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; Provonsia, 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 Provonsia & 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; Provonsia & McCafferty, 1995).

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

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

Relationships in the Caenidae

chys, Afro cerc us and Madecocercus. From the latter two genera the larval stages are unknown up to now.

The subfamily CAENINAE: with the genera Caenis, Brasilocaenis, Clypeocaenis, Americaenis, 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 caudal 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 foremargin of the 9th sternite to 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).

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
hand the well developed forceps-muscle goes
forward until the basolateral-sclerite that marks
therefore the lateral part of the border. Conse­
quently 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 possibil­
ity 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 opin­
ion in the developmental line of the Caenidae
this reduction culminated in genitalia with
short, one-segmented forceps without any func­
tion. This seems to me to be the initial stage for
the evolution of the Caenidae. The lack of func­
tion 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 Tasmanocaenis (Fig. 5) and as it seems in Wundacaenis, too. That is to say: Tasmanocaenis 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 genes. 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 Tasmanocaenis (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


