

SISTER RELATIONSHIP OF THE NEOPHEMERIDAE AND CAENIDAE (EPHEMEROPTERA: PANNOTA)^{1,2}

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ABSTRACT: A consistent structural characteristic has been found to be unique to the mayfly families Neophemeridae and Caenidae. It is termed a sutural ommation and is present on the adult mesonotum. The structure is described and illustrated. Its unique presence supports the hypothesis of a sister relationship of Neophemeridae and Caenidae among the pannote mayflies, a cladistic arrangement that has been somewhat debatable in the past. The Baetiscidae and Prosoptomatidae, which previously have been hypothesized to be closely related to either Neophemeridae or Caenidae by various authors, are considered to constitute an aberrant clade of mayflies with still dubious relationships within the Ephemeroptera.

Neophemerid mayflies, the "large squaregills" (McCafferty 1981), were considered among the burrowing mayflies in the first half of this century. For example, Traver (1935) considered them as one of the subfamilies of Ephemeridae (= families of Ephemeroidea), and Ulmer (1939) considered them in the family Potamanthidae. This association was based on the common possession of basally arched MP₂ and CuA veins in the forewings. Edmunds and Traver (1954) placed the neophemerids with the Caenidae, the "small squaregills" (McCafferty 1981), in a separate superfamily Caenoidea. This association was based on larval morphology, in particular the similar gill structure. Since that time, all workers, with the exception of Demoulin (1958), have grouped Neophemeridae with Caenidae rather than Ephemeroidea. McCafferty and Edmunds (1979) placed the Caenoidea among other mayflies that possess the apomorphic characteristic of more or less fused developing wingpads and are known as the pannote mayflies.

Given the general relationships of large groupings of mayfly families (e.g., see McCafferty 1991), it appears that adult similarities (wing venation) of neophemerids and burrowing mayflies (Ephemeroidea) were present in their immediate common ancestor, and of the pannote mayflies, only retained in the neophemerids. On the other hand, the larval similarities of neophemerids and other pannotes, including caenids, (e.g., fused wingpads) appear to be derived in these groups. Edmunds (1965), McCafferty (1972), and McCafferty and Edmunds (1976) have discussed how differential rates of evolution in the larval and adult stages can lead to such disparate stage characterization in certain

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Ephemeroptera taxa (i.e., with relatively ancestral characterization in one stage and relatively derived characterization in another stage).

Among the pannote mayflies, three major historical schemes of familial relationships are noteworthy. McCafferty and Edmunds (1979) recognized Neophemeridae as a phyletic sister group of Caenidae. Landa and Soldán (1985) recognized Neophemeridae as a sister group of Baetiscidae, with the two derived with another lineage consisting of Caenidae and Prosopistomatidae. McCafferty (1991) followed Landa and Soldán (1985) in recognizing Neophemeridae as a sister group of Baetiscidae, but derived this lineage from near the base of the Pannota. He also included Prosopistomatidae and Caenidae as sister groups (see also Tshernova 1970). None of the previous arguments supporting these various schemes have been compelling.

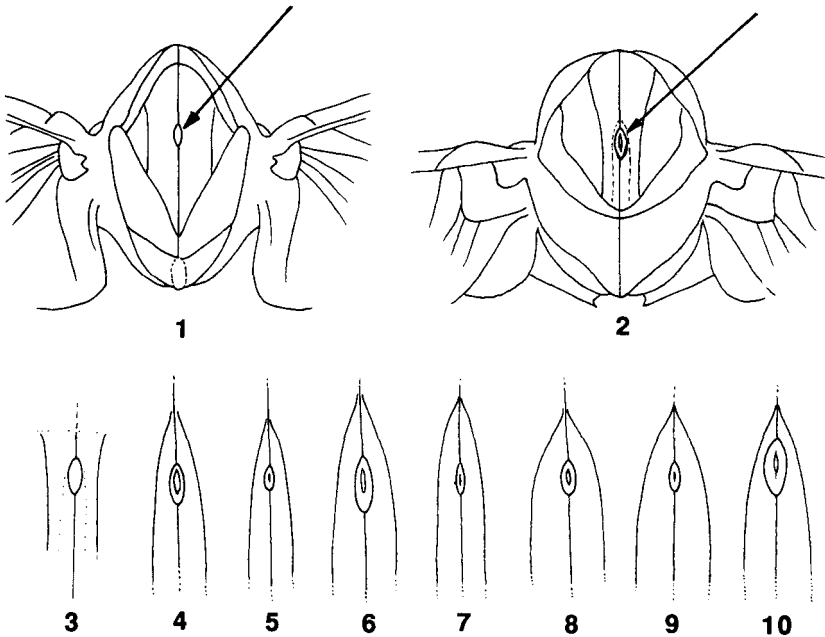
The Landa and Soldán (1985) scheme was based on data from internal anatomy, especially the ureterlike (their term) characteristics of Malpighian tubules in the case of Neophemeridae and Baetiscidae, and the arrangement of the alimentary canal in the case of Prosopistomatidae and Caenidae. Although these internal anatomical data provided valuable descriptions for certain pannote mayflies, any interpretation of them as synapomorphic is suspect because of not only the very small number of representatives sampled from families (Landa 1969) but also the current inability to substantiate cladistic polarity with respect to them.

McCafferty (1991) suggested that the operculate gills of abdominal segment 2 in Neophemeridae and Caenidae were fundamentally different. However, based on our recent comprehensive morphological studies, these gills are indeed essentially the same with respect to shape, ridge development and armature. McCafferty (1991) also stated that the carapacelike development of the larval thorax was not similar in Baetiscidae and Prosopistomatidae. Nonetheless, among Ephemeroptera, the carapace is found only in the Baetiscidae and Prosopistomatidae. We have additional data (Wang and McCafferty unpublished) showing that underlying gill morphology and certain mouthpart structures are similar and unique in these two families. These data strongly suggest that the carapace was commonly derived in the Baetiscidae and Prosopistomatidae. Kluge *et al.* (1995), without stating any reason, removed these latter two families from the Pannota and considered them sister families in a separate suborder of Ephemeroptera.

Although we have not been able to find any larval characteristics common to both Neophemeridae and Caenidae that are, without a doubt, apomorphic and unique (not subject to homoplasy), we have recently discovered a stable adult characteristic that strongly supports the hypothesis of a sister relationship of the two families. We present this characterization herein.

NEW CHARACTERIZATION AND DISCUSSION

A small, elongate eye-shaped membrane located medially on the mesonotum of adult caenids was noted and illustrated by Provonsha (1990). This appears as a short, primordial split along the medial suture, comprised of a clear membrane (Figs. 1, 3). We have found that this structure also occurs in adults throughout the Neophemeridae (Figs. 2, 4-10), but in no other mayflies (obviously all possible outgroups) that we know of. It differs somewhat in the Neophemeridae in terms of how membranous the structure is; sometimes it is not membranous. We call this structure the sutural *ommation* because of its eye shape. We hypothesize that it evolved in the immediate common ancestor of the Neophemeridae and Caenidae: its uniqueness among all mayflies is strongly suggestive of a sister relationship of the two families. Since we cannot surmise a likely function of this ommation, it is highly possible that it is non-adaptive. If that is the case, it may be an excellent stable character for not only defining the Neophemeridae + Caenidae clade but diagnosing the Edmunds and Traver (1954) and McCafferty and Edmunds (1979) concept of the superfamily



Figs. 1-10. Sutural ommation of the adult mesonotum. 1. *Caennis latipennis*. 2. *Neophemera youngi*. 3. *Brachycercus nasutus*. 4-5. *Potamanthellus amabilis*. 6-7. *P. chinensis*. 8-9. *N. purpurea*. 10. *P. compressa*.

Caenoidea in the adult stage.

The relative phylogenetic position of the hypothesized Neophemeridae + Caenidae clade among the Pannota is still not clear. None of the previously published proposals are convincing because of the use of characteristics with unsubstantiated polarity. In any case, we are now convinced that the two families form a distinct clade within the Pannota.

Baetiscidae and Prosopistomatidae, which have been variously associated with Neophemeridae or Caenidae previously, appear to be sister lineages that form a separate clade based on the carapace and certain mouthpart and gill characteristics as mentioned above (Wang and McCafferty ms). The clade is aberrant, and its relationship to the Pannota is unclear at this time. For example, if the shared trait of the A₁ vein of the forewings ending in the outer margin (see Fontaine 1958) is plesiomorphic in Prosopistomatidae + Baetiscidae, then all other mayflies constitute a separate grouping because they would share the apomorphic modified forewings with a reduced anal area and shortened A₁. This would also indicate that the carapace of Prosopistomatidae + Baetiscidae is not derived in common with the fused wingpads of the Pannota, including the Ephemerellidae, Leptohiphidae, Tricorythidae, Neophemeridae, and Caenidae. Obviously, more cladistic research is needed before these further questions can be completely resolved.

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