

NEW DIAGNOSTIC CHARACTERS FOR THE MAYFLY FAMILY BAETIDAE (EPHEMEROPTERA)¹

T.-Q. Wang, W. P. McCafferty²

ABSTRACT: Two newly discovered universal characteristics are proposed to distinguish larvae of the family Baetidae (Ephemeroptera) from those of all other families of mayflies. These include the orientation of the lateral branches of the epicranial suture anterior of the lateral ocelli, and the ventral orientation of the dorsal lobe at the apices of the femora. Use of these new characters should eliminate the previously necessary use of complex combinations of characters that have been used in keys and that have continued to meet with exceptions.

The family Baetidae usually can be distinguished in the larval stage by a combination of general characteristics. These include a streamlined body, hypognathous head, relatively long antennae, antennae originating anteriorly or anterolaterally on the head, long and narrow glossae and paraglossae of the labium, abdominal segments without well-developed posterolateral projections, and in mature male larvae, developing turbinate compound eyes (e.g., Edmunds, *et al.* 1976). Unfortunately, on a world level, each of these characteristics fails in certain genera of Baetidae, and several of them fail in a few genera. For example, *Platybaetis* Müller-Liebenau (1980) has a prognathous head with short antennae originating dorsally (Fig. 5), and a depressed body. Recently, Lugo-Ortiz and McCafferty (1996) described a new genus of Baetidae that, remarkably, lacks the male turbinate eyes, one characteristic that historically has been considered a unique and consistent characteristic for the family. The turbinate eyes of baetids continue to be regarded as a synapomorphy defining the family phylogenetically, and are regarded to have been secondarily lost in this one particular baetid lineage (Lugo-Ortiz and McCafferty 1996).

In the Northern Hemisphere, diagnosis of all baetids from Ameletidae and Siphonuridae [previously equal to Siphonuridae (see McCafferty 1991)], has been problematic because there could be exceptions to the key couplets involving the relative length of the antennae and development of the posterolateral processes, even if augmented with mouthpart characters, as was discussed by McCafferty (1981). In the Southern Hemisphere, a somewhat similar problem is found in distinguishing the Baetidae from Metamoniidae [previously considered Siphonuridae in part (see McCafferty (1991))] in keys to Australian mayfly families (e.g., Peters and Campbell 1991). The dilemma in North America was partly rectified by McCafferty (1981), who showed that, in North America, two-tailed baetid larvae were easily distinguished from Siphonuridae and Ame-

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² Department of Entomology, Purdue University, West Lafayette, IN 47907.

letidae, and that these latter three-tailed mayflies could then be separated from three-tailed baetid larvae by the relative length of the antennae. This, of course, meant keying out the family Baetidae in multiple places in keys to families.

An exception to all three-tailed baetids having relatively long antennae subsequently became apparent with the discovery of the new genus *Barbaetis*, which possesses a well-developed median caudal filament and relatively short antennae (Waltz *et al.* 1985). Even in a recently published key to the families of mayflies by Edmunds and Waltz (1995) in the third edition of "An Introduction to the Aquatic Insects of North America," a characteristic – included in the couplet leading to Baetidae to account for the variability expressed by *Barbaetis* – is stated as "or, antennae shorter than twice width of head, but labrum with notched distal margin." Quite unintentionally, this causes the genus *Ameletus* and the family Ameletidae to be incorrectly keyed out as Baetidae.

An obvious way to alleviate these identification problems, and the complex key couplets that result, would be to have at least one characteristic that would separate all Baetidae larvae from all other mayflies with which they might be confused. Historically, this grouping would include only mayflies with minnowlike bodies (pisciform mayflies), but recently "flatheaded" baetid larvae have been discovered in the Orient (Müller-Liebenau 1980, Mol 1989) that are reminiscent of Heptageniidae as well as some Leptophlebiidae.

NEW CHARACTERS

We have discovered external morphological larval traits that appear to distinguish larvae of the family Baetidae from those of all other mayflies throughout the world. In larval specimens of Baetidae that we have examined (representatives of all known and some undescribed genera), lateral ocelli are posterior to the initial lateral branches of the epicranial suture (e.g., Figs. 1-6). In all specimens of other mayflies, the initial lateral branches of the epicranial suture either connect with the lateral ocelli, usually near the center of the ocelli, but also at the posterior edges of the ocelli, or are slightly posterior to the ocelli (e.g., Figs 7-12). In all female larvae and males of broad-headed baetid larvae, the branches of the epicranial suture are easy to see. In very mature male larvae of Baetidae with narrow heads, some manipulation of the overshadowing large eyes may be required.

In certain instances among non-baetid families, lateral ocelli may not be readily evident and the epicranial suture, itself, may be obscure. Closer observation, however, will usually reveal these structures, although lateral branches can be extremely short, for example, on the aberrant head of *Ametropus* (Ametropodidae) larvae. Unfortunately, many published figures of mayflies, especially whole larval drawings, do not show details of the epicranial suture, and thus it can be futile to attempt comprehensive comparisons based only on published figures.

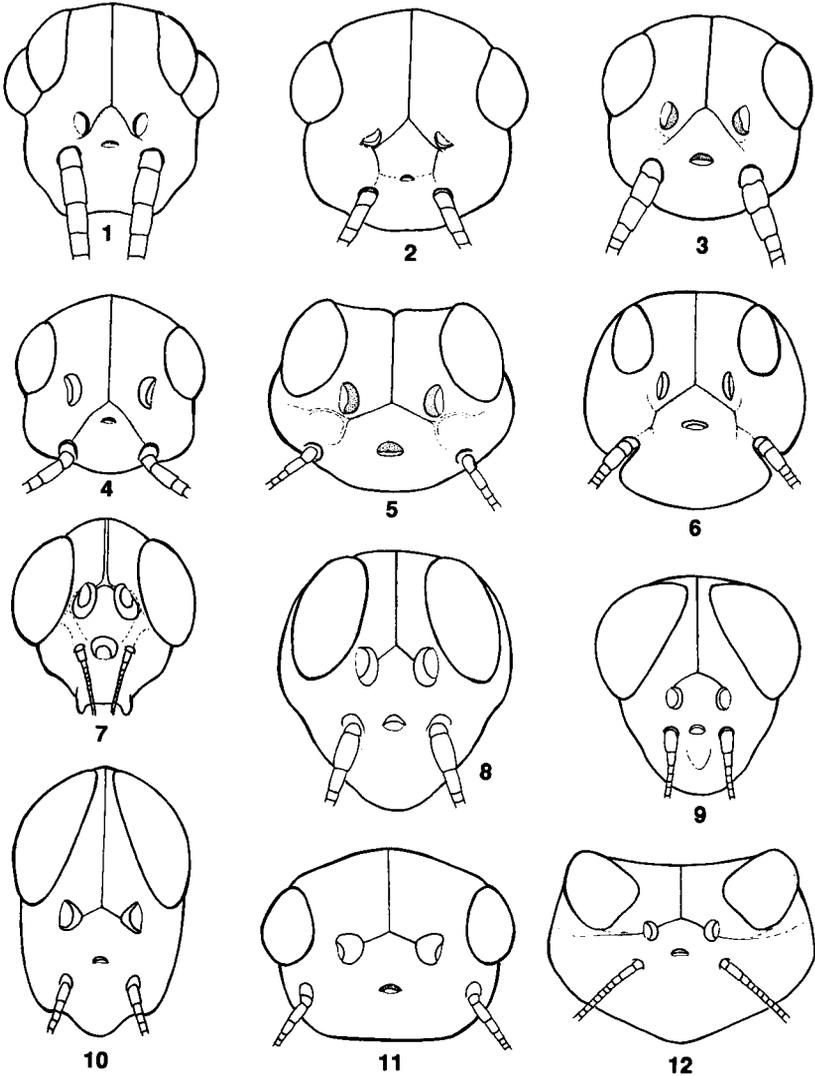
The initial lateral branches of the epicranial suture in Baetidae larvae not only run anterior to (below) the lateral ocelli, but in many, they continue for

some distance beyond the lateral ocelli (Figs. 2-6), and in some groups, each initial lateral branch becomes subsequently branched (Figs. 2, 3, 5, 6). In many other mayflies, the lateral branches of the epicranial suture end at the ocelli (Figs. 8-11). In Heptageniidae and genera of some other families, however, the lateral branches continue to extend laterally beyond the lateral ocelli (Fig. 12), and a somewhat extreme example of this is seen in *Atopopus* [Fig. 1 of Wang and McCafferty (1995)]. In Siphlaenigmatidae, the initial lateral branches directly meet the lateral ocelli, but a weak suture line also connects the anterior edge of the lateral ocelli with the median ocellus (Fig. 7).

A second useful character appears to be the shape of the apices of the larval femora. In representatives of all genera of Baetidae known as larvae, we have found that the apex of the dorsal lobe of the femoral apex is oriented ventrally (e.g., Figs. 13-16). To fully understand this somewhat more complex character, it must be kept in mind that we follow the terminological suggestion of Hubbard (1995) in recognizing the narrow edges of the femora as dorsal and ventral aspects. The tibia adducts toward the ventral edge of the femur. (In some Ephemeroptera literature, the dorsal aspect of the larval femur is referred to as posterior, and the ventral aspect as anterior because of the *in situ* orientation of legs often encountered.) It must also be realized that there is a distinguishable separation of the apex of the femur into an ventral portion (sometimes appearing as a lobe) and dorsal portion (always a lobe in baetids). These ventral and dorsal areas are evidenced by a slight to moderately deep medial incision (sometimes a clear furcation, sometimes only a fusion line) or by obvious differences in shape and development.

In Baetidae, the dorsal and ventral femoral lobes, when both are developed, can together give the impression of an entirely convex femoral apex (Figs. 13, 14), although the dorsal lobe makes up the greater part of the convexity because it is oriented ventrally and thus tends to wrap around the ventral lobe, or part of it. R. D. Waltz (pers. comm.) has pointed out to us that, in certain *Callibaetis* and some other genera, the dorsal lobe is not rounded but more truncate (e.g., Figs. 15, 16). However, even in these baetids, we found that the ventral orientation of the dorsal lobe is still obvious from its oblique medial margin.

In all non-baetid mayfly larvae that we have examined, the apex of the femur does not have a ventrally oriented dorsal lobe (e.g., Figs. 17-20). Oftentimes, the dorsal lobe is not developed (e.g., Figs. 18, 19), whereas the ventral lobe may be variously developed and sometimes highly developed (e.g., Fig. 19). In some Oligoneuriidae (e.g., Figs. 20), the apex of the femur is convex, but the two lobes are essentially symmetrical. In some Leptophlebiidae, a similar situation is found, but lobes are not as well developed [e.g., see *Notachalcus* (Fig. 59) of Peters and Peters (1981)]. The dorsal lobe is never ventrally oriented in non-baetids, even in some Leptophlebiidae whose dorsal lobe is slightly larger than the ventral lobe [e.g., see *Fasciamirus* (Fig. 87) of Peters *et al.* (1990)].

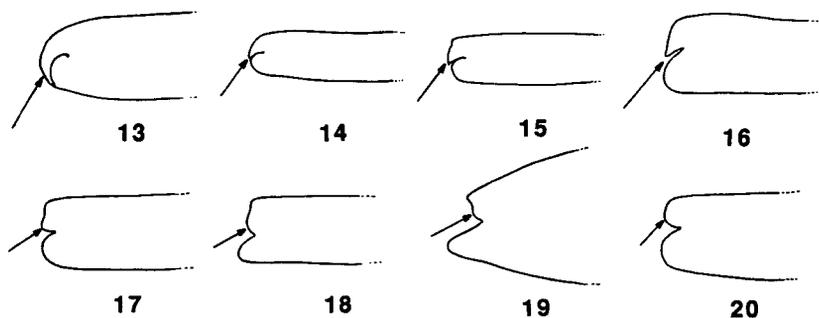


Figs. 1-12. Epicranial sutures of the larval heads of mayflies. 1. *Callibaetis* sp. (Baetidae). 2. *Barbaetis* sp. (Baetidae). 3. *Acentrella* sp. (Baetidae). 4. *Baetodes* sp. (Baetidae). 5. *Platybaetis* sp. (Baetidae). 6. *Echinobaetis* sp. (Baetidae). 7. *Siphlaenigma* sp. (Siphlaenigmatidae). 8. *Ameletus* sp. (Ameletidae). 9. *Siphloplecton* sp. (Metreopodidae). 10. *Ameletoides* sp. (Metamoniidae). 11. *Paraleptophlebia* sp. (Leptophlebiidae). 12. *Compsoeuriella* sp. (Heptageniidae).

We have found the femoral apex character easy to see and use. Again, however, illustrators of mayfly larvae have often neglected or incorrectly figured details of this new character, or, often, the orientation of legs in their drawings do not clearly show apical femoral structure.

The non-baetid orientation of the initial lateral branches of the epicranial suture and the non-baetid shape of the apices of the femora also apply to the family Siphlaenigmatidae, a group of New Zealand mayflies shown by McCafferty and Edmunds (1979) to be intermediate between certain other pisciform mayflies and the Baetidae proper. These differences would appear to provide additional arguments for not considering this grouping as a subfamily of Baetidae (McCafferty 1991), as was done previously by McCafferty and Edmunds (1979) and Landa and Soldán (1985).

We are learning, in the study of Ephemeroptera, that entirely universal and exclusive character states are difficult, if not impossible, to find for very diversified and ubiquitous higher taxa (i.e., extant families Baetidae and Leptophlebiidae). Due to their highly radiated nature and worldwide distribution, they are prone to convergences and secondary losses in at least some of their many lineages. With this in mind, we would not be surprised if, in the future, a convergence of one or both of the new baetid characteristics reported here are found at perhaps the genus or species level in some other group of mayflies. We would predict, however, that the epicranial suture character is probably the most stable of the two. The shape of the apices of the femora, on the other hand, may be more susceptible to homoplasy because there is considerable variation both within Baetidae and within non-Baetidae mayflies although we have yet to find any overlap. Leptophlebiid lineages are always candidates for such homoplasy, as witnessed by the incredible convergences in certain lineages of this family for character states usually associated with other groupings of mayflies [e.g.,



Figs. 13-20. Distal apices of larval right hindfemora of mayflies (anterior view, pointer to dorsal lobe; see text for explanation of directional terms). 13. *Baetis* sp. (Baetidae). 14. *Cloeon* sp. (Baetidae). 15. *Cloeodes* sp. (Baetidae). 16. *Callibaetis* sp. (Baetidae). 17. *Ameletus* sp. (Ameletidae). 18. *Siphonurus* sp. (Siphonuridae). 19. *Afronurus* sp. (Heptageniidae). 20. *Elassoneuria* sp. (Oligoneuriidae).

the pannota-like thorax of adult *Traverella* (McCafferty and Edmunds 1979) and the ephemereid-like wing venation of *Melanemerella* (Wang and McCafferty 1996)]. One other caveat is that a large fraction of Baetidae of the Southern Hemisphere is as yet unknown.

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