 10). The bristles are approximately as long as the trichomas covering the surface. Species of this group are distributed mainly in the Holarctic and a small number in the Oriental Region. The forceps of some species are very similar and also variable e.g. the North American *Caenis anceps* and the European *Caenis beskidensis* and *Caenis pseudorivulorum* (b,c). In *Caenis hilaris* (d) and *Caenis punctata* (e) very short bristles are stuck together

forming a tiny little tip. A little longer tips consisting of stuck bristles can be seen in *Americaenis ridens* (f) (see: PROVONSHA & McCAFFERTY 1985, fig. 14), in the Mediterranean *Caenis pusilla* and in some related Middle and Eastern Palaearctic species (g).

4. group: forceps with terminal tuft of strong spines which are longer than the trichomas of the surface. Most of the species of this group can be found in the Aethiopical Region (the greatest part of the African species belong to this group) and some others in the Palaearctic and the Oriental Regions. The size of the spines as well as length and shape of the whole forceps often are valuable diagnostic characters. Fig. 11 shows some combinations. Though it must be taken into account that one or more of those characters can be highly variable: fig. 12 shows different forceps-shapes from the paratype-series of *Caenis kivuensis*.

Thew described in his revision the new genus *Caenomedea* the characters of which are identical with those of this group. But he didn't know hat *Caenis macrura*, the Type-species of the genus *Caenis*, has tufts of long spines (fig. 11c). Also the forceps of *Caenodes*, described as barbed by THEW, have those tufts (fig. 11a). Certainly they are not to be seen in the figures of the original descriptions by ULMER (1924, fig. 6), KIMMINS (1956, fig. 22) and GRANDI (1951, fig. 5/1).

5. group: apically rounded forceps. They are known from Africa and South America, but the simplest forms occur only in West Africa (*Caenis elouardi*, fig. 13a) and in the northeastern part of South America (species of the *Caenis reissi*-group, fig. 13 c-e). There are little more differentiated forms in all parts of South and Middle America (f-i). Sometimes they have small sclerotized tips (like a species from Cuba, k) that could be an intermediate stage to forceps with strongly sclerotized apexes.

Besides the previously described forceps-types there are other intermediate forms and those which can not be assigned with confidence to one of the groups (fig. 14) e.g. *Caenis basuto* with very different apexes (b) and an Indian species (a). *Afrocaenis major* (c), *Caenopsella meridies* (e) and *Caenis valentinae* (d) have two separated apical spines. But sometimes there is only one spine or even one and a half.

From the genital-morphological point of view the following evolution of the family seems to me to be possible. The functioning of the forceps of the Caenidae is different from that in other families. They are too short, too weak and too inflexible to hold the female abdomen. I think they function as titillatores because of their armed apexes and surfaces. As these forceps are new aquisitions not to be found in other families, they must have developed inevitably from apically rounded forms under reduction of the length and the number of the segments. The *Potamanthellus-Neoephemeropsis*-group of the Neoephemeridae that Edmunds considers to be the sister-group of the Caenidae, show transitional stages. In the Caenidae the most reduced, apically rounded forms that have obviously lost their original function occur only in West Africa and the northeastern parts of South America, two regions which had been connected before the continental shifting. This indicates a

unique origin and a maximum age of about 150 million years. The relative abundance of plesiomorph features in the former Gondwanian region - there are also examples besides the genital morphology - let assume that the ancestry of the Caenidae was here.

The more differentiated forceps-types must have developed then from the reduced, apically rounded ones. You can't tell with certainty *how* they have developed and how they are related nor whether they are monophyletic. Especially the development of the grooved forms is unclear and because of that the question when and where the Brachycercinae branched off. In some cases the limited geographical distribution seems to indicate a monophyletic origin of a group, e.g. the tufts of spines that may have originated in the Aethiopic Region and spread out northeastwards. The rounded forceps in South America could have led to forms with strongly sclerotized apexes. This line may have taken a western way and distributed all over the Holarctic.

ACKNOWLEDGEMENTS

Besides fig. 7a and f all figures are taken from Malzacher 1984, 1986, 1987 and in press, or are new drawings.

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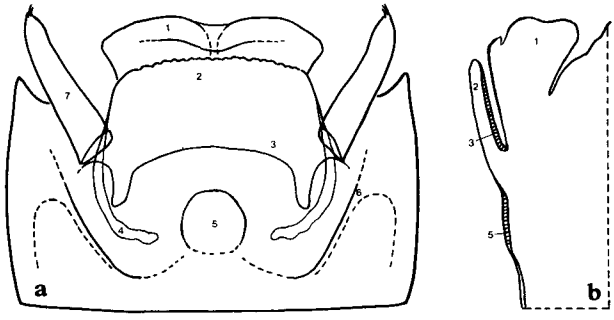

Fig. 1. Male genitalia, schematic. - a. *Caenis*, ventral, - b. *Caenis*, longitudinal section, 1 = penis, 2 = caudal part of the styliger, 3 = styliger-sclerite, 4 = lateral-sclerite, 5 = central-sclerite, 6 = basolateral-sclerite, 7 = forceps.

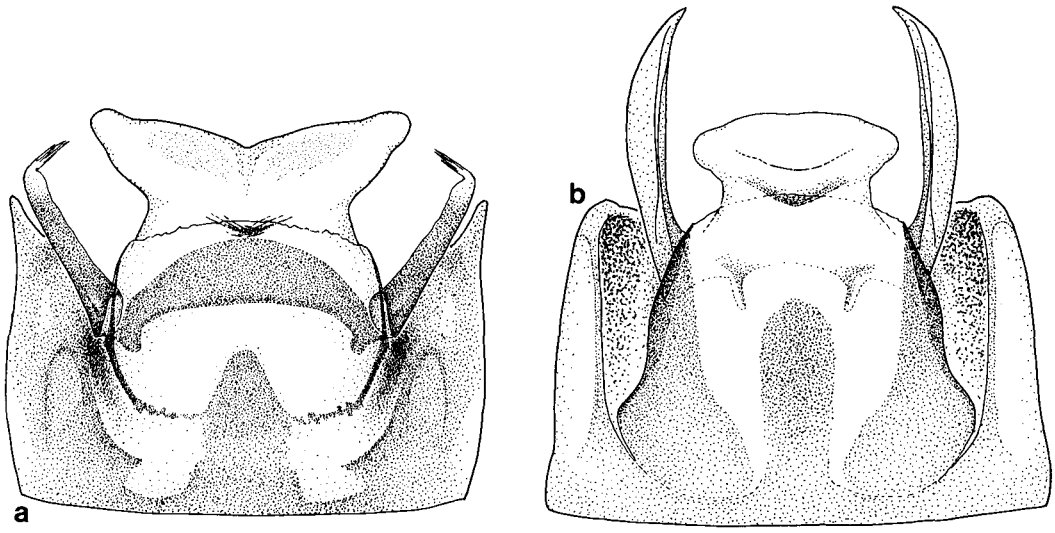

Fig. 2. Male genitalia. - a. *Caenis luctuosa* (subfamily Caeninae), - b. *Brachycercus harrisella* (subfamily Brachycercinae).

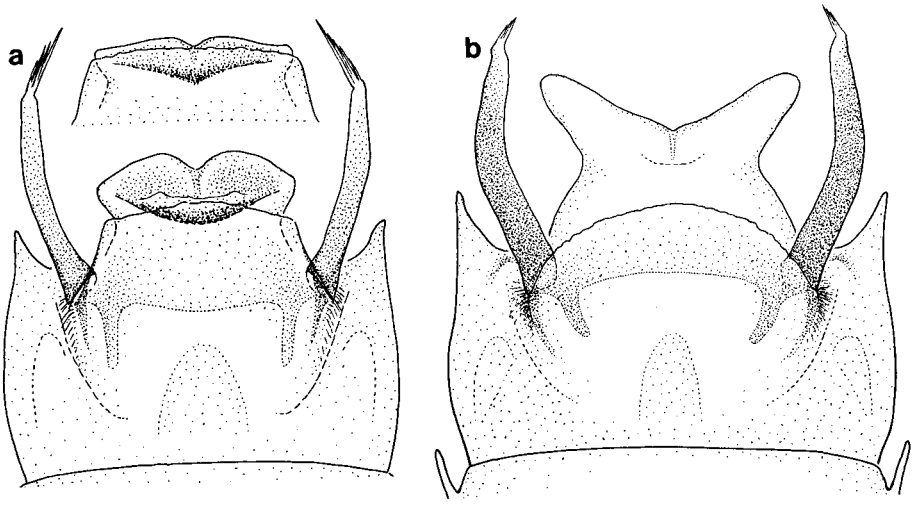

Fig. 3. Male genitalia. a. *Caenis cibaria*, - b. *Caenis pallida*.

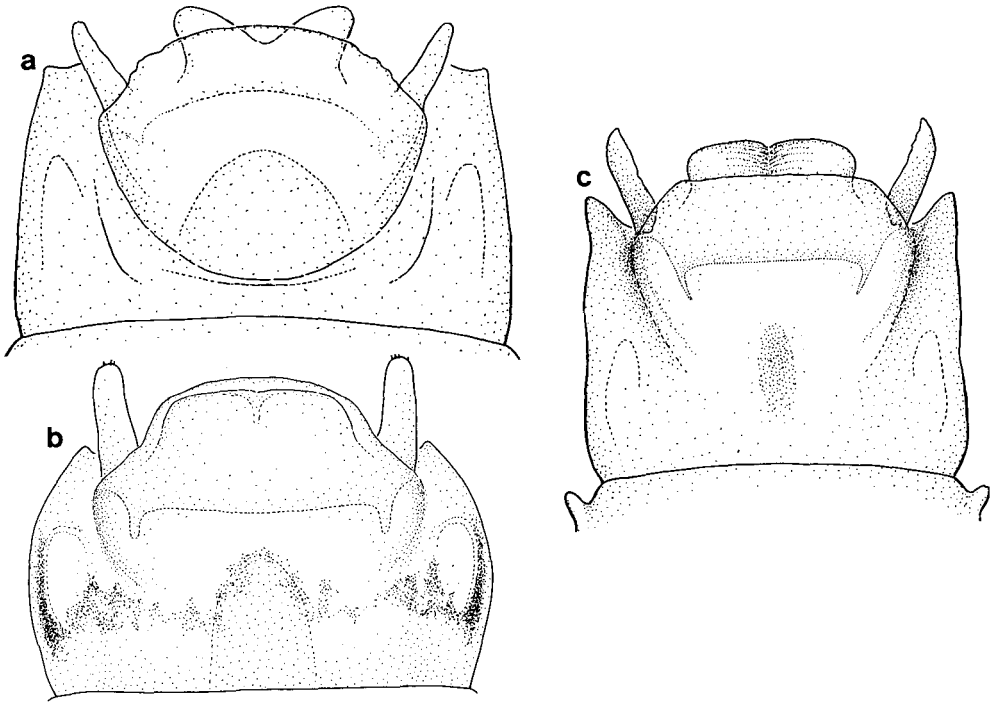

Fig. 4. Male genitalia. - a. *Caenis elouardi*, b. *Caenis quatipuruica*, - c. *Caenis ghibana*.

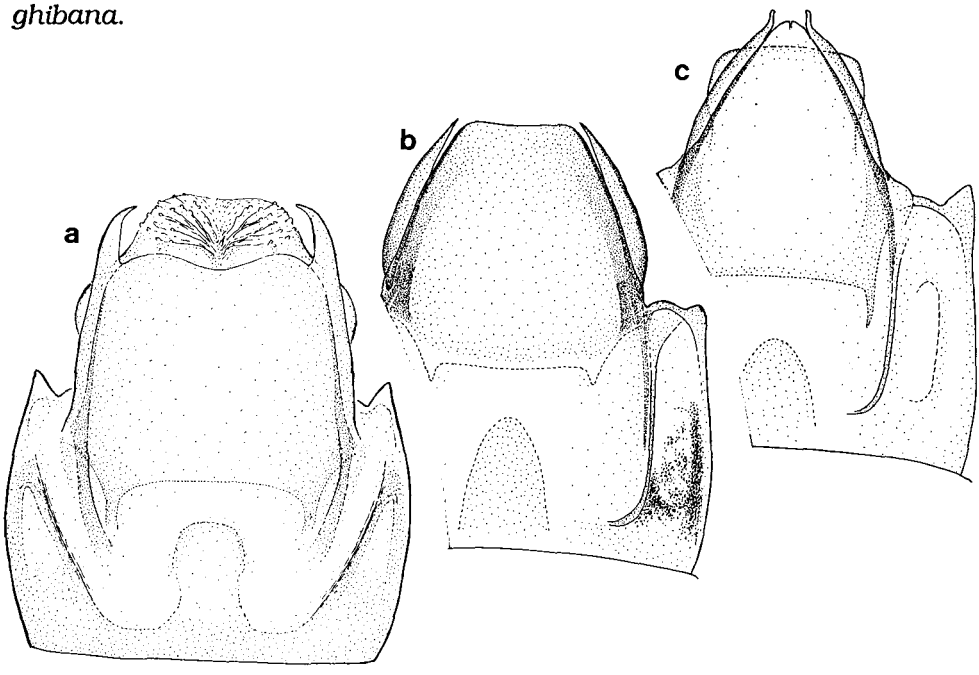

Fig. 5. Male genitalia. - a. *Brasilocaenis septentrionalis*, - c. *Brasilocaenis renata*, c. *Brasilocaenis puthzi*.

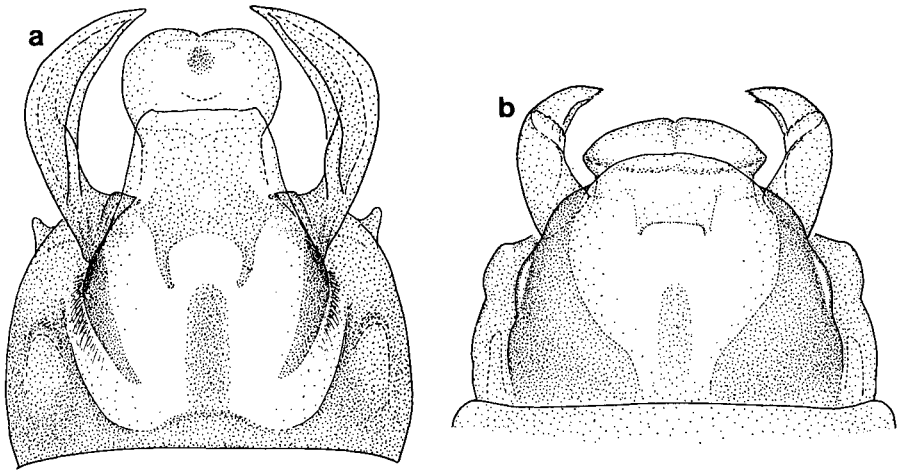

Fig. 6. Male genitalia. - a. *Tasmanocoenis tillyardi*,- b. *Afrocercus forcipatus*.

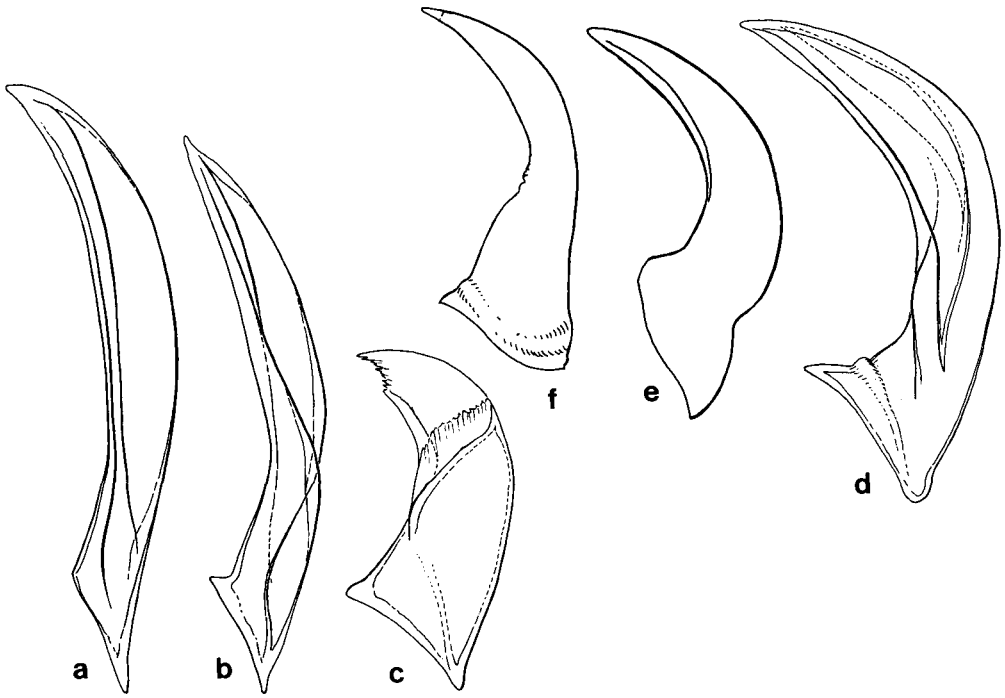

Fig. 7. Forceps. - a. *Brachycercus harrisella*,- b. *Cercobrachys etowah*, - c. *Afrocercus forcipatus*, - d. *Tasmanocoenis tillyardi*,- e. *Tasmanocoenis jillongi* (after Harker, 1957), - f. *Tasmanocoenis tonnoiri* (after Suter 1984).

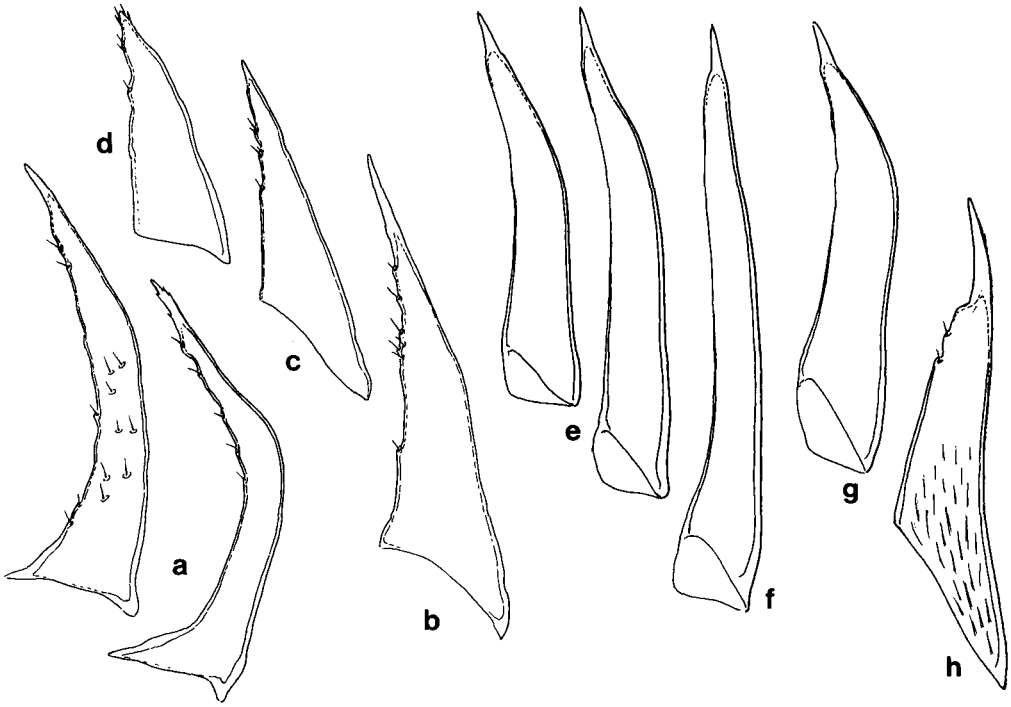

Fig. 8. Forceps. - a. *Caenis rivulorum*, - b. *Caenis horaria*, - c. *Caenis robusta*, - d. *Caenis strugaensis*, - e. *Caenis simulans*, - f. *Caenis jocosa*, - g. *Caenis pseudamica*,- h. *Caenis burmeisteri*.

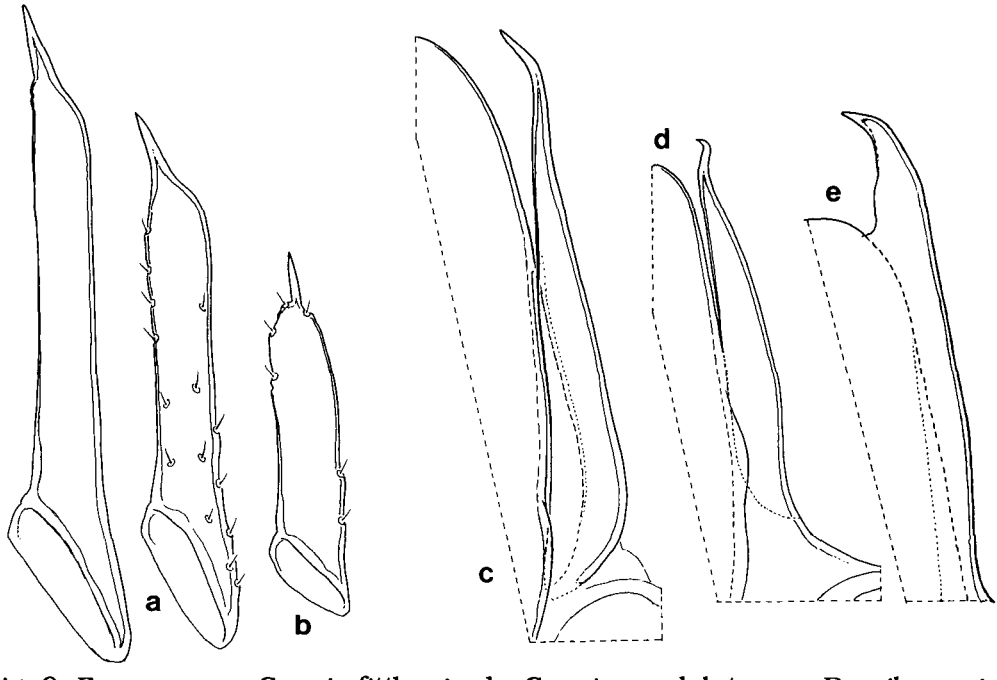

Fig. 9. Forceps. - a. *Caenis fittkaui*, - b. *Caenis candelata*, - c. *Brasilocaenis irmleri*,- d. *Brasilocaenis puthzi*, - e. *Brasilocaenis septentrionalis*.

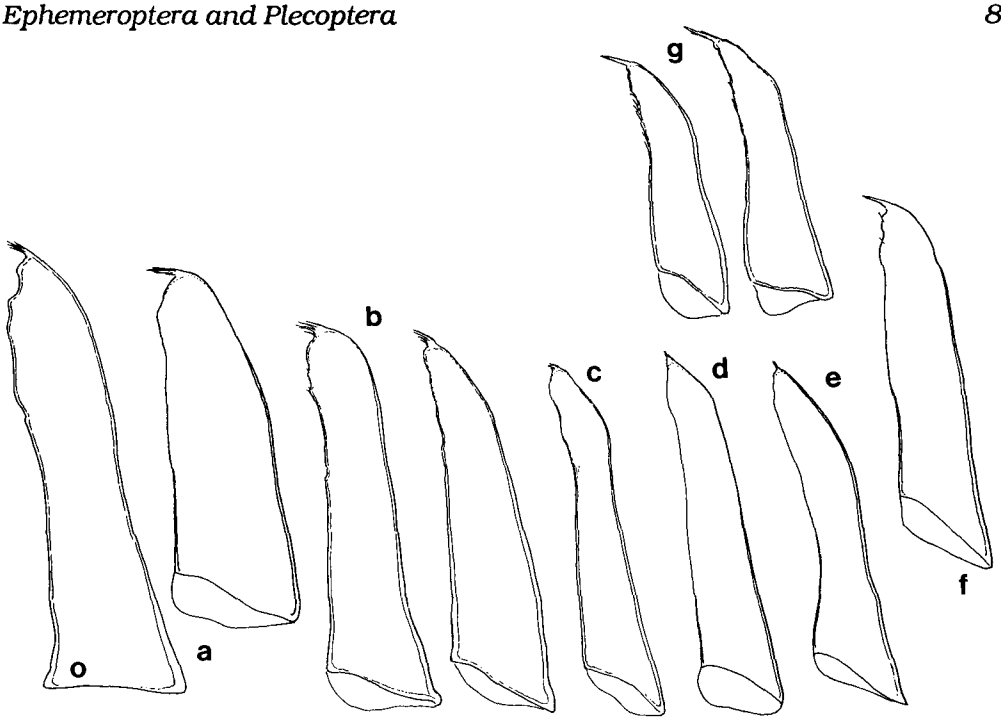

Fig. 10. Forceps. - o. *Caenis lactea*, - a. *Caenis picea*, - b. *Caenis beskidensis*, c. *Caenis pseudorivulorum*, - d. *Caenis hilaris*,- e. *Caenis punctata*, - f. *Amercaenis ridens*,- g. *Caenis pusilla*.

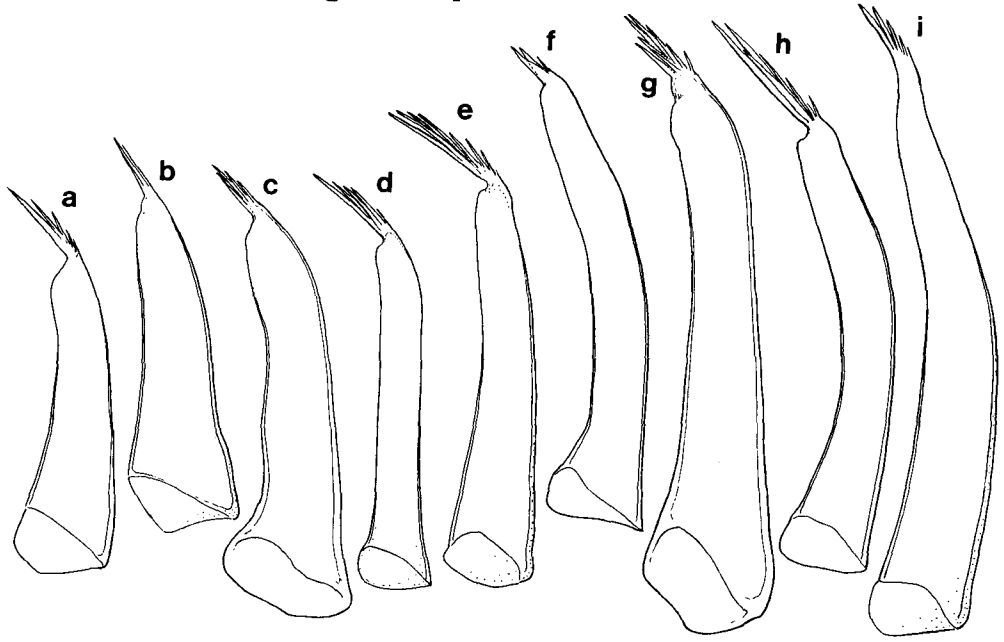

Fig. 11. Forceps. - a. *Caenis ulmeri*, - b. *Caenis liebenauae*, - c. *Caenis macrura*, d. *Caenis margherita*, - e. *Caenis magnipilosa*, - f. *Caenis gilliesi*, - g. *Caenis luctuosa*, - h. *Caenis cibaria*, - i. *Caenis pallida*.

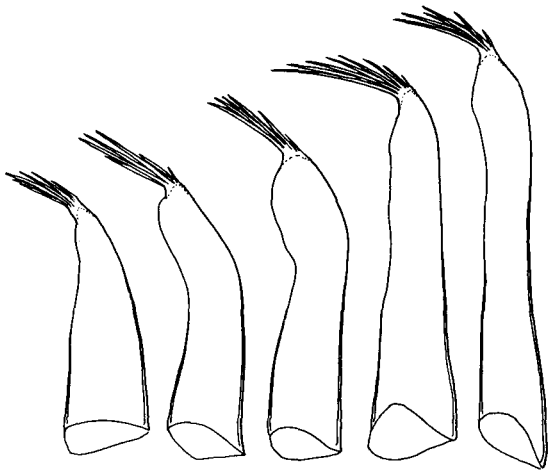

Fig. 12. Forceps of different paratypes of *Caenis kivuensis*.

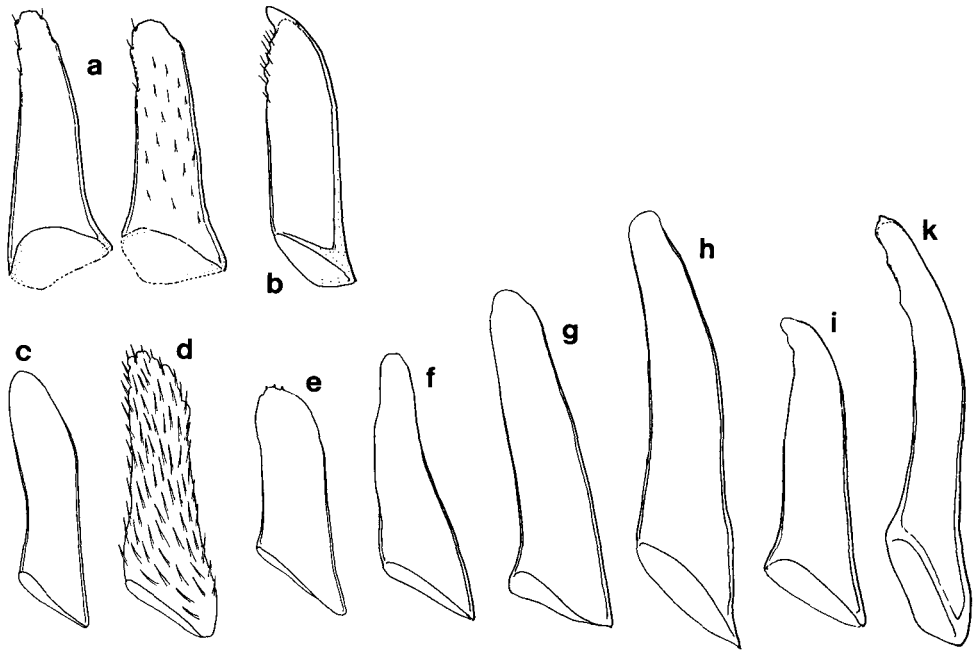

Fig. 13. Forceps. - a. *Caenis elouardi* , - b. *Caenis ghibana*, - c. *Caenis reissi*, - d. *Caenis quatipuruica*, - e. *Caenis sigillata*,- f. *Caenis* spec. (Argentina), - g. *Caenis* spec. (Argentina), - h. *Caenis argentina*,- i. *Caenis pflugfelderi*, - k. *Caenis* spec. (Cuba).

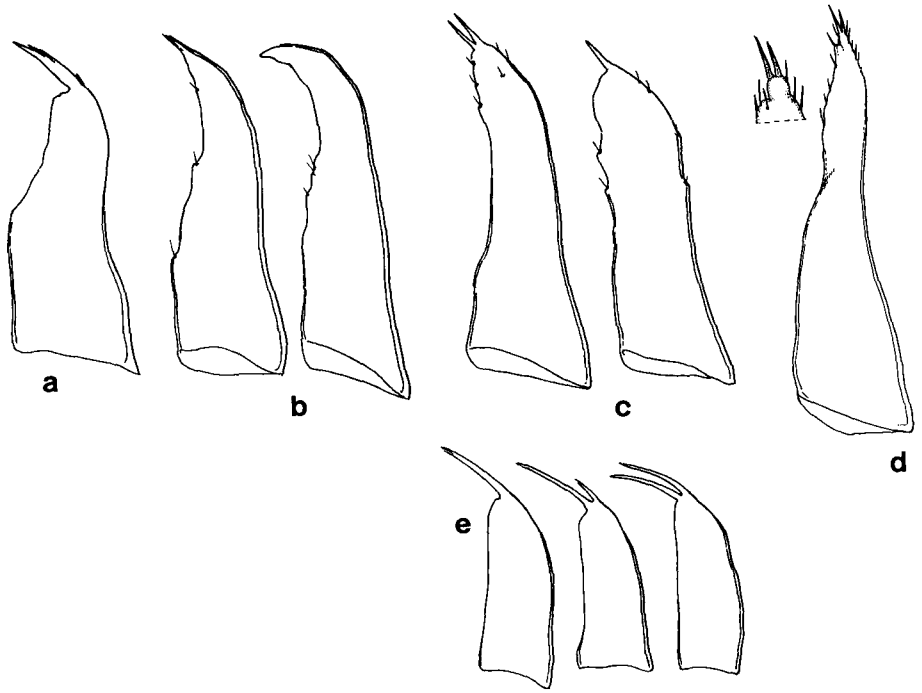

Fig. 14. Forceps. - a. *Caenis* spec. (India), - b. *Caenis basuto*, - c. *Afrocaenis major*, - d. *Caenis valentinae*, - e. *Caenopsella meridies*.