30 Ephemeroptera tusks and their evolution

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Review and synthesis of available and new data on morphology and function of mandibular tusks in light of fossorial behaviour, habitat and phylogenetic data suggest that tusks in Ephemeroidea may have originated from hump-like protusks present in some plesiotypic Leptophlebioidea, that tusks of Potamanthidae represent an ancestral form, and that tusks are related variously to interstitial dwelling. Parallel evolution involving discrete burrow formation, enhanced tusk robustness and armature, and ability to excavate compact substrates occurred in Polymitarcyidae and Ephemeridae. Tusk setation is related to filter feeding. Tusk homologies in Ephemeroptera are discussed. Phylogenies and evolutionary trends of Ephemeroidea are depicted.

Introduction

Among the Ephemeroptera, all larvae of Ephemeroidea and larvae of a few species of the related superfamily Leptophlebioidea possess anteriorly directed mandibular processes. These so-called tusks are morphologically diverse and sometimes reminiscent of the tusks of elephants or *défenses* of wild boars. Mayfly tusks have often been used as characters for both diagnostic and phylogenetic purposes (e.g., Eaton 1883-88; Murphy 1922; Spieth 1933; Edmunds 1973; McCafferty 1975, 1979; Bae and McCafferty 1991). Morgan (1913) first suggested that tusks were used for feeding and burrowing. Since then, some workers have experimentally demonstrated the function of tusks as burrowing devices and in some cases feeding devices also (e.g., Sattler 1967; Keltner and McCafferty 1986; McCafferty and Bae 1992), and sophisticated videomacroscopic techniques (see McShaffrey and McCafferty 1991) have been used for such by Keltner and McCafferty (1986) and McCafferty and Bae (1992).

Although behavioural adaptations of burrowing mayflies have been addressed in phylogenetic studies (Edmunds 1972, 1973; McCafferty 1979; McCafferty and

Edmunds 1979) and functional morphology of tusks has been variously studied (Sattler 1967; Strenger 1970, 1973, 1975, 1977; Keltner and McCafferty 1986), such data have often been fragmentary and have not been developed into a uniform theory of tusk evolutionary adaptations. Our study aims at providing a more comprehensive understanding of the comparative functional morphology and evolution of mayfly tusks via a thorough review and synthesis of new and existing data. To accomplish this, we compared tusk morphology in 27 genera and 54 species among seven families from around the world, as shown in Table 1. Most specimens were housed in the Purdue Entomological Research Collection. The materials were examined and measured with both dissecting and electron scanning microscopy. We also reviewed an extensive literature base (Table 2), and this together with our own unpublished studies provided comparative behavioural and habitat data on genera and most species of tusked mayflies.

Tusks and Their Origins

We regard tusks of Ephemeroidea as anteriorly directed outgrowths of mandibles that result in elongate processes. The fact that these tusks are derived from the outer body of the mandible was recognized by Needham et al. (1935) and Strenger (1973). Ephemeroid tusks are not homologous with mandibular canines as intimated by some early workers, although canines are prolonged in some predacious mayflies in other groups (see e.g., McCafferty and Provonsha 1986), and certain Leptophlebiidae (*Paraleptophlebia bicornuta, P. helena, P. packi,* and *P. zayante*) possess blade-like tusks (Fig. 4) that are derived from the outer incisor of the mandible (Needham et al. 1935). Ian Campbell (Monash University, personal communication) has informed us that he has found a new leptophlebiid from Australia with tusks derived from the body of the mandibles similar to those of Ephemeroidea. All other tusk-like projections found in Ephemeroptera are not mandibular.

We have discovered rudimentary expansions (humps) of the body of the mandible (Fig. 1) in some Leptophlebioidea. Given the close phylogenetic relationship of the Ephemeroidea and Leptophlebioidea (Landa and Soldán 1985; McCafferty 1991a), it is probable that tusks originated from structures similar to these "protusks." Protusks are present in certain extant species of the plesiotypic leptophlebiid genera, *Leptophlebia* and *Paraleptophlebia.* We have not witnessed the function of these protusks, although they do possess bipectinate filtering setae, as shown in Figure 5 (see Trends, below). Some other Ephemeroptera larvae have enlargements of the bodies of their mandibles [e.g., Afrotropical *Tricorythus* (Corbet 1960) and certain Atalophlebiinae Leptophlebiidae]. In case of the former, C. Palmer (Institute for Water Research, personal communication) and the second author (unpublished) have found the enlarged mandibles to be related to orienting the mandibular setal fans into the stream current for passive filter feeding; in case

Table 1. Ephemeroptera taxa studied for comparative tusk morphology.

- Leptophlebiidae
  - *Leptophlebia cupida* (USA)
  - *L. nebulosa* (USA)
  - *Choroterpes trifurcata* (Korea)
  - *Paraleptophlebia chocolata* (Korea)
  - *P. bicornuta* (USA)
  - *P. packi* (USA)
  - *Thraulodes* sp. (USA)
- Behningiidae
  - *Behningia lestagei* (Poland)
  - *Dolania americana* (USA)
- Polymitarcyidae
  - *Asthenopus* sp. (S.E. Ecuador)
  - *Campsurus* sp. (Uruguay)
  - *Campylocia* sp. (Brazil)
  - *Ephoron album* (USA)
  - *E. leukon* (USA)
  - *E. shigae* (Korea)
  - *Exeuthyplocia* sp. (S. Africa)
  - *Povilla adusta* (Ghana)
  - *P. corporaali* (Java)
  - *Proboscidoplocia sikorai* (Madagascar)
  - *Tortopus incertus* (USA)
- Potamanthidae
  - *Anthopotamus distinctus* (USA)
  - *A. myops* (USA, Canada)
  - *A. verticis* (USA)
  - *Potamanthus formosus* (Japan, Thailand)
  - *P. huoshanensis* (China)
  - *P. idiocerus* (Taiwan)
  - *P. longitibius* (China)
  - *P. luteus* (Switzerland)
  - *P. sabahensis* (E. Malaysia)
  - *P. yooni* (Korea)
  - *Rhoenanthus coreanus* (Korea)
  - *R. obscurus* (Thailand)
  - *R. speciosus* (E. Malaysia)
  - *R. youi* (China)
- Ephemeridae
  - *Afromera siamensis* (Thailand)
  - *Cheirogenesia decaryi* (Madagascar)
  - *Ephemera danica* (Spain)
  - *E. guttulata* (USA)
  - *E. orientalis* (Korea)
  - *E. simulans* (USA)
  - *E. strigata* (Korea)
  - *Hexagenia limbata* (USA)
  - *H. rigida* (USA)
  - *Ichthybotus hudsoni* (New Zealand)
  - *Litobrancha recurvata* (USA)
  - *Palingenia fuliginosa* (Czechoslovakia)
  - *P. longicauda* (Hungary)
  - *P. orientalis* (Iran)
  - *Pentagenia vittigera* (USA)
- Ephemerellidae
  - *Drunella aculea* (Korea)
  - *D. cryptomeria* (Korea)
  - *D. triacantha* (Korea)
- Tricorythidae
  - *Tricorythus* sp. 1
  - *Tricorythus* sp. 2

Table 2. Sources of larval habitat and behavioural data regarding tusked mayflies.

Species	Sources
Leptophlebiidae	
Jappa edmundsi (Australia)	Harker 1954; Riek 1970; Skedros & Polhemus 1986; Campbell 1990
J. serrata (Australia)	Riek 1970
Paraleptophlebia bicornuta (USA)	Lehmkuhl & Anderson 1971
P. packi (USA)	Needham 1927
Behningiidae	
Behningia lestagei (Poland)	Keffermüller 1959
Dolania americana (USA)	Berner 1959; Peters & Jones 1973; McCafferty 1975; Edmunds et al. 1976; Peters & Peters 1977; Berner & Pescador 1988
Protobehningia asiatica (Far East Russia)	Tshernova & Bajkova 1960
P. merga (Thailand)	Peters & Gillies 1991
Polymitarcyidae	
Afroplocia sp. (Africa)	Barnard 1937; Gillies 1980
Asthenopodichnium ossibiontum (Austria)	Thenius 1988a 1988b
A. xylobiontum (Germany)	Thenius 1979
Asthenopus sp. (Brazil)	Sattler 1967
Campsurus decoloratus (USA)	McCafferty 1975
C. notatus (Brazil)	Nolte 1987
Campsurus sp. 1 (Peru)	Roback 1966
Campsurus sp. 2 (Venezuela)	Cressa 1986
Campylocia anceps (Brazil)	Traver 1944
C. bocainensis (Brazil)	Pereira & Silva 1990
Ephoron album (USA)	Edmunds 1948; Edmunds et al. 1956; McCafferty 1975 unpublished; Edmunds et al. 1976
E. leikon (USA)	Ide 1935; Britt 1962; McCafferty 1975 unpublished; Edmunds et al. 1976

Table 2. (continued)

E. savigni (S. Africa)	Crass 1947
E. shigae (Korea, Japan)	Bae unpublished; N.C. Watanabe pers. comm.
Euthyplocia hecuba (Costa Rica)	B.W. Sweeney pers. comm.
Euthyplocia sp. (Peru)	Roback 1966; Strenger 1973; Edmunds et al. 1976
Exeuthyplocia sampsoni (S. Africa)	Crass 1947
Exeuthyplocia sp. (Africa)	Gillies 1980
Povilla adusta (Africa)	Kimmins 1949; Corbet 1957; Hartland-Rowe 1958; Petr 1970 1973; Strenger 1973; Hubbard 1984; Hare & Olisedu 1987
P. corporaali (Indonesia)	Ulmer 1939; Hubbard 1984
P. junki (Thailand)	Hubbard 1984
P. teprobanes (Sri Lanka)	Hubbard 1984
Povilla sp. (Thailand)	Vejabhongse 1937
Proboscidoplocia sikorai (Madagascar)	Strenger 1977; G.F. Edmunds unpublished; A.G.B. Thomas pers. comm.
Tortopus incertus (USA)	Scott et al. 1959; Knight & Cooper 1989
Tortopus sp. (Canada, USA)	Berner 1959; McCafferty 1975; Edmunds et al. 1976; Keltner & McCafferty unpublished
Potamanthidae	
Anthopotamus distinctus (USA)	Bae & McCafferty 1991
A. myops (USA)	Bartholomae & Meier 1977; Munn & King 1987; Bae & McCafferty 1991
A. verticis (USA)	Bae & McCafferty 1991 unpublished; McCafferty & Bae 1992
Potamanthus formosus (Japan, Thailand)	Uéno 1928; Watanabe 1988; Bae & McCafferty 1991
P. luteus (Europe)	Bae & McCafferty 1991
P. sabahensis (E. Malaysia)	Bae et al. 1990; Bae & McCafferty 1991
P. yooni (Korea)	Bae & McCafferty 1991
Rhoenanthus coreanus (Korea)	Bae & McCafferty 1991

Table 2. (continued)

R. obscurus (Thailand)	Bae & McCafferty 1991
R. speciosus (E. Malaysia)	Bae & McCafferty 1991
Ephemeridae	
Afromera evae (Gambia)	McCafferty & Gillies 1979
A. siamensis (Thailand)	McCafferty & Edmunds 1973
Afromera sp. (S. Africa)	McCafferty unpublished
Cheirogenesia sp. (Madagascar)	McCafferty & Edmunds 1976
Eatonica schoutedeni (S. Africa)	Crass 1947
Eatonigenia sp. (Thailand)	McCafferty 1973
Ephemera blanda (USA)	McCafferty 1975
E. danica (England)	Strenger 1973 1975; Wright et al. 1981
E. guttulata (USA)	McCafferty 1975
E. japonica (Japan)	Uéno 1928
E. mooiana (S. Africa)	McCafferty 1971b
E. orientalis (Korea)	Bae unpublished
E. simulans (USA)	Spieth 1936; Britt 1962; Eriksen 1963 1964 1968; McCafferty 1975
E. strigata (Korea)	Bae unpublished
E. varia (USA)	McCafferty 1975
Hexagenia albivitta (Brazil, Costa Rica)	McCafferty 1970
H. atrocaudata (USA)	McCafferty 1975
H. bilineata (USA)	Berner 1959; Swanson 1967; Fremling 1973; Wright & Mattice 1981; Berner & Pescador 1988
H. limbata (Canada, USA)	Hunt 1953; Berner 1959; Eriksen 1963 1964 1968; Swanson 1967; Fremling 1973; McCafferty 1975 unpublished; Rutter & Wissing 1975; Zimmerman & Wissing 1980; Kelter & McCafferty 1986; Berner & Pescador 1988; Rasmussen 1988
H. rigida (USA)	McCafferty 1975
Hexagenia sp. (USA)	Lyman 1943
Ichthybotus bicolor	Tillyard in Phillips 1930; Phillips 1931

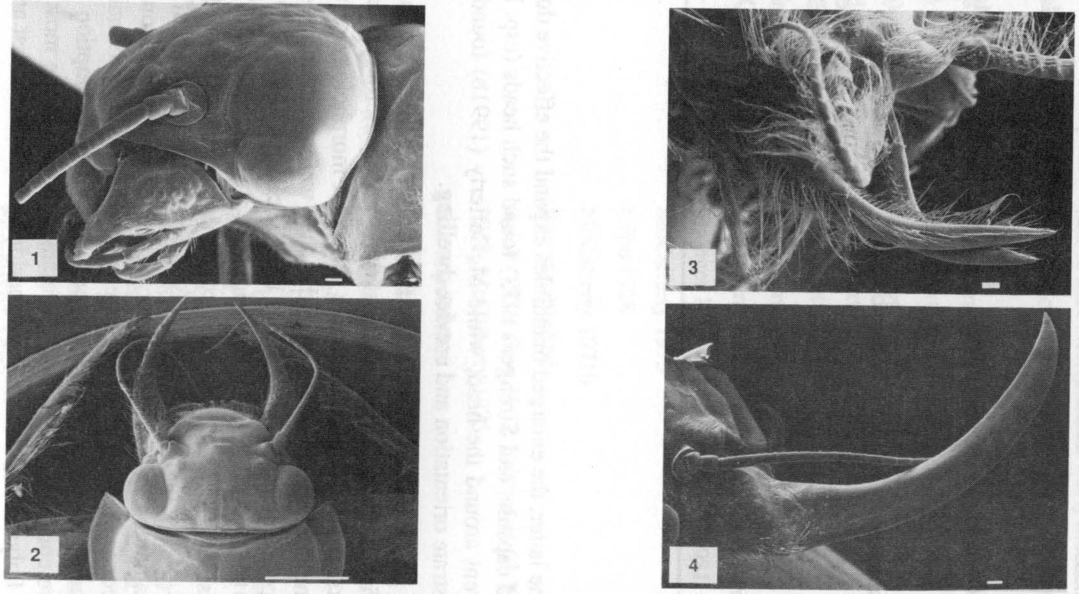
Table 2. (continued)

I. hudsoni (New Zealand)	Phillips 1931
Ichthybotus sp. (New Zealand)	Phillips 1930 1931; W.P. Chisholm unpublished
Litobrancha recurvata (USA)	Needham 1920; Morgan & Grierson 1932; Morgan & Wilder 1936; McCafferty 1971a 1975
Palingenia fuliginosa (Czechoslovakia)	Soldán 1978
P. longicauda (India, Europe)	Gravely 1920; Strenger 1970 1973; Csoknya & Ferencz 1972; Soldán 1978; Russev 1987
Pentagenia vittigera (USA)	Berner 1959; McCafferty 1975; Keltner & McCafferty 1986

of the latter, the enlarged mandibles expand the effective dorsal surface area of the head capsule, and Strenger (1973) found such heads (esp. Heptageniidae) to alter current around the head, while McCafferty (1991b) found them to be related to substrate orientation and crevice dwelling.

Based on the phylogeny of Lanceolata mayflies (McCafferty 1991a) (depicted in Fig. 9), the hypothetical ancestor of the Ephemeroidea possessed fully developed tusks. It is difficult to estimate the exact morphology of these primordial tusks. Some workers have suggested that they were potamanthid-like (Fig. 2), at least in shape and orientation (Edmunds 1973; McCafferty 1979, 1991a; Bae and McCafferty 1991). If the branching positions of the three families of Ephemeroidea are considered, the ancestral tusks could have been like those of plesiotypic lineages in any of the families. Since Polymitarcyidae tusks are all convergent anteriorly, Potamanthidae tusks are convergent anteriorly (at least somewhat convex laterally or concave medially), and those of the plesiotypic subfamily Ichthybotinae of the Ephemeridae are also convergent, it is a fair assumption that the ancestral tusks were convergent. Also, since Potamanthidae and the most plesiotypic lineages of the Polymitarcyidae and Ephemeridae possess tusks that are more-or-less round in cross-section basally (Fig. 9; Tables 3 and 4; Appendix A), that would appear to be the generalized ancestral condition. With regard to setation, both simple-stout and hairlike setae are present on the tusks of all Potamanthidae (Fig. 6) and the most plesiotypic lineages of the Polymitarcyidae and Ephemeridae, with simple-stout

Figures 1-4. SEM's of larval morphology. (1) *Leptophlebia nebulosa*, lateral head (bar = 0.1 mm). (2) *Anthopotamus distinctus*, dorsal head (bar = 1 mm). (3) *Hexagenia limbata*, mandibular tusk, lateral (bar = 0.1 mm). (4) *Paraleptophlebia bicornuta*, mandibular tusk, lateral (bar = 0.1 mm).



Figures 5-8. SEM's of larval morphology (continued). (5) *Leptophlebia nebulosa*, setae on mandibular protusk (bar = 0.01 mm). (6) *Anthopotamus myops*, setae at base of mandibular tusk (bar = 0.01 mm). (7) *Rhoenanthus obscurus*, bipectinate-hairlike seta on basolateral area of mandibular tusk (bar = 0.001 mm). (8) *Ephoron album*, bipectinate-hairlike setae on basolateral area of mandibular tusk (bar = 0.01 mm).

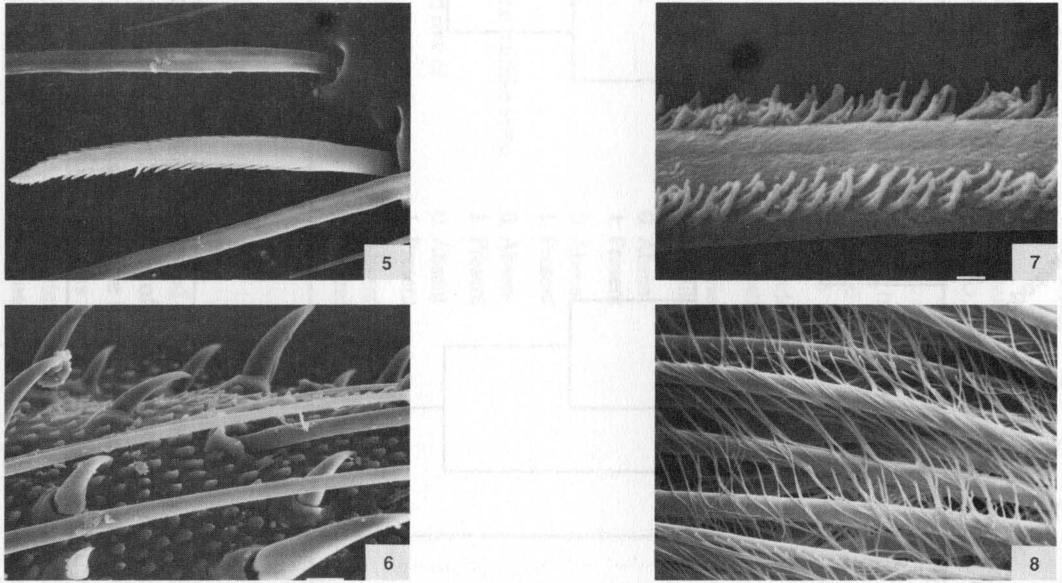


Figure 9. **Cladogram of the superfamilies of Lanceolata and families and subfamilies of Ephemeroidea (after McCafferty 1991a).**

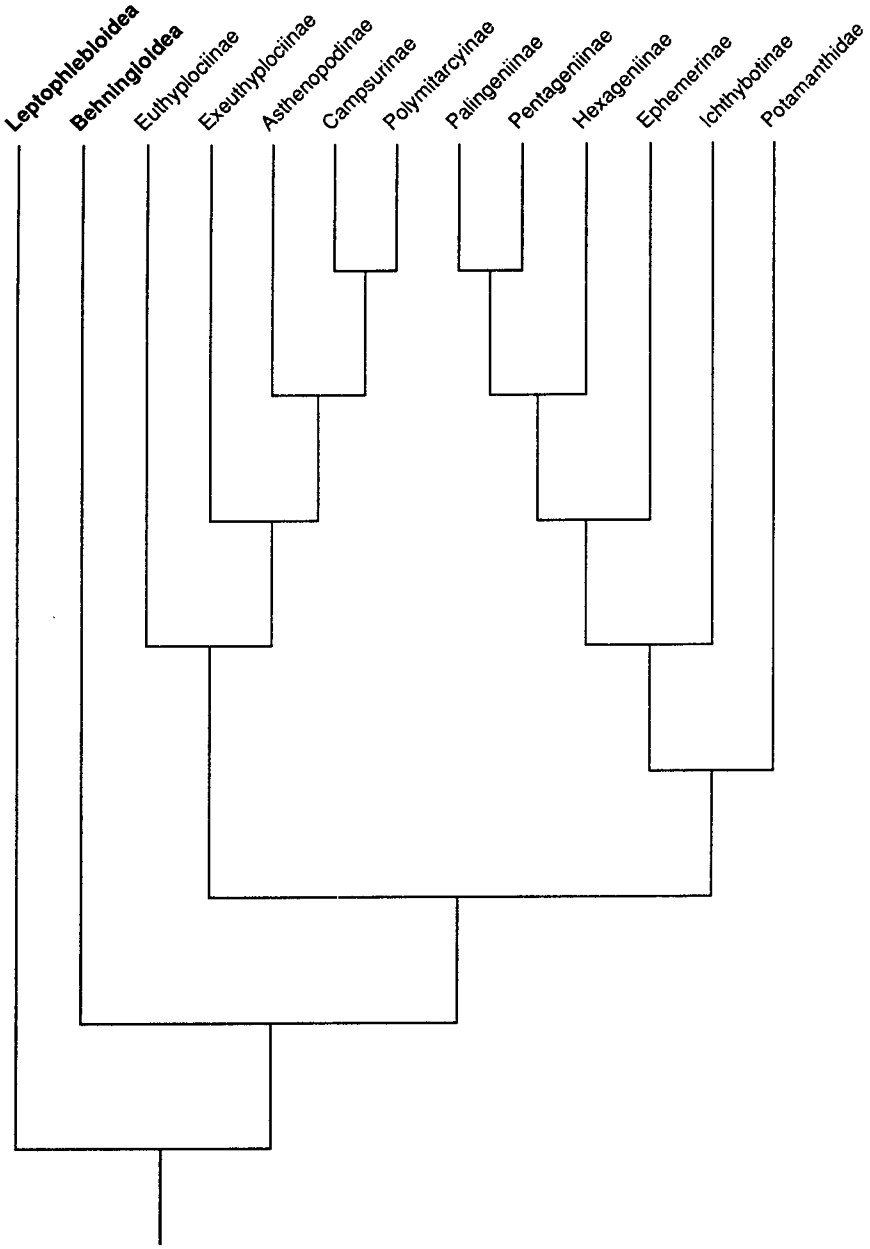


Table 3. Comparative tusk characters and assumed polarities of character states used for formulating the alternative cladogram of the subfamilial relationships of Polymitarcyidae (Figure 10). (0 = plesiomorphy, 1 = apomorphy, +1 and - 1 = bidirectional apomorphy).

	Character	Character state
1.	Ratio, tusk length to head length	0. 0.5-3.0 +1. > 3.0 -1. < 0.5
2.	Basal shape	0. Rounded 1. Dorsally flat with lateral angle
3.	Setal type	0. Simple-stout and hairlike 1. Hairlike only
4.	Large mediobasal spine	0. Absent 1. Present
5.	Medioapical crenulation	0. Absent 1. Present
6.	Row of medial and lateral hairlike setae	0. Absent 1. Present
7.	Basal inverted U-shaped row of hairlike setae	0. Absent 1. Present
8.	Ventral hairlike setae	0. Absent 1. Present

setae absent in Polymitarcyinae, Asthenopodinae, and Hexageniinae (Fig. 9; Tables 3 and 4; Appendix A). The presence of both types of setae on the tusks therefore can be inferred for the hypothetical ancestor, and the loss of the simple-stout setae is obviously subject to convergence. Also, various specialized tusk conditions, such as a inverted U-shaped row of setae basolaterally, ventral hairlike setae, strong lateral spurs, and specialized fields or positions of setae, spines and crenulations among some of the clearly apotypic lineages (Fig. 9; Tables 3 and 4; Appendix A), may be assumed to have been absent in the ancestral tusk. The placement of setae or spines, however, can be highly subject to convergence among lineages (see Diversity, below).

Table 4. Comparative tusk characters and assumed polarities of character states used for formulating the alternative cladogram of the subfamilial relationships of Ephemeridae (Figure 11). (0 = plesiomorphy, 1 = apomorphy).

Character	Character state
1. Dorsolateral curvature	0. Slightly downward to slightly upward 1. Greatly arched to upward
2. Mediolateral curvature	0. Convergent 1. Divergent
3. Basal shape	0. Rounded 1. Dorsally flat with lateral angle
4. Presence of setae	0. Simple-stout and hairlike setae present 1. Only hairlike setae present
5. Distribution of simple-stout setae	0. Dorsobasal and laterobasal 1. Whole dorsal area and lateral margin
6. Development of simple-stout setae	0. Not developed into spurs 1. Developed into spurs
7. Presence of round bare area at basolateral mandible	0. Absent 1. Present

Although the sister group to the Ephemeroidea, the Behningioidea, are also burrowing mayflies (McCafferty 1975), they do not possess tusks or protusks. The common ancestor of the Behningioidea-Ephemeroidea lineage (Fig. 9) may or may not have possessed tusks, although protusks may have been present, considering the phylogenetic position of the Leptophlebioidea. There are known instances of tusks becoming highly reduced among some Potamanthidae and Ephemeridae (see Diversity, below), and tusks or protusks may have become lost in the aberrant Behningioidea. Of note, the larvae of Behningioidea are interstitial dwellers that do not form burrows. This is also the case among Potamanthidae and likely among plesiotypic lineages of Polymitarcyidae and Ephemeridae (Table 5). From this we deduce that larvae of the ephemeroid common ancestor had not developed the ability to form burrows as is found in the Ephemeridae and apotypic lineages of Polymitarcyidae (Fig. 9; Table 5).

Table 5. Summarized habitat data for tusked mayflies.

Taxa	Substrate	Dwelling
Leptophlebiidae		
Tusked *Paraleptophlebia*	Mixed substrate	Interstitial
Jappa	Mixed substrate	Interstitial
Polymitarcyidae		
Campylocia	Mixed substrate (?)	Interstitial (?)
Euthyplocia	Mixed substrate	Interstitial
Proboscidoplocia	Mixed substrate	Interstitial
Afroplocia	Mixed substrate (?)	Interstitial (?)
Exeuthyplocia	Mixed substrate (?)	Interstitial (?)
Ephoron	Mixed substrate, clay	Interstitial/burrow
Campsurus	Silt	Burrow
Tortopus	Clay	Burrow
Asthenopus	Hard substrate, wood	Burrow
Povilla	Clay, hard substrate, wood	Burrow
Potamanthidae		
Rhoenanthus	Mixed substrate	Interstitial
Anthopotamus	Mixed substrate	Interstitial
Potamanthus	Mixed substrate	Interstitial
Ephemeridae		
Ichthybotus	Mixed substrate	Interstitial/burrow
Ephemera	Mixed substrate, sand, silt	Interstitial/burrow
Afromera	Silt	Burrow
Hexagenia	Silt, silt/clay	Burrow
Litobrancha	Silt	Burrow
Eatonica	Silt	Burrow
Pentagenia	Clay	Burrow
Cheirogenesia	Silt	Burrow
Palingenia	Silt, clay	Burrow

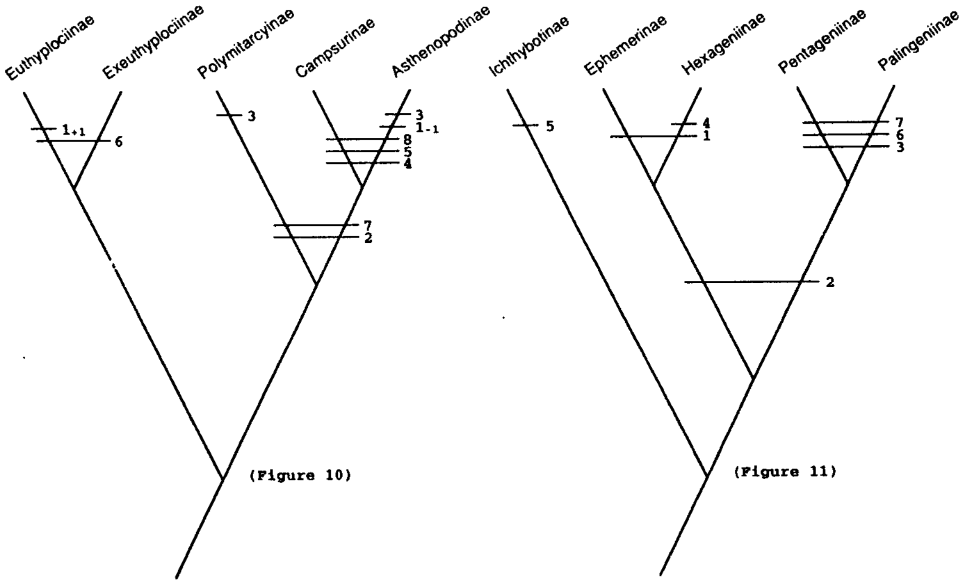
The earliest known mayfly fossils with tusks (*Mesopalingea lerida*) are from the Lower Cretaceous (Whalley and Jarzembowski 1985); however, the species' tusks are clearly not of the Palingeniinae (or any other Ephemeridae) type. The species may be a Polymitarcyidae [perhaps Pristiplociinae (McCafferty 1991a)], but could also be a member of the Australiphemeridae, which was described from Lower Cretaceous adults from Brazil by McCafferty (1990). It is not clear whether this tusked fossil is actually an ephemeroid since its gills are indeterminate. From the Oligocene, larvae of *Hexagenia* (Hexageniinae) were discovered from North America (Lewis 1978); larvae of *Litobrancha* (Ephemerinae) were discovered from Far East Asia (McCafferty and Sinitshenkova 1983). While Ephemeroidea is at least as old as the Lower Cretaceous based on adult fossils (e.g., McCafferty 1990), other fossil larvae thought to be ephemeroids, such as *Mesogenesia* (?Palingeniinae) from the Jurassic (Tshernova 1977) and *Torephemera* (Torephemeridae) from the Mesozoic (Sinitshenkova 1989), do not demonstrate any tusk-like processes in their head, although they have expanded foretibiae possibly indicating fossorial (or raptorial) habits. Thus, we find placement of these latter larvae and *Mesopalingea* dubious (see also McCafferty 1990). Trace fossils of U-shaped burrows in bones and teeth as well as in wood were found from the Late Tertiary (Miocene) by Thenius (1979, 1988a, 1988b). His placement of these burrows in a separate genus *Asthenopodichnium* (Asthenopodinae) is tenuous in our opinion, since they are not even clearly insect burrows.

Ephemeroid Diversity

We present a compendium of comparative morphology of tusks of the families and subfamilies of Ephemeroidea in Appendix A. In Tables 3 and 4 we present the morphological character state distributions we used in our phylogeny construction. In Table 5 we present a summary of all known burrowing habit and habitat data for tusked mayflies, based on our literature review and unpublished observations (Table 2). There is considerable diversity both in morphological detail, function and habitat. There is also a strong correlation between tusk morphology and substrate type as predicted by McCafferty (1975) and shown by Keltner and McCafferty (1986). The discovery of the habitat of *Pentagenia* larvae by the second author, for example, was based on the prediction that the heavily armoured and robust tusks of those larvae were adapted for excavating a hard compacted substrate, such as clay, where they were eventually found in abundance.

In Figures 10 and 11, we present possible alternative cladograms that would be generated regarding McCafferty's (1991a) subfamilies of Polymitarcyidae and Ephemeridae (Fig. 9), if only comparative tusk data based on our present interpretation (Tables 3 and 4) were used, respectively, as a character set. While these cladograms strongly support the monophyletic nature of the Polymitarcyinae-Campsurinae-Asthenopodinae and the Pentageniinae-Palingeniinae lineages, they

Figures 10-11. Alternative cladograms of Ephemeroidea taxa based only on presumed polarities of tusk characters. (10) Subfamilies of Polymitarcyidae (see Table 3). (11) Subfamilies of Ephemeridae (see Table 4).



differ in other details. We cannot be fully confident of these alternative cladograms for three reasons. First, some polarities, as assumed and shown in Tables 3 and 4, are subject to interpretation because an outgroup for the entire Ephemeroidea lineage technically does not exist in that there are no mayflies with homologous tusks outside the Ephemeroidea. We, therefore, have been limited to using the combined Potamanthidae-Ephemeridae lineage as the outgroup for the analysis of Polymitarcyidae tusks (Table 3, Fig. 10), but were able to use Potamanthidae as the outgroup for Ephemeridae (Table 4, Fig. 11). In determining an ancestral type tusks for the entire ephemeroid lineage, we could have incorrectly assumed that some tusk characters of plesiotypic potamanthids represent an ancestral state (see Origin, above). For example, rows of medial and lateral hairlike setae such as found in Euthyplociinae and Exeuthyplociinae (Table 3) may just as reasonably have been the ephemeroid ancestral condition rather than an absence of them as we assume. In either case, convergences must be explained; parsimony does not help solve the question. Second, positions of setae and armature associated with mouthparts are known often to be related to modes of feeding or to various environmental factors associated with large numbers of aquatic invertebrates, regardless of relationships. For example, unrelated filter feeders (even Crustacea) have similar setae in predictable places (Farmer 1974; Wallace and O'Hop 1979), and unrelated predators have pronounced mandibular convergences (Edmunds 1975). Convergences in mouthpart functional morphology of mayflies are many. Third, we are cognizant of the fact that to draw conclusions about phylogeny from one character set is indecisive and sometimes inconsistent with principles of parsimony [see e.g., the somewhat aberrant phylogeny of Ephemeroptera by Koss and Edmunds (1974), which was based on egg morphology only].

In Table 5, we have distinguished burrowing mayflies as either interstitial dwellers or burrow dwellers. The former are those that do not form a distinctly defined burrow or tube in substrates. As such they are often variously oriented and some seek out crevices on the undersides of larger parts of mixed substrates such as stone and wood. *Anthopotamus* larvae are good examples of interstitial dwellers (Bae and McCafferty unpublished), and incisor-tusked *Paraleptophlebia* may be similar (G.F. Edmunds, University of Utah, personal communication). Of note, the tuskless burrowers of the Behningioidea also fall into this category, except their substrates are consistently coarse sand. Burrow dwellers form burrows. Some of these burrows may be very well defined such as the clay burrows of *Tortopus* (Scott et al. 1959) and *Palingenia* (Russev 1987). In *Asthenopus*, burrows are silken lined (Sattler 1967), while others, such as those formed in silt or silt/sand, must be maintained in part by a current, sometimes generated by the larvae itself [e.g., *Hexagenia* (Keltner and McCafferty 1986)]. In a few burrow dwellers, the integrity of the burrow changes with the substrate. For example, larvae of *Ephoron leukon* form tubes in clay but have ill-defined burrows in mixed substrate.

Evolutionary Trends

The accumulated phylogenetic data, regardless of the branching alternatives presented herein (Figs. 9-11), along with available morphological data (Tables 3 and 4, Appendix A) and behavioural and habitat data (Tables 2 and 5) have allowed us to hypothesize trends in the evolution of tusk form (Fig. 12) and behavioural and habitat adaptations (Fig. 13) in the Ephemeroidea. Our conclusions are basically an elaboration of those first set down in this regard by McCafferty (1979).

Beginning with an *Anthopotamus*-like prototype tusk form and the habit of interstitial dwelling in mixed substrate, which is common in all of the plesiotypic lineages, there are some major tendencies that are independently developed in the Polymitarcyidae and the Ephemeridae lineages. Burrow formation and dwelling became developed in the Polymitarcyinae-Campsurinae-Asthenopodinae lineage of the Polymitarcyidae and in the Ephemerinae-Hexageniinae-Pentageniinae-Palingeniinae grouping in Ephemeridae. We see this as a natural tendency in becoming more proficient burrowers once the ability to live within the substrate was established ancestrally. In the Polymitarcyidae, this coincided with the invasion of more compacted clay substrates, while in the Ephemeridae it coincided with the invasion of less cohesive fine substrates such as silt and sand/silt (Fig. 13). In the Polymitarcyidae, the tusks retained the basically apically convergent orientation found ancestrally and that is efficient for moving, and living in, coarse mixed substrate (Bae and McCafferty unpublished), whereas the apical orientation became divergent and ventrally convex in silt burrowers (Ephemerinae and Hexageniinae) in the Ephemeridae. Keltner and McCafferty (1986) found this latter orientation to be efficient for burrowing into silt, since it provided a plow-like function; it also aids the mandibles in raising the head for shovelling silt with the frontal process (McCafferty unpublished). Ephemeridae in general appear more efficient at shovelling substrate than the Polymitarcyidae or Potamanthidae due to their much more developed frontal processes.

Another independent tendency found in the evolution of the Polymitarcyidae and Ephemeridae is the enhanced robustness of the tusks in the most apotypic lineages (Campsurinae, Asthenopodinae, Pentageniinae, and Palingeniinae). Campsurinae larvae became well adapted for burrowing into compacted clay with their heavy mandibles, and even further enhancement of the tusks took place in the Asthenopodinae, a group in which larvae are able to cut and burrow into wood. The Pentageniinae and Palingeniinae also became well adapted for burrowing into clay. A behavioural corroboration that this is another example of convergence in the two major families of Ephemeroidea was uncovered by videomacroscopy work by Keltner and McCafferty (1986 unpublished). *Pentagenia* larvae were found to initiate burrowing by digging much like the related Hexageniinae and Ephemerinae (sweeping motions of both forelegs and head, which allowed the tusks to excavate).

Figure 12. **General trends in the evolution of tusk form in Ephemeroidea.**

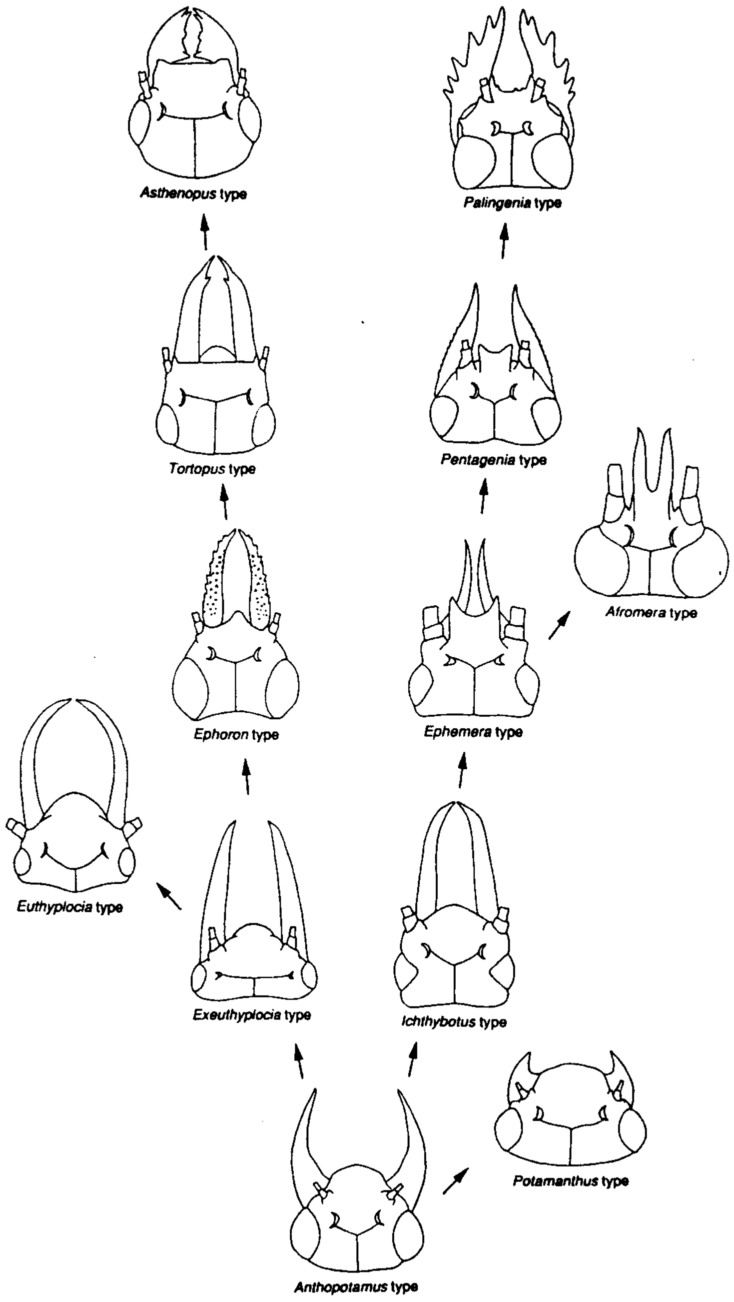
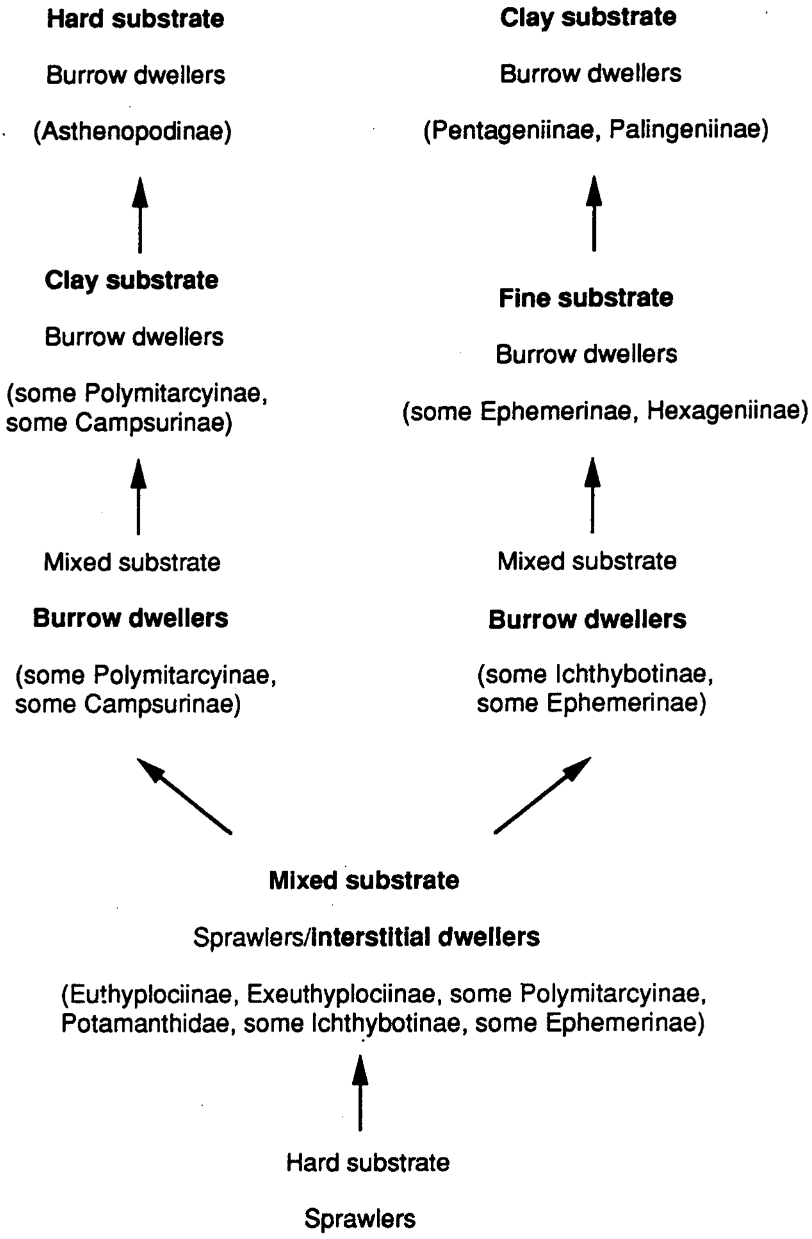


Figure 13. **General trends in the evolution of burrowing behaviour and habitat adaptation in Ephemeroidea.**



Tortopus (Polymitarcyidae, Campsurinae), on the other hand, initiated burrowing by thrusting the head against the substrate and "cork-screwing" and chiselling into the substrate, effectively allowing the tusks to cut into the clay. The different modes of burrowing into compacted substrate in the different lineages appear related to some fundamental differences of the tusks (again whether the tusks are essentially convergently or divergently oriented apically) and in the development of the frontal process. The plowing/digging type of burrowing and divergently oriented tusks found in the more ancestral silt burrowing Hexageniinae (Fig. 3) and Ephemerinae are carried over in the Pentageniinae and Palingeniinae, the major difference in the latter two groups being their much more robust tusks and other fossorial structures. The apically convergent oriented tusks along with the absence of well-developed frontal processes evidently are related to the chiselling type of excavation seen in apotypic lineages of Polymitarcyidae.

There are some tendencies in the evolution of relative size of the tusks also. In the Euthyplociinae, the tusks became greatly elongated. (It will be interesting to eventually learn the exact function of these elongated tusks.) Drastic size reduction of tusks has occurred independently in the Potamanthidae and the Ephemeridae. Bae and McCafferty (1991) showed the reduction of tusk size in *Potamanthus* to be an apomorphy. Likewise, McCafferty and Edmunds (1973) showed the specialized nature of highly atrophied tusks found in *Afromera* and the peculiar asymmetrical size reduction in the subgenus *Aethephemera* of *Ephemera* (both Ephemerinae). Considering the role of the frontal process in digging in the Ephemeridae, as discussed above, it is of interest to note that the bifurcate frontal processes of *Afromera* and *Aethephemera* are greatly enlarged and presumably compensate for the loss of effective tusks in these groups. There evidently is a similar functional situation in the larvae of the Australian leptophlebiid genus *Jappa*, which possess greatly elongated frontal horns (or cephalic "tusks") on their heads (see Fig. 1 in Skedros and Polhemus 1986). Harker (1954) and Campbell (1990) indicated that these structures were convergent with the mandibular tusks of *Ephemera*, however, we regard them as most analogous with the tusks of *Rhoenanthus* (Potamanthidae) (see especially *J. edmundsi* and *R. speciosus*), and their function may be identical (Bae unpublished).

Finally, with regard to evolutionary trends in feeding habits of Ephemeroidea, filter feeding is developed throughout the group. Bipectinate setae, which are used in filter feeding (Farmer 1974; Wallace and Merritt 1980), are present on the protusks of Leptophlebiidae (Fig. 5). In the Potamanthidae, although there are filtering setae at the base of the tusks (Figs. 6 and 7) (Bae and McCafferty 1991), the tusks function more in raking the filtering setae of the forelegs (McCafferty and Bae 1992). Filtering setae are greatly developed on the tusks of Polymitarcyidae and to a lesser extent in Ephemeridae. Extensive inverted U-shaped fields of filtering setae are found basolaterally on the tusks of Polymitarcyinae, Campsurinae, and Asthenopodinae [see Pl. 25, Fig. 8 and Pl. 28, Fig. 9 in Eaton (1883-88)], and are found in rows along the length of the tusks of Euthyplociinae (Strenger 1977) and Exeuthyplociinae (Gillies 1980). These setal fields reportedly function as catch baskets (Hartland-Rowe 1953; Sattler 1967). Setules of the bipectinate setae in these groups are well developed (Fig. 8). In the Pentageniinae, where filter feeding has been shown to be highly developed in the Ephemeridae (Zimmerman and Wissing 1980; Keltner and McCafferty 1986), a filtering catch basket is formed mainly by the setae of the forelegs and other mouthparts.

Acknowledgements

The SEM was made available by Electron Microscope Center at Purdue University with support from NSF grant PCM-8400133. This article is published as Purdue University Experiment Station Journal No. 13497.

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Appendix A. Comparative morphology of mandibular tusks of Ephemeroidea families and subfamilies.

Polymitarcyidae	Tusks 1-18 mm, 0.5-5.0 x length of head, either basally round in cross section or flattening dorsobasally, convergent apically, dorsoventrally straight to curved downward, and slightly upcurved apically; either with simple-stout and hairlike setae or with hairlike setae only, variously shaped, numbered and arranged.
Euthyplociinae	Tusks 6-18 mm, 2.0-5.0 x length of head, basally round in cross section, straight, with simple-stout and hairlike setae, without spines or crenulations; simple-stout setae dorsally and in lateral rows; bipectinate-hairlike setae arranged in mediolateral row along length of tusks.
Exeuthyplociinae	Tusks 2-3 mm, ca. 1.5 x length of head, basally round in cross section, straight, with simple-stout and hairlike setae, without spines or crenulations; simple-stout setae dorsally and in lateral rows; bipectinate-hairlike setae in mediolateral row along length of tusks.
Asthenopodinae	Tusks 1-2 mm, ca. 0.5 x length of head, flattening dorsobasally, curved downward, with only hairlike setae, with large mediobasal spine, and with 2-3 medioapical crenulations; bipectinate-hairlike setae in distinct inverted U-shaped row basolaterally and scattered dorsally and ventrally.
Campsurinae	Tusks 1.5-2.5 mm, 0.6-1.2 x length of head, flattening dorsobasally, curved downward, with simple-stout and hairlike setae, with large mediobasal spine, and with 0-4 medioapical spines; simple-stout setae laterally and dorsobasally distributed; bipectinate-hairlike setae in distinct inverted U-shaped row basolaterally and dense ventrally.
Polymitarcyinae	Tusks 1.5-2.5 mm, ca. 1.0 x length of head, flattening dorsobasally, curved downward, with only hairlike setae, with dorsal tubercles, without spines or crenulations; bipectinate-hairlike setae in distinct inverted U-shaped row basolaterally; simple-hairlike setae sparse dorsally.
Potamanthidae	Tusks 0.1-4.6 mm, 0.1-2.3 x length of head, basally round in cross section, convergent apically, and slightly upcurved dorsoventrally; mixed simple-stout and hairlike setae in dorsobasal area.
Ephemeridae	Tusks 0.3-3.0 mm, 0.2-1.5 x length of head, either basally round in cross section or depressed dorsobasally, convergent or divergent apically, curved dorsoventrally either slightly downward to greatly upward; either with simple-stout and hairlike setae or with hairlike setae only, variously shaped, numbered and arranged.

Appendix A. (continued)

Ichthybotinae	Tusks 1.5-2.0 mm, ca. 1.0 x length of head, basally round in cross section, convergent apically, curved downward, with simple-stout and hairlike setae, without spines or crenulations; simple-stout setae dorsally and in dorsolateral rows; bipectinate-hairlike setae dense in dorsobasal area and sparse in ventral area.
Ephemerinae	Tusk 0.3-3.0 mm, 0.2-1.5 x length of head, basally round in cross section, divergent apically, greatly upcurved, with simple-stout and hairlike setae, without spines or crenulations; setae basolaterally distributed. (Tusks atrophied in some.)
Hexageniinae	Tusks 1.5-2.0 mm, 0.6-1.0 x length of head, basally round in cross section, divergent apically, greatly upcurved, with only hairlike setae, without spines or crenulations; setae distributed either laterally or more generally.
Pentageniinae	Tusks ca. 2.0 mm, ca. 1.0 x length of head, flattening dorsobasally, divergent apically, slightly upcurved, with simple-stout and hairlike setae, with spurs and slight crenulations laterally; bipectinate-hairlike setae distributed generally except in basolateral area.
Palingeniinae	Tusks ca. 2.0-2.3 mm, ca. 1.0 x length of head, flattening dorsobasally, divergent apically, slightly upcurved, with only hairlike setae, with spurs and crenulations (sometimes very large) laterally; bipectinate-hairlike setae distributed generally except in basolateral area.