
26 Comparative functional morphology of larval *Stenacron interpunctatum* and *Rhithrogena pellucida* (Ephemeroptera: Heptageniidae) and *Ephemerella needhami* (Ephemeroptera: Ephemerellidae), with application in mayfly taxonomy and ecology

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*Examination of the functional role of mouthparts and attached structures of *Stenacron interpunctatum*, *Rhithrogena pellucida* and *Ephemerella needhami* using videomacroscopy and scanning electron microscopy begins to replace speculation about ecological roles and taxonomic significance of such structures with observational data. Detailed study of these three species, along with casual observations of seven additional taxa, gives observational data to support a hypothesis tying increased development of the maxillary palps in heptageniids to increased current speed in the microhabitat. Detailed study of feeding also gives important insight into the selective pressures placed on taxonomically important structures and helps distinguish between homology and convergence in these structures.*

Introduction

The mouthparts of most organisms are highly adapted for the essential role of obtaining food from the environment. The crucial nature of their task and the structural diversity needed to deal with the mechanical problems associated with ingesting a wide variety of food sources in manifold microhabitats has led to evolution of many diverse mouthpart structures. In addition, as organisms compete for food, many of them narrow their niches with regard to the microhabitats they exploit or the particular food they consume within that microhabitat; such specialization often leads to species-specific mouthpart structures. Thus, the mouthparts of ephemeropteran larvae can make excellent taxonomic characters

because they vary between species and are intimately associated with the evolutionary processes that lead to differentiation between species. Likewise, since the morphology of these structures is often determined by physical factors unique to different modes of feeding, the mouthparts of larval Ephemeroptera can be important predictors of ecological function.

Traditionally, taxonomists have used mouthpart characters only after some appreciation of the range of variation in a series of specimens. If sufficient specimens are available, such a procedure may be feasible, but it will never be on scientifically solid ground until the selective pressures and ecological roles of the structures involved are fully understood. This understanding can arise from detailed studies of the functional morphology of mouthparts and other feeding structures. With this information, the taxonomist can move from merely describing the variation to actively explaining it in terms of differences in microhabitat and diet. The taxonomist will also be in a position to evaluate the significance of variations between populations or taxa. If there are sufficient taxa with associated valid functional-morphological data, potential problems in distinguishing between homology and convergence can be avoided.

The ecologist can likewise use functional-morphological data to make predictions of the ecology of taxa that have morphology similar to that of other, better-studied taxa. Such predictions can be important in attempting to understand community dynamics where study of all individual species would be impractical.

To date, unfortunately, taxonomists have often been forced to use mouthpart characters without the benefit of a firm understanding of their function, and ecologists have likewise been limited to making assumptions about feeding ecology based on scanty, indeed, often incorrect data. Much of the ephemeropteran literature is littered with anecdotal information or pure speculation concerning the function of larval mouthparts. There is, however, a rapidly growing body of evidence on the detailed functional morphology of the mouthparts of larval Ephemeroptera, and this paper will attempt to show how it can be applied in several specific cases to problems in taxonomy and ecology.

Strenger (1953) made a careful examination of feeding structures in *Ecdyonurus* and *Rhithrogena*; later she turned her attention to the role of the mandibles (Strenger 1973) and more generalized aspects of feeding in larval Ephemeroptera (Strenger 1979), as well as additional studies of the functional morphology of *Palingenia* (Strenger 1970), *Ephemera* (Strenger 1975) and *Proboscidiplacia* (Strenger 1977). Her student, Schonmann, also made detailed studies of feeding in *Siphonurus* (Schonmann 1979, 1981) and *Lepeorus* (Schonmann 1981). Brown (1960, 1961a, 1961b) studied functional morphology in *Cloeon* and *Baetis*. Froehlich (1964) and Soldán (1979) described the functional morphology of the filter-feeding heptageniid *Arthroplea*; Soluk and Craig (1988) examined the carnivore *Ametropus*. *Isonychia*

has been the subject of Wallace and O'Hop (1979) as well as Braimah (1987a, 1987b). Elpers and Tomka (1992) used videomacroscopy to study *Oligoneuriella*. Bae and McCafferty (1991, 1992) examined *Anthopotamus*. Arens (1989) conducted detailed morphological examinations of European species of *Rhithrogena*, *Epeorus*, *Ecdyonurus* and *Baetis*. My own studies have focussed on *Stenacron* (McShaffrey and McCafferty 1986), *Rhithrogena* (McShaffrey and McCafferty 1988) and *Ephemerella* (McShaffrey and McCafferty 1990, 1991); I also have made some observations of feeding in *Callibaetis*, *Isonychia*, *Anthopotamus*, *Heptagenia*, *Stenonema*, *Caenis* and *Ephoron* (McShaffrey 1988).

Materials and Methods

Videomacroscopic and scanning electron microscopic techniques for observation of feeding behaviour and the examination of feeding structures have been described elsewhere (McShaffrey 1988; McShaffrey and McCafferty 1986, 1987, 1988, 1990, 1991).

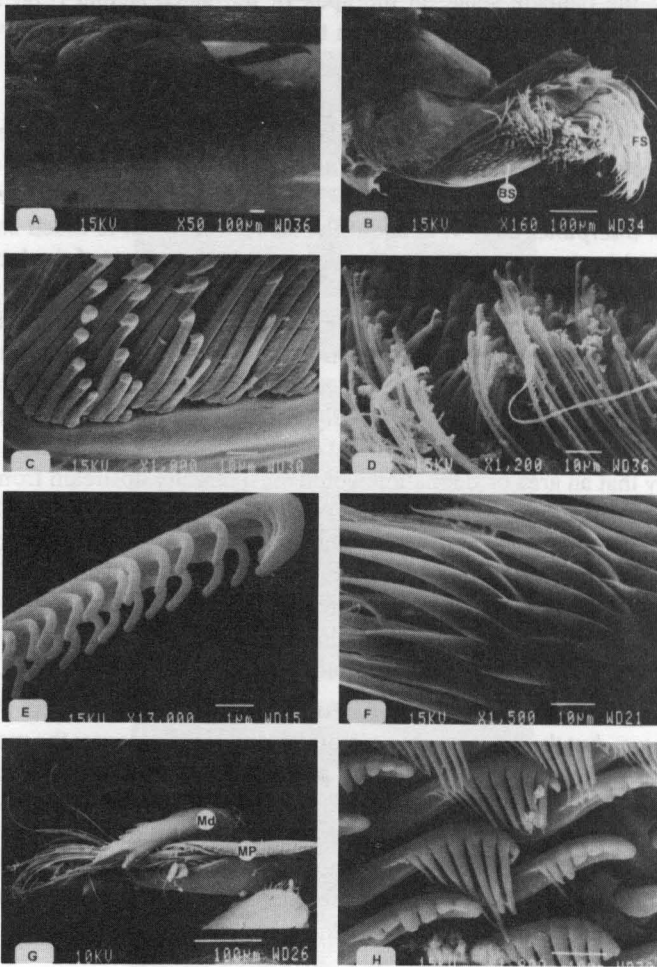
The three organisms studied in detail were not chosen at random. Because of its secretive ways and prognathous mouthparts, *S. interpunctatum* (Fig. 1a) was viewed as the most challenging to film, hence the decision to study it first. *Rhithrogena pellucida* (Fig. 1b) was selected next because it was related to *S. interpunctatum* and was found at the same site, though in a different microhabitat; *R. pellucida* also has distinctive mouthpart morphology. Together these species represent microhabitat extremes among the non-predacious Heptageniinae and provide a good basis for explaining some of the peculiarities of heptageniid mouthpart morphology. *Ephemerella needhami* (Fig. 1c) possesses more generalized, hypognathous mouthpart morphology and was chosen for comparative purposes. All data reported here are based on mature larvae; the many interesting questions concerning shifts in feeding with development have not been addressed.

Results and Discussion

Stenacron and Rhithrogena: Morphology, Microhabitat and Taxonomy

Field data gathered at the Tippecanoe River in Indiana (U.S.A) from 1983 to 1989 showed *Stenacron interpunctatum* to prefer microhabitats with slower currents and *Rhithrogena pellucida* to prefer microhabitats with faster currents. *Stenacron interpunctatum* and *R. pellucida* use their flattened body shapes to utilize quite different food sources. A flattened body gives *S. interpunctatum* access to crevices where it feeds on detritus (Wodsedalek 1912; Lamp and Britt 1981; McShaffrey and McCafferty 1986). *Stenacron interpunctatum* feeds on detritus using its labial

Figure 2. A. Heptageniid in feeding position. B. Labial palp of *Stenacron interpunctatum*, from the "viewpoint" of a food particle on the substrate. BS = brushing setae, FS = filtering setae. C. Closer view of brushing setae. D. Closer view of brushing setae. E. View of individual bipectinate filtering setae. F. Palmate seta on the apex of the galea-lacinia. G. Maxillary palp of *Stenacron interpunctatum* being combed through the mandible. Md = mandible, MP = maxillary palp. H. Stout pectinate setae on the surface of the maxillary palp of *Rhithrogena pellucida*. Scale bars on each figure are accurate; magnifications are for a 4 x 5 inch image size and are retained here for comparative purposes only.



The setae on the galea-lacinia of *R. pellucida* perform the same tasks as their counterparts in *S. interpunctatum*. There is a great degree of similarity in numbers and size of setae on the galea-laciniae of the two species, with a slight trend towards smaller numbers and reduced sizes in *R. pellucida*. The reductions correspond to the reduced food gathering role of the labium in *R. pellucida*.

The superlinguae are reduced in *R. pellucida*; this reduction corresponds to the reduced role of the labium in food gathering and thus the reduced need for food transport via the hypopharynx. A similar reduction is seen in the labium of *R. pellucida*; because of the increased role of the maxillary palps, the labium in *R. pellucida* has a reduced role overall.

The study of *S. interpunctatum* and *R. pellucida* suggests some general trends in mouthpart morphology among heptageniids in particular, and mayflies and aquatic invertebrates in general. The increased size and setation of the maxillary palpus of *R. pellucida* not only allows more efficient uptake of tightly accreted material (McShaffrey and McCafferty 1988), but they also allow for more effective feeding in currents (Strenger 1953). Correlated with the increase in size of the maxillary palpus is the modification of the mandible apex, and a reduction in importance of the labium as a food-gathering organ. The reduction in importance of the labium also means a lesser food load for the palmate pectinate setae on the crown of the galea-lacinia, and thus for the hypopharynx also. This in turn is correlated with a reduction of these structures.

Similar modifications of mouthparts in correlation with current velocity of microhabitats are found throughout the Heptageniidae. Unfortunately, accurate data on microhabitat and current velocity in such areas are lacking for most heptageniids. If sufficient data can be gathered in support of this correlation, it will link taxonomically important characters to their ecological function.

There are also a number of related modifications found in the mouthparts of carnivorous heptageniids. For example, the comb structures on the mandibles and maxillae are lacking, the molae are greatly reduced, and the superlinguae are small (McCafferty and Provonsha 1986). Since these structures are used for transport of microscopic particles in other heptageniids, their disappearance in the carnivorous heptageniids, which feed on macroscopic particles, is predictable.

Carnivorous heptageniids are also the only members of the taxon to ingest macroscopic food. The restrictive nature of the tricondylic mandibles may explain why feeding on macroscopic food is rare among mayflies. In the carnivorous heptageniids, the reduction of the molae increases the size of the opening to the pharynx. The carnivorous Heptageniidae, as well as most carnivorous mayflies, are midge predators, and midges are macroscopic only in one direction, length. The critical dimension of a midge larva, insofar as passage through the mandibles of a mayfly is concerned, is its diameter, which is small compared to its length.

The absence of any shredders among the Heptageniidae is not surprising, since the prognathous orientation and structure of the mouthparts is not suited to shredding.

In particular, there are no hardened, pointed mouthparts in position to bite into vascular plant material.

Ephemerella needhami and Hypognathous Mouthparts

Functional-morphological trends that are apparent in the Heptageniidae are also present in other mayflies, even those with hypognathous mouthparts. Detailed study of *Ephemerella needhami* shows that the main difference between hypognathous and prognathous mouthparts is a shift in the food gathering site from the maxillary and labial palps to the tips of the maxillae and the mandibles. Associated with this shift is a reduction in the roles of the palps and a corresponding reduction in the role of the mandibles as a comb for removing food material from the maxillary palps. Comparison of the morphology of *E. needhami* with that of *Siphonurus aestivalis* (Schonmann 1979, 1981), *Cloeon dipterum* (Brown 1961a) and *Baetis rhodani* (Brown 1961a) shows a clear correlation between increased use of the maxillary palps as food gathering structures and the increased development of the distal end of the mandible as a comb to remove those particles. In *E. needhami* and other hypognathous mayflies the ability of the heavily sclerotized tips of the mandible to reach the substrate opens a realm of feeding possibilities, as the mandibles are strong enough to cut or shear off a wide range of materials including algal filaments, while other mouthparts (and the forelegs) are still available to gather fine particles by brushing the substrate or filtering. As is the case for heptageniids, shredding also seems to be rare among other mayflies, although hypognathous species such as *E. needhami* do have mouthparts that could bite into plant material. The paucity of mayfly shredders is perhaps again due in part to the nature of the mandibles, although other constraints such as evolutionary history and ecological factors are no doubt also very important.

Behavioural observations of *E. needhami*, when compared to those made of *S. interpunctatum* and *R. pellucida* and the descriptions of feeding behaviour in *Cloeon*, *Baetis*, *Siphonurus* and others, reveal an overall pattern of similarity in terms of the sequence of mouthpart movement. While there are differences, those who would like to use behavioural data as a taxonomic tool should realize that it takes meticulous observation to elucidate the differences in behaviour, and that from a diagnostic standpoint it is much easier to work with structures on a preserved specimen than to make detailed observations on a live one.

The Roles of Setae: Implications for Taxonomy and Ecology

Detailed observations have revealed the roles of many distinct types of setae. Whereas simple straight setae play too many roles (brushes, sensors, food particle holders, filters, etc.) to be characterized functionally, several other types of setae apparently play limited roles, which characterize their function.

Pectinate and bipectinate setae (Fig. 2e) are usually associated with trapping and retaining small food particles; their presence is an indication of feeding on small particles. Their presence on outer mouthparts (mouthparts exposed to the current) or legs is an indication of filtering function; their presence on inner mouthparts shows where food is held as it is processed. Such pectinate and bipectinate setae are widespread throughout the Ephemeroptera, and are common in other aquatic organisms. The convergence is striking and widespread, probably reflecting basic biophysical principles of filter design (Rubenstein and Koehl 1977; LaBarbera 1984; Nilsson 1984). Such setae have been demonstrated to act as filter structures in Heptageniidae (McShaffrey and McCafferty 1986, 1988), Isonychiidae (Brimah 1987a; Wallace and O'Hop 1979), Oligoneuriidae (Elpers and Tomka 1992), Potamanthidae (Bae and McCafferty 1991, 1992), Culicidae (Dahl et al. 1988) and Crustacea (Farmer 1974). I have additional observations of similar structure and function in the mayflies *Ephoron* (Polymitarcyidae), *Callibaetis* (Baetidae) and *Ephemerella needhami* (Ephemerellidae), the caddisfly *Macrostemum* (Hydropsychidae), ostracods, amphipods and polychaetes. The fact that these setal types evolve so readily reduces their usefulness as taxonomic characters.

Stouter forms of pectinate setae are often used to remove small particles from the substrates to which they are attached; a prime example would be the setae on the maxillary palps of *R. pellucida* (Fig. 2h). These setae, in turn, are very similar to scraping structures on certain gastropod radulae (compare Barnese and Lowe 1990, Figures 1a and 1b with Fig. 2h). Arens (1989) also documents a variety of scraping structures and comments on the convergence in scraping structures. Palmate setae such as those on the tip of the galea-laciniae in *Stenacron* (Fig. 2f) are used to remove food material from opposing sets of pectinate setae.

Conclusions

Detailed functional-morphological studies allow predictions about the variance of taxonomic characters and the ecological niche of organisms to be made with some accuracy. In an ideal world all species would be studied in detail, but, where that is impractical, some carefully chosen extrapolations can be made from species that have been examined in detail.

Among heptageniids there appears to be a positive correlation between current speed and increased development of the maxillary palps. Ecologically, this means that specimens with well-developed maxillary palps are likely to have been taken from higher-current microhabitats, and that their diet has proportionally less detritus and more living material such as diatoms. Taxonomically, one would expect to see fewer palmate setae on the galea-laciniae, a smaller labium and hypopharynx, and more developed mandibular denticles in specimens from higher-current microhabitats. Species that are taken from a wider range of microhabitats will likely exhibit more variation in regards to these characters.

Species with hypognathous mouthparts are often more flexible in their feeding than the prognathous heptageniids. The mandibles and the maxillae can be used to ingest food, and, if such is the case, the maxillary and labial palps will be relatively simple. The presence of more elaborate structures on the palps is an indication of their use in feeding, and in these species the food source is likely to be detritus; there is also some evidence that this in turn means a microhabitat with slower current speed, which would allow the detritus to settle out.

Acknowledgements

This paper is based on research performed as part of a Ph.D. dissertation at Purdue University under the direction of W.P. McCafferty, whose guidance was greatly appreciated and whose editing is sorely missed. Arwin Provonsha, John Keltner, Y.J. Bae and Dan Bloodgood assisted with illustrations, techniques, fieldwork and ballistics, respectively. The SEM was made available by the Electron Microscope Center in Agriculture with support from NSF grant PCM-8400133.

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