RELATIONSHIPS IN THE CAENIDAE (INSECTA: EPHEMEROPTERA)

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Problems with the construction of a natural phylogenetic system of the family Caenidae are shown. In many species either the larvae or the imagines are unknown. This increases the difficulties in the assessment of characters and their taxonomic value. An attempt is made to explain synapomorphies that seem to exclude each other.

INTRODUCTION

Since the revision of the family Caenidae by THEW (1960) the genera have changed in a dramatic manner. There were several new descriptions in the seventies and eighties (PUTHZ, 1975; GILLIES, 1977, 1982; SOLDAN, 1978, 1986; PROVONSHA, 1985; MALZACHER, 1987). Five genera have been declared as synonyms (SUTER, 1984; KLUGE, 1991; MALZACHER, 1993). Recently three new genera were described: the genus *Wundacaenis* from Australia by SUTER (1993), the genus *Madecocercus* from Madagascar by MALZACHER (1995) and the genus *Barnarda* from South Africa by PROVONSHA & MCCAFFERTY (1995).

At present the family Caenidae includes fifteen genera forming two groups: genera which are in the broader sense *Caenis*-like and those which are *Brachycercus*-like. In the *Caenis*-like genera many species are described only from the males while in *Brachycercus*-like genera often only the larvae are known. It is therefore sometimes hard to say if a diagnostic feature is valid for all species of an assumed group.

RESULTS AND DISCUSSION

Table 1 shows the genera together with the characters that are to be considered as synapomorphic. These are:

1 The shape of the imaginal prosternum. It is either broad and rectangular or narrow and triangular. I think the triangular prosternum is apomorphic because in the related families the prosternum is always broad. It occurs in all *Caenis*-like genera, in the large-eyed African genera, in the Australian genera and in *Caenoculis*. As this feature is recognizable already in the larval stage it is known sufficiently in all taxa.

2 The row of Microtrichia on the ventral side of the 2nd gill. It consists of a large number of denticulated scales that are to be found in the same genera as the triangular prosternum.

3 The ocellar tubercles on the larval head.

4 The lateral spines of the abdomen which are bent dorsally, to protect the gills.

5 The 2-segmented maxillary and labial palps. 3-5 occur in the *Brachycercus*-like genera. In *Clypeocaenis* and in *Barnarda* only the maxillary palps are 2-segmented (SOLDAN, 1978; PROVONSHA & MCCAFFERTY, 1995).

With these characters it seems possible to subdivide the family into two subfamilies:

The subfamily BRACHYCERCINAE: with the genera *Brachycercus, Cercobrachys, Insulibra-*

Table 1. Generic synapomorphies in the Caenidae. im = imagines - la = larvae.

	Brachycercus	Cercobrachys	Insulibrachys	Afrocercus	Madecocercus	Tasmanocoenis	Wundacaenis	Caenopsella	Afrocaenis	Caenoculis	Caenis	Amercaenis	Brasilocaenis	Clypeocaenis	Barnarda
1	–	–	–	–	–	X	X	X	X	X	X	X	X	X	X
2	–	–	–			X	X	X	X	X	X	X	X	X	X
3	X	X	X			–	–	–	–	–	–	–	–	–	–
4	X	X	X			–	–	–	–	–	–	–	–	–	–
5	X	X	X			–	–	–	–	–	–	–	–	(–)	(–)
6	X	X	X	X	X	X	X	–	–	–	–	–	–	–	

1	im/la	Prosternum triangular. Fore coxae contiguous
2	la	Row of microtrichia on the ventral side of the 2nd gill
3	la	Ocellar tubercles on the larval head
4	la	Lateral spines of the abdomen large and bent dorsally
5	la	Two-segmented maxillary and labial palps
6	im	Functional unit of forceps, forceps-muscle and lateral-sclerite

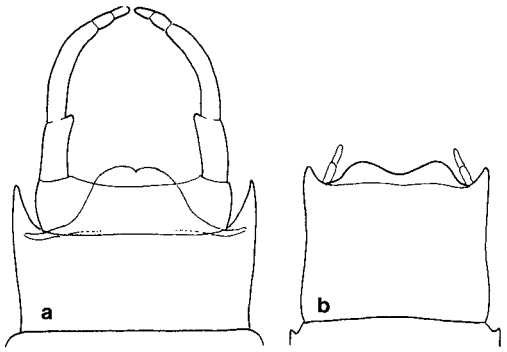

Fig. 1. Male genitalia of Neoephemeridae. a: *Neoephemera*; b: *Potamanthellus*.

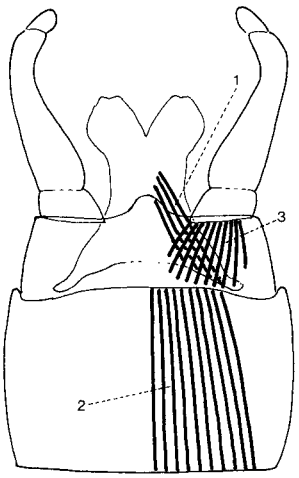

Fig. 2. Male genitalia of *Ephemerella (Serratella) ignita* with the right inner penis-muscle (1), the right half of the styliger-muscle (2) and the right forceps-muscle (3).

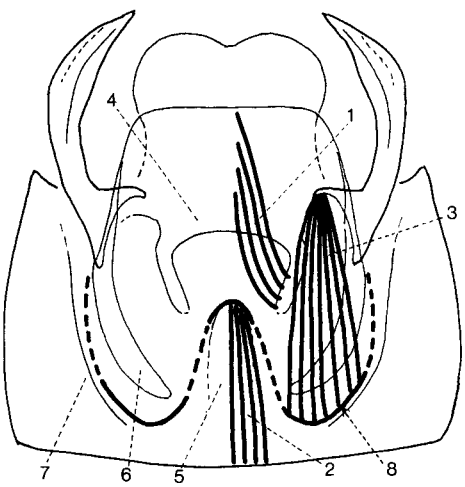

Fig. 3. Male genitalia of *Brachycercus harrisella* with the right inner penis-muscle (1), the right half of the styliger-muscle (2), the right forceps-muscle (3), the styliger-sclerite (4), the central-sclerite (5), the lateral-sclerites (6), the basolateral-sclerites (7) and the fore margin of the styliger (8).

chys, Afrocercus and *Madecocercus*. From the latter two genera the larval stages are unknown up to now.

The subfamily CAENINAE: with the genera *Caenis, Brasilocaenis, Clypeocaenis, Amercaenis, Barnarda, Caenopsella, Afrocaenis, Caenoculis, Tasmanocoenis* and *Wundacaenis*.

There are some other larval characters to distinguish the two subfamilies; in fact the whole appearance of the larval body is different.

I shall now go into diagnostic features of the male genitalia, but first I shall try to derive their structure from that of the related families.

Concerning shape and arrangement of the styliger and the forceps we have rather similar conditions in the Pannota-Superfamily Ephemerelloidea and the families Baetiscidae and one part of the Neoephemeridae. The long forceps, normally with 3 or 4 segments, are articulated caudolaterally to the broad and more or less rectangular styliger, like in *Neoephemera* (Fig. 1a).

In *Potamanthellus*, a genus that belongs to that group of the Neoephemeridae that EDMUNDS (1979) considers to be the sister-group of the Caenidae, the forceps are distinctly shortened, only 2-segmented and the articulation with the styliger has moved forward and lies level with the base of the caudolateral spines of the 9th sternite (Fig. 1b). We can find the same position in the Caenidae (Figs 4, 6).

Also the styliger itself has moved forward, so to speak into the 9th sternite. In the Caenidae there is no suture that marks the border between styliger and 9th sternite. But it is possible to reconstruct this border with the position of some muscles. These muscles are shown in the figures 2 to 6 (right half).

1st The styliger-muscle, running from the fore-margin of the 9th sternite to the border between the 9th sternite and the styliger.

2nd The forceps-muscles, running from the base of the forceps to this border, too, but from behind.

3rd The inner penis-muscles, running from the ventromedian part of the penis to the lateral fore-margin of the basal-plate of the penis.

In *Brachycercus* (Fig. 3) the very narrow styliger-muscle runs far backwards and marks the median part of the border on the hind margin of the central-sclerite. On the other

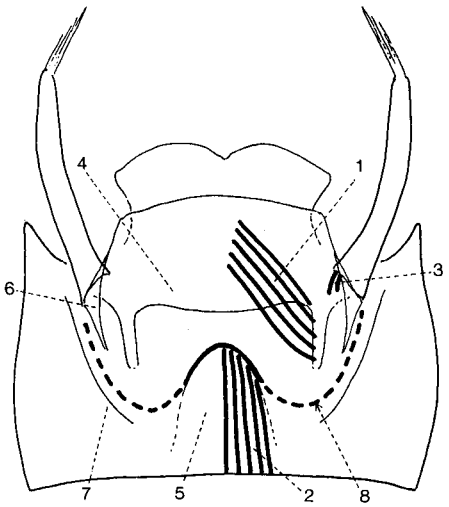

Fig. 4. Male genitalia of *Caenis cibaria*. Numbers see Fig. 3.

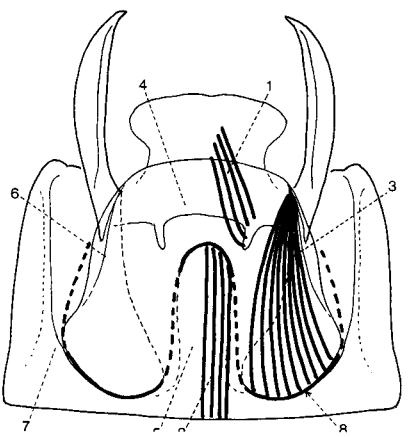

Fig. 5. Male genitalia of *Tasmanocoenis tillyardi*. Numbers see Fig. 3.

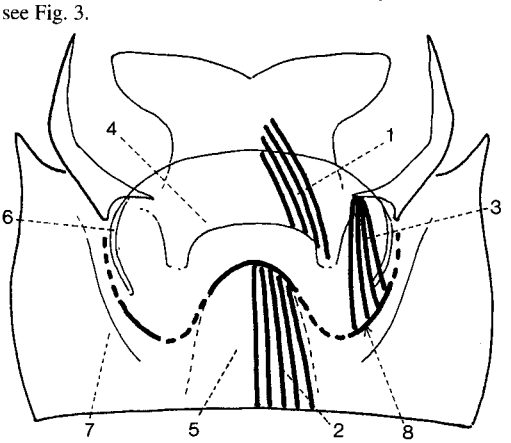

Fig. 6. Male genitalia of *Caenis rivulorum*. Numbers see Fig. 3.

hand the well developed forceps-muscle goes forward until the basolateral-sclerite that marks therefore the lateral part of the border. Consequently the fore-margin of the styliger proves to be a very strongly curved line ending at the bases of the forceps.

In *Brachycercus* the penis-muscles end on the styliger-sclerite; in particular on the apophyses. That means almost certainly that the styliger-sclerite is homologous with the basal-plate of the penis of other Ephemeroptera lying closely to the styliger. GRANDI (1960) already took this possibility into consideration. As she did not notice the styliger-muscle, she questioned the existence of the styliger. But she investigated only *Caenis macrura* and could find only very short forceps-muscles, because in nearly all *Caenis* species and other *Caenis*-like genera these muscles are reduced and often invisible. Therefore in these species the forceps-muscles cannot give an indication of the styliger-margin. Compared with the Brachycercinae it may lie between the lateral-sclerite and the basolateral-sclerite.

In summary, one can say: In the Caenidae there are two different types of genitalia:

1st type. Styliger with curved fore-margin. The lateral-sclerites are small, often totally reduced. The forceps-muscles are nearly invisible in most cases. The forceps are of different shape, often weakly developed and never grooved. Proper motion seems to be nearly out of the question.

2nd type. Styliger with very strongly curved fore-margin. All parts of the functional complex of lateral-sclerite, forceps-muscle and the nearly always grooved forceps are strongly developed. Proper motion of the latter is given. There is no conclusive proof that the *Potamanthellus*-group and the Caenidae are sister-groups but in both groups a reduction of the forceps and styliger took place. In my opinion in the developmental line of the Caenidae this reduction culminated in genitalia with short, one-segmented forceps without any function. This seems to me to be the initial stage for the evolution of the Caenidae. The lack of function is the requirement for the development of the great number of forceps-shapes as well as for the two genital-types.

Regarded in this way it seems clear that the functional unit of the strongly differentiated

genital-type 2 is apomorphic within the family. Because of its complexity it can be considered synapomorphic in all taxa where it occurs.
And where does it occur? In all *Brachycercus*-like genera but also in *Tasmanocoenis* (Fig. 5) and as it seems in *Wundacaenis*, too. That is to say: *Tasmanocoenis* and *Wundacaenis* belong to the Brachycercinae judging by the genital features whereas two other features, 1 and 2, give cause to coordinate them to the Caeninae (see Table 1).
There are synapomorphies excluding each other. Does that mean that the one or the other is in reality a convergence? I do not think so, because a real convergence is only given when the similar structures have developed in a different manner and from different organs or morphological structures and that presupposes strongly different genomes.
But the following seems to me to be possible: the genomes of all involved taxa are more or less identical regarding the concerning diagnostic features, but the factors which initiate or prevent the transcription of the concerning genes are specific or generic. Unfortunately this can go for the one or for the other of the above mentioned features so that it does not enable us to say with certainty to which subfamily the Australian genera may belong. But such a - naturally hypothetical - mechanism could explain the fact that there are sometimes highly differentiated characters that turn up, apparently without any rule, here and there in the family.
One example: In all examined *Caenis* species the forceps-muscles are strongly reduced (Fig. 4). But the European *Caenis rivulorum* (Fig. 6) does not only show well developed forceps-muscles but also a dilated forceps-base and a curved forceps-shape like in *Tasmanocoenis* (Fig. 5).
There is no doubt that the species is a real member of the genus *Caenis*. But on can imagine that, for some reason or another, there was a change in the transcription-mechanism so that the phenotypical realization of movable forceps became possible.
If this hypothesis or a similar one could be verified, the construction of a natural system for lower taxa by means of synapomorphies would become exceedingly questionable.

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REFERENCES

EDMUNDS, G.F. 1979. Biogeographical relationships of the Oriental and Ethiopian mayflies. Proc. 2nd Int. Conf. on Ephemeroptera: 11-14.

GILLIES, M.T. 1977. A new genus of Caenidae (Ephemeroptera) from East Africa. J. nat. Hist. 11: 451-455.

GILLIES, M.T. 1982. A second large-eyed genus of Caenidae (Ephemeroptera) from Africa. J. nat. Hist. 16: 15-22.

GRANDI, M. 1960. Contributi allo studio degli Ephemeroidei italiani XXIII. Gli organi genitali esterni maschili degli Ephemeroidei. Boll. Ist. Ent. Univ. Bologna 24: 67-120.

KLUGE, N. Yu. 1991. Mayflies of the Genus *Brachycercus* (Ephemeroptera, Caenidae) of the USSR Fauna. Vestn. zool. 2: 14-23.

MALZACHER, P. 1987. Eine neue Caeniden-Gattung *Afrocercus* gen. nov. und Bemerkungen zu *Tasmanocaenis tillyardi* (Insecta: Ephemeroptera). Stuttgarter Beitr. Naturk. (Ser. A) 407: 1-10.

MALZACHER, P. 1993. Caenidae der äthiopischen Region (Insecta, Ephemeroptera). Teil 2. Systematische Zusammenstellung aller bisher bekannten Arten. Mitt. schweiz. ent. Ges. 66: 379-416.

MALZACHER, P. 1995: Caenidae from Madagascar (Insecta: Ephemeroptera). Stuttgarter Beitr. Naturk. (Ser. A) 530: 1-12.

PROVONSHA, A.V. 1985. *Amercaenis:* new Nearctic genus of Caenidae (Ephemeroptera). Int. Quart. Ent. 1: 1-7.

PROVONSHA, A.V. & MCCAFFERTY, W.P. 1995. New Brushlegged Caenid Mayflies from South Africa (Ephemeroptera Caenidae). Aquatic Insects 17(4): 241-251.

PUTHZ, V. 1975. Eine neue Caenidengattung aus dem Amazonasgebiet (Insecta: Ephemeroptera: Caenidae). Amazoniana V(3): 411-415.

SOLDAN, T. 1978. New genera and species of Caenidae (Ephemeroptera) from Iran, India and Australia. Acta ent. bohemoslov. 75: 119-129.

SOLDAN, T. 1986. A revision of the Caenidae with ocellar tubercles in the nymphal stage (Ephemeroptera). Acta Universitatis Carolinae - Biologica (5-6), 1982-1984: 289-362.

SUTER, P.J. 1984. A redescription of the genus *Tasmanocoenis* LESTAGE (Ephemeroptera: Caenidae) from Australia. Trans. r. Soc. S. Aust. 108(2): 105-111.

SUTER, P.J. 1993. *Wundacaenis*, a New Genus of Caenidae (Insecta: Ephemeroptera) from Australia. Invertebr. Taxon. 7: 787-803.

THEW, T.B. 1960. Revision of the genera of the family Caenidae (Ephemeroptera). Trans. Am. ent. Soc. 76: 187-205.