

NOTE

Phylogenetics and the Reconfirmation of *Dentatella* Allen  
(Ephemeroptera: Ephemerellidae)

The history of Ephemeroptera taxonomy has involved instances of one species described as an adult and another species described as a larva proving to be the same species once rearing associations of the two stages have taken place. For some of the more recent examples establishing such associations, see Whiting and Lehmkuhl (1987), McCafferty and Provonsha (1988), McCafferty and Silldorff (1998), and Burian (2002). Lugo-Ortiz and McCafferty (1996a) argued that some such associations were inevitable but because of the present imperative to document the biodiversity of the world, the possibility of such eventual associations should not preclude the description of species based on either stage. In a recent instance (Burian 2002), adults of *Eurylophella coxalis* (McDunnough) (previously unknown as larvae) were shown to be associated with the known larvae of the genus *Dentatella* Allen, as both *D. bartoni* (Allen) and *D. danutae* McCafferty (previously unknown as adults). *Dentatella* and the more speciose genus *Eurylophella* Tiensuu had previously been shown to be sister branches within the Ephemerellidae subfamily Timpanoginae (McCafferty and Wang 1994, 2000). Burian's placement of the species in *Eurylophella* and dissolution of *Dentatella*, however, discounted compelling cladistic evidence (McCafferty 1977, 1978, 2000; McCafferty and Wang 1994, 2000) that, within a framework of strict phylogenetic hierarchical classification, allows this species to reside in a separate genus.

To support his position, Burian (2002) proposed an arbitrary rule that both adult and larval stages of lineages must possess defining morphological apomorphies in order to be recognized at the genus level. This

effectively eliminated the genus *Dentatella* because its divergence with *Eurylophella* is based on larval apomorphies. We reject Burian's rule because it is both unrealistic and unnecessary to phylogenetic systematics, and would prove devastating to the higher classifications of metamorphic organisms. For example, we estimate that Burian's rule would eliminate well over half of the mayfly genera, by discounting genera that are now based on phenetic data and thus taken as hypothetical groupings yet to be tested with cladistics, and by discounting genera now unknown in one or the other stage, including nearly all extinct genera. A consideration of groups that have undergone cladistic analysis [for example, in the *Baetodes* complex (McCafferty and Baumgardner 2003), the *Bugilliesia* complex (Lugo-Ortiz and McCafferty 1996b), the *Hermanella* complex (Flowers and Domínguez 1991), the *Miroculus* complex (Savage and Peters 1982), Neoephemeridae (Bae and McCafferty 1998), Potamanthidae (Bae and McCafferty 1991), Teloganodidae (McCafferty and Wang 1997, McCafferty and Benstead 2002), and Timpanoginae (McCafferty and Wang 1994)] indicates that a combination of both adult and larval synapomorphies or autapomorphies does not exist at the point of generic branching in a large proportion of genera. Such does not even exist at more basal branchings involving several families and higher taxa of mayflies. For example, a single adult synapomorphy common to the Leptohiphidae is the basis of that taxon being recognized as a non-paraphyletic family separate from Coryphoridae (Molineri et al. 2001). Even if Burian intended to qualify his rule by limiting it only to monospecific genera [the largest category of genera in all biota (see

e.g., Raup 1991)], his rule would still decimate higher classifications and undermine their potential applications.

Monophyly and branching sequence are the essential bases for phylogenetic higher classifications (e.g., Hennig 1966), with no specification of what life stage or multiple life stages of a lineage must contribute the apomorphies supporting hypotheses of monophyly and no specification of the degree of synapomorphy required at any branch for defining taxonomic categories. Because rates of morphological evolution vary considerably between larval and adult stages of mayflies (e.g., see McCafferty and Edmunds 1976, fig. 1) and other metamorphic organisms when different selection environments are involved, there is no logical reason to expect morphological apomorphies to be expressed in multiple life stages of every lineage and clade. These life stages are "character-bearing semaphoronts," the basic comparable elements of biology, in the terms of Hennig (1966), and any one semaphoront of an evolving lineage may sufficiently demonstrate morphological character evolution for the purposes of phylogenetics. Burian's rule, insisting on layered evidence from both adults and larvae for a particular taxonomic category is tantamount to an arbitrary gap criterion. McCafferty (1991) rejected the use of all gap criteria, following Wiley's (1981) admonition that phylogenetic classifiers must reject gaps and definitions of taxonomic categories based on such criteria. Finally and not in the least, imposition of Burian's rule and the resultant severe reduction of genera would significantly lessen the valuable indications of comparative biology (the "explanatory powers") that are inherent in the complex hierarchies of phylogenetic classifications (Ross 1974, Farris 1979, Wiley 1981, Ax 1987).

In keeping with a philosophy of providing strictly phylogenetic classifications of Ephemeroptera when possible, with a maximum of information content and unconstrained by gap or special criteria, or any

selective use of such, we are regarding the above treated recently associated species as *Dentatella coxalis* (**new combination**), and thus continue to recognize the cladistic-founded genus *Dentatella*—a highly distinctive taxon in the larval stage and sister lineage to *Eurylophella*. These sister genera are phylogenetically distinct within the tribe Eurylophellini of the subfamily Timpanoginae. In the case of *Dentatella*, for example, the broadened larval femur is autapomorphic within the subfamily, and the relatively enlarged size of operculate gill 4, covering much of abdominal tergum 8 is autapomorphic within the order. For *Eurylophella*, the much elongated larval abdominal tergum 9 is a unique synapomorphy within the order. We know of no evidence, out-group or otherwise, that suggests alternative polarities with respect to these characters.

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