

INFERENCES REGARDING THE FEEDING BEHAVIOR AND MORPHOECOLOGICAL PATTERNS OF FOSSIL MAYFLY NYMPHS (INSECTA, EPHEMEROPTERA) FROM THE LOWER CRETACEOUS SANTANA FORMATION OF NORTHEASTERN BRAZIL

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ABSTRACT: The life habit and diet of fossil mayflies nymphs can be understood based on the characters of their head. The mouthparts are poorly preserved, and the inferences based on the head and the habits of extant families help to obtain a "image" of the paleoecology. This work intends to show that only a simple single image of the paleoenvironment is not enough to the knowledge about fossil mouthparts and diet, that can be enriched with the head morphology. We used here fossils of the Santana Formation (Lower Cretaceous, northeastern Brazil) and also illustrations of species descriptions, while the conclusions regard to mouthparts were based on extant families and their phylogenetic relationship, as well data of functional feeding group tables. The results demonstrate that in the Santana Formation there are nymphs which feed as collectors and shredders, such as the Hexagenitidae, and nymphs which are filterers of suspended particles, for example Oligoneuriidae and Polymitarcyidae. A discussion of the systematic of the Ephemeroidea and the possible Leptophlebiidae of Santana Formation is provided.

Key word: Feeding behaviour, Nymphs, Mayflies, Morphology of insects, Lower Cretaceous, Santana Formation, northeast Brazil.

RESUMO: Os hábitos e a dieta de ninfas de Ephemeroptera fósseis podem ser compreendidos com base nas características de suas cabeças. As peças bucais são malpreservadas e as inferências baseadas na cabeça e nos hábitos de famílias atuais ajudam a obter uma "imagem" da paleoecologia. Este trabalho pretende mostrar que somente uma simples imagem do paleoambiente não é suficiente para o conhecimento sobre peças bucais e dieta de fósseis, o que pode ser enriquecido com a morfologia da cabeça. Nós usamos aqui fósseis da Formação Santana (Cretáceo Inferior, nordeste brasileiro) e também ilustrações de descrições de espécies. As conclusões sobre peças bucais foram baseadas em famílias atuais e suas relações filogenéticas, bem como dados de tabelas de grupos alimentares funcionais. Os resultados demonstram que, na Formação Santana, há ninfas coletoras e fragmentadoras, tais como os Hexagenitidae, e ninfas filtradoras de partículas em suspensão, por exemplo Oligoneuriidae e Polymitarcyidae. É também apresentada uma discussão da sistemática dos Ephemeroidea e dos possíveis Leptophlebiidae da Formação Santana.

Palavras-chaves: Hábitos alimentares, Ninfas, Morfologia de insetos, Cretáceo inferior, Formação Santana, Nordeste do Brasil.

Introduction

The fossil nymphs of Ephemeroptera, and other orders of insects, often leave poor records of their mouthparts, although frequently the entire head, eyes, and other structures of the body are well preserved (Labandeira, 1997). However, through analysis of the head proportions and their relationship to the body, and with the knowledge about ecology and behavior of the extant mayfly fauna, it is possible to make general conclusions about the general diet of the fossil ephemeropteran nymphs, using a well developed theoretical basis. Consequently, one can investigate (1) the principal feeding strategies, and (2) the dominant diet, following the established classification of functional feeding groups, as outlined in Williams and Feltmate (1992). Additionally, inferences can be made about (3) the occupied substrate, such as leaves, wood, stone, sand and silt, and (4) properties of the water and of the ambient habitat. A weak association can be established between mouthpart structure and insect ecological position, but a stronger association is possible between mouthparts, diet, and behavior. Some important works on mouthparts, diet and ecology are Labandeira (1997), Arens (1989, 1990, 1994). Any contributions toward understanding the feeding habits of fossil Ephemeroptera should involve an investigation of shape based on (1) structural and biomechanical possibilities, and (2) an exploration of phylogenetic and adaptative trends. An important basis is the classification in functional feeding groups (FFG) of aquatic insects, and the knowledge about mouthparts and principal habits of species which represent living families. Within Ephemeroptera, the more plesiomorphic are filterer-burrowers, such as the Ephemerioidea. The Baetidae, Siphonuridae, Leptohyphidae, Caenidae, and others, are collectors or shredders. A very specialized type consists of scrapers and filterers, or collector-filterer in many works, such as Cummins (1973), and is

represented by Leptophlebiidae, Heptageniidae and Oligoneuriidae, not burrowers. Although there is variations in details, the phylogenetic groups show a well delimited general pattern in functional morphology. The collectors and shredders bear mouthparts hard and without abundant bristles. The filterers-burrowers have abundant bristles for filtering suspended particles. The scrapers bear strong clusters of hard bristles and sclerotized projections. Some details of these differences are found in Arens (1989), Froehlich (1964), McShaffrey and McCafferty (1988), Polegatto (1998), and Strenger (1954).

Material and Methods

Fossil of mayfly nymphs of the Early Cretaceous (Aptian-Albian) Santana Formation, collected from Araripe Basin of Northeastern Brazil, were examined from the illustrations and photographs documented in Martins-Neto (1996), Martins-Neto & Caldas (1990), and McCafferty (1990), as well some fossils were examined. Maisey (1990) presented important data about the Araripe Basin. According to that author, the Araripe Basin today forms an elevated plateau (Chapada do Araripe), reaching altitudes of between 600 and 900m, which extends some 200km east-west and 70km north-south. The basin contains approximately 700m of a Mesozoic sedimentary sequence, thought to be of Upper Jurassic and Lower Cretaceous age. There is a considerable amount of lithological and paleontological data to support the view that the Crato Member of the Santana Formation is lacustrine. Subenvironments are found, one of these is the deeper lake center, while the other probably represents a marginal environment. The Araripe plateau has long been a source of spectacular fossil vertebrates, especially fishes, turtles, crocodilians, and pterosaurs. Insects, plants, and goniorhynchiform fishes are among the more common fossils

occurring in lacustrine laminated carbonates of the Crato Member. Some of these data are found in Braun (1966), Brito (1984), Moraes *et al.* (1976), and Silva (1983).

The interpretation was based on the photographs, draws, and fossils. The patterns used in the figures 10 and 11 were established based on the phylogenetic of Landa and Soldán (1985), on the works about habits of each family, and on the functional feeding group (FFG) of the order Ephemeroptera, such as Edmunds *et al.* (1976), Illies (1968), Merritt and Cummins (1978), Roldán-Pérez (1988), Williams and Feltmate (1992). Thus, comparing the patterns of the extant taxa, regarding head shape and general habits, with the fossils concluded the functional morphology of the nymphs.

The fossil mayfly nymphs of Santana Formation

The immature stages of mayfly species that were described by Martins-Neto (1996), Martins-Neto & Caldas (1990), and McCafferty (1990) from the Santana Formation, are the Hexagenitidae, Oligoneuriidae, Siphonuridae, Ephemeridae, Polymitarcyidae and Potamanthidae, and possibly Leptophlebiidae. Imagoes were recorded as well principally for Ephemeroidea group. The following is a brief review of the occurrence of taxa from these families in the Santana Formation.

Hexagenitidae

In the Santana Formation, the Hexagenitidae is the most commonly represented family (see Martins-Neto, 1996; McCafferty, 1990). This family includes many records in several regions of the Gondwana. Interestingly, these regions lack extant species that are associated to the Hexagenitidae, indicating that this clade is extinct. The closest extant relatives of the Hexagenitidae are the Siphonuridae (McCafferty, 1990).

Hexagenitid nymphs bear in dorsal view spherical heads, such as *Cratogenites corradinae* (Figure 1), *Paleobaetodes costalimai* (Figure 2), and *P. britoi* (Figure 3), or less commonly vertically-oriented and oval heads, including *Protoligoneuria limai* (Fig. 4). McCafferty (1990) presented a photo with a lateral view of this species, showing the baetid-like head (Figure 4, D).

Siphonuridae

The Siphonuridae are very similar structurally to the Baetidae, and both clades are closely related. *Siphogondwanus occidentalis* (Fig. 5) is hypognathous and the head is relatively similar to that of *Protoligoneuria limai*, a member of the Hexagenitidae. Both species are compared and reviewed by McCafferty (1990), who states that both species are similar in form and the inferences about ecological patterns for the latter are corresponding to those for *S. occidentalis*.

Oligoneuriidae

The Oligoneuriidae is the only family from the Santana Formation that is consistently associated with a lotic habitat. *Cratoligoneuriella leonardii* (Fig. 6) and *Colocrus indicum* (Fig. 7) are ecologically similar to extant Oligoneuriidae, and are specialized filterers that dwell in running water.

Ephemeroidea

Among the Ephemeroidea, *Carirynympha mandibulata* (Ephemeridae; Fig. 8, C), *Cratonympha microcelata* (Polimitarcyidae; Fig. 8, A), and *Olindinella gracilis* (Pothamantidae; Fig. 8, B), inhabit lentic water according to Martins-Neto & Caldas (1990). For the ecology of Ephemeroidea nymphs, Martins-Neto & Caldas (1990), refers to a benthic habitat with silt, sand, and mud in bottoms of streams and lakes, based on Edmunds *et al.* (1963), although there is not a clear ecological definition for each family. The mandibles and head capsule of these three species are very similar.

Leptophlebiidae

A fossil of possible Leptophlebiidae (Fig. 9), presented by McCafferty (1990) is insufficiently complete for identification. McCafferty (1990) described the fossil as possessing a "squarish head, less in length than the thorax, narrow in the cervical region and possibly hypognathous."

Other morphological data by McCafferty (1990) assists in reconstructing the paleoenvironment, such as the presence on Hexagenitidae nymphs of cerci for swimming in lentic waters such as peripheral pools within streams. Moreover, it was recorded imagoes of Oligoneuriidae, *Pristiplocia rupestris*, Euthyplociidae, and possible Pothamantidae (McCafferty, 1990) in Santana Formation.

Life Habits and Functional Morphology

Regarding paleoecology, McCafferty (1990) states that lotic habitats of the immediate area of the Santana Formation are evidenced by the presence of Oligoneuriidae and Euthyplociidae, and possibly Pothamantidae. Additionally, McCafferty (1990) suggests that the possible Leptophlebiidae is possibly a member of a group associated with a lotic habitat. Martins-Neto (1996) described the benthos for *Protoligoneuria* and *Cratogenites* as consisting of the silty and sandy bottoms with running and shallow water. By contrast, the sediment substrate for the habitat occupied by *Paleobaetodes* is stagnant shallow water within vegetated lakes, "with nymphs swimming freely" (Martins-Neto, 1996).

According to a previous theoretical model, presented herein as Figure 10, there is a predictable relationship between head- and mouthpart shape. In this model, hypognathous heads often have very basic, hard mouthparts, with portions well sclerotized, and without abundant bristles. The prognathous heads bear broad, specialized mouthparts, with abundant bristles, and they can to present also

sclerotized projections. Additionally, in the prognathous heads the mouthparts present modified articulations, and the median portions are dorsally-oriented, as demonstrated by Arens (1989), Brown (1961) and Polegatto (1998).

Examinations of the functioning of mayfly nymphal mouthparts increase our knowledge regarding this model, and demonstrate that details of the mouthparts and behavior of the nymphs are stereotyped for each head and mouthpart shape, such as the Baetidae, of Brown (1961), and Heptageniidae, of McShaffrey and McCafferty (1988) and Froehlich (1964). The most specialized structures occur in mouthparts and head of the Heptageniidae, Oligoneuriidae, Leptophlebiidae, and Ephemeroidea. By contrast, the Leptohyphidae and their allies, as well as the Baetidae-Siphonuridae group, bear more generalized mouthparts and heads (see Fig. 10 and 11). The figure 11 demonstrates some the basic types of head and mouthparts, and some variations.

Regarding functional feeding groups, the table 1 presents our summary of such classification, simplified of Merritt and Cummins (1978), and Williams and Feltmate (1992).

Discussion

The head structures used by Martins-Neto (1996), Martins-Neto & Caldas (1990), and McCafferty (1990) in the classification of Santana Ephemeroptera are the same that we employ for a morphological-functional understanding of the mouthparts and diet. We suggest that biomechanically-based and phylogenetic characters should be used as basis for interpretation. To this, we included supplemental data about paleoenvironment by those authors. We focused principally on the labial and maxillary tips and the distal portions of their palps, which were compared with extant species in order to provide

Table 1 - Functional Feeding Groups of Ephemeroptera; simplified of Merritt and Cummins (1978) and Williams and Feltmate (1992).

Feeding Strategy		Dominant Food	Structures Associated	Examples
Collector	Gatherer	Detritus, algae, fungi, leave pieces	Mandibles, tips of the maxillae, maxillary and labial palps	Baetidae, Siphonuridae, Caenidae, Leptohyphidae
	Filterer*	Suspended particles, single-celled algae (diatoms)	Long bristles of the maxillae, labium or mandible	Polymitarcyidae, Euthyplociidae, Heptageniidae, Oligoneuriidae
Shredder		Leave pieces, wood, detritus	Mandibles, tips of the maxillae	Baetidae, Leptohyphidae, Polymitarcyidae
Scraper		single-celled algae (diatoms), fine detritus, fungi, other biofilm associated matter	Clusters of hard bristles, and tooth-like projections in the maxillae and the labium	Leptophlebiidae, Heptageniidae
Predator		Arthropods and other invertebrates	Mandibles and maxillae	Leptophlebiidae

* The filtering strategy of nymphs of the Heptageniidae, Oligoneuriidae, and Leptophlebiidae, is very different of those of Ephemeroidea, in structures, behavior and evolution, and is associated with scraping, such as found in Heptageniidae and Leptophlebiidae.

ecologically relevant characters (Fig. 10). Our theoretical model shows that hypognathous heads are associated with more generalized or phylogenetically basal mouthparts within the Ephemeroptera, whereas prognathous heads are related to phylogenetically derived and specialized mouthparts and contain varied structures (see Fig. 10 and 11). We present the following ecological inferences for the Santana Formation Ephemeroptera families.

Hexagenitidae

Nymphs of the Hexagenitidae are hypognathous and feed as detritus collectors. This condition is typical of a generalized body-form associated with a facultative diet, such as occurs in extant Baetidae (see Figure 11). Functionally, it is not possible to characterize these mouthparts as bearing broad regions of bristles that are inclined allowing scraping or filtering (see McCafferty and McShaffrey 1988, Polegatto 1998). Additionally, there are mouthpart hard surfaces that are used for processing of solid food, such as in extant Leptohiphidae. For this type of mouthparts, shredding would complement the gathering of detritus, although the two processes are difficult to distinguish in many ephemeropterans, such as of first stage Caenidae nymphs that simultaneously employ both processes (Polegatto, unpublished data). Shredding apparently is associated with more spherical heads, such as *Cratogenites corradinae* (Figure 1), *Paleobaetodes costalimai* (Figure 2), and *P. britoi* (Figure 3), and occurs in extant Leptohiphidae. Alternatively, *Protoligoneuria limai* (Fig. 4), has a more vertical and oval head, and illustrates the predominance of collecting as found in typical Baetidae. McCafferty (1990) photographically documents a lateral view of this species, with exhibits a baetid-like head (Fig. 4, D). Moreover, the largest, longitudinally directed heads, such as the three previously discussed species, bear a greater space for housing more extensive, sclerotized mouthparts, especially mandibles - features which would allow more powerful

movement of robust mouthparts (see Polegatto, 1998).

Siphonuridae

Siphondwanus occidentalis (Fig. 5), based on the presence of hypognathous mouthparts, would be typically a collector, as well *Protoligoneuria limai*, a member of the Hexagenitidae, consistent with data provided by McCafferty (1990). *S. occidentalis* has a head that, although projecting somewhat forward and broad in width, seems not to be spherical, but rather is similar to that of a grasshopper in shape. Many extant Baetidae and Siphonuridae bear this type of head shape. Although the statement by McCafferty (1990) is correct because of the general similarities, which are buttressed by the close phylogenetic relationship of both families, there are some differences in head and body shape between these species. As a trend, it is probable that the Hexagenitidae would present less variation in ecology and diet than the Siphonuridae, based on the spatial and temporal distribution of Siphonuridae and some but important morphological variation (see Edmunds, 1976).

Oligoneuriidae

Morphological characters of *Cratoligoneuriella leonardii* (Fig. 6) and *Colocrus indicum* (Fig. 7) correspond closely to those of living Oligoneuriidae. *Colocrus indicum* possesses more developed mouthparts and deployment of regions with abundant bristles, attributable to the broad area mouthpart attachment observed in the fossil, as well as a head larger than the thorax. Thus there is relatively detailed data on mouthpart structure, and not only of the head shape. In *C. indicum* the wide head is more similar to those of some Heptageniidae, a related group, than the most cofamilial living Oligoneuriidae. Interestingly, Figure 7 of McCafferty (1990) (Fig. 7), shows a fossil in a ventral position that reveals probable glossae, paraglossae, and labial palps.

Ephemeroidea

Within the Ephemeroidea, the Polymitarcyidae and Ephemeridae are associated with lentic water by Martins-Neto & Caldas (1990), where currently burrowing mayflies are common. However, primitive species with sprawling gaits in the two families (Bae and McCafferty, 1996) and such species inhabit marginal lentic habitats where detritus and various items are abundant, as well as lotic habitats. Regarding Pothamantidae, the extant species are found in mixed substrates (Bae and McCafferty, 1996), with species occurring variously in sand and mud (Edmunds, 1976), and representing sprawling and burrowing life-habits, respectively. Both types of life-habits are found in the lotic habitat of McCafferty (1990). McCafferty (1975), also states that the North-American Ephemeroidea "sprawl more than burrow", but the work of Bae and McCafferty (1996), on the Polymitarcyidae, Pothamantidae, Ephemeridae, and Leptophlebiidae indicate that species with burrower and sprawler life-habits occur in the same genus. The Ephemeroidea are filterers that obtain food while the body is enclosed within burrows (in burrowers) or among the interstitial spaces (in sprawlers). We suggest that there is a difference in diet, albeit weak, between burrowers and sprawlers. Sprawlers are capable of obtaining a more varied diet, principally regard to size, than burrowers, as evidenced by the presence of more numerous bristles in *Campsurus* (Polymitarcyidae), than in *Campylocia* (Euthyplociidae). In burrowers, the clypeal-genal region often has projections and bristles, and the head is flattened; the body is soft and light in color. In sprawlers, the head is smooth and rounded, and the body is robustly sclerotized and dark-hued. In fossil Ephemeroidea, the existence of this association is unique; for example, bodies in different degrees of preservation bear varying detail of head capsule and mouthpart structure (see Martins-Neto & Caldas, 1990). Thus, in the Santana Formation, *Caririnympa mandibulata* (Ephemeridae;

Figure 8, C) and *Cratonympha microcelata* (Polymitarcyidae; Figure 8, A) (Martins-Neto & Caldas, 1990), appear to be burrower, corresponding to an interpretation by Bae and McCafferty (1996) for extant taxa. The ecology of *Caririnympa mandibulata*, discussed by Martins-Neto & Caldas (1990), and based on earlier study by Edmunds *et al.* (1963), is similar to that of extant descendant taxa, consisting of occupation of the firm bottoms of streams and lakes that are composed of silt and sandy mud (see Bae and McCafferty, 1996; Edmunds *et al.*, 1976). However, the Polymitarcyidae also occurs in mixed substrate, for example primitive sprawler species (Bae and McCafferty, 1996). *Olindinella gracilis*, considered as a pothamantid by Martins-Neto & Caldas (1990) (Fig. 8, B), could be assigned to another family, the Polymitarcyidae, principally because of mandibular structures, [although McCafferty (1990) described a possible pothamantid from Santana Formation]. If *O. gracilis* is a member of the Pothamantidae, it would have inhabited mixed substrates based on modern descendant taxa (see Bae and McCafferty, 1996), therefore indicating that it would have been a sprawler, in opposition to the interpretation of Martins-Neto & Caldas (1990), who suggested that it colonized a silty or muddy habitat. These opposing interpretation highlight the problem the classification of *O. gracilis*, and indicate that most species in the Santana Formation would be burrowers and not sprawlers.

Leptophlebiidae

Possible Leptophlebiidae of the Santana Formation do not allow a robust interpretation, because the fossil specimen is insufficiently preserved. In this context another hypothesis, not suggested by McCafferty (1990), is that this fossil occurred in a non-lentic habitat attributable to the fact that the extant subfamily Leptophlebiinae, presently occurring in Central- and North America, typically consists of sprawler species. Therefore members of this taxon are

filters, and some species are predators, and inhabit lentic water (see Bae and McCafferty, 1996). McCafferty (1990) states that this fossil has a "squarish head, lesser than the thorax, narrow in the cervical region and possibly hypognathous". This analysis is difficult to evaluate because the head is poorly preserved. A discernable "neck" for this fossil is typical of the Atalophlebiinae, which bear prognathous mouthpart, allowing a wider movement of the head (Polegatto, 1998). Additionally, a squarish head is associated with prognathous heads and is typical in many extant Atalophlebiinae, such as the *Hermanella* group, indicating that a "squarish hypognathous head" is inconsistent (see Polegatto, 1998). However, the squarish head in the photograph of McCafferty (1990) could indicate that only the dorsal area of the head is preserved, and thus it would be inappropriate to say the head is "squarish". Therefore, the head of this specimen is similar to those of taxa such as *Paraleptophlebia* (Leptophlebiinae), and is partly similar to those of some Atalophlebiinae, such as *Hagenulopsis*. Heads that are smaller than the thorax would be more typical in the Leptophlebiinae and not the Atalophlebiinae (see Edmunds, 1976; Bae and McCafferty, 1996; Hubbard *et al.*, 1992), including hypognathous species similar to the Baetidae (see Edmunds *et al.*, 1976). An important character is the relatively narrow body, found in Leptophlebiinae, such as *Leptophlebia*, and in some Atalophlebiinae, including *Hagenulopsis*. If the Santana specimen is a member of the Leptophlebiinae, the mouthparts would be of scraper-collector structure, based on descriptions of the family (see Figure 2). The diet would be more generalist, as showed in Edmunds *et al.* (1976), such that mature nymphs would have inhabited more lentic water, in contradistinction to the Atalophlebiinae, with more specialized mouthparts for the scraping of periphyton and for filtering suspended particles (Polegatto, 1998). The latter case is restricted to lotic and

oligotrophic habitats (Roldán-Pérez 1988). Thus, based on the ~~death~~ of the running-water species in the Santana Formation, and the distribution of these two subfamilies, this fossil could be allocated to the Atalophlebiinae.

Other data presented by McCafferty (1990), such as the body-form of nymphal Hexagenitidae and nymphs with cerci designed for a swimming in calm waters such as pools within streams, help to establish the Santana paleoenvironment. This rendering is in accord with our data on collector-shredding Hexagenitidae as well, and is consistent with the presence of allochthonous organic particulate matter in Santana insect-bearing deposits and ephemeropteran access to peryphiton in areas with more luminosity. Lastly, the imagoes of Oligoneuriidae, *Pristiplocia rupestris*, Euthyplociidae, and possible Pothamantidae (McCafferty, 1990), would suggest even an abundance of streams, corresponding also to the presence of Atalophlebiinae and Oligoneuriidae, and the coexistence of filtering-sprawling and scraping-filtering species.

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References

- ARENS, W., 1989. Comparative functional morphology of the mouthparts of stream animals feeding on epilithic algae. (Monographische Beiträge). *Arch. Hydrobiol. Suppl.*, **83**(3): 253-534.
- _____, 1990. Wear and tear of mouthparts: a critical problem in stream animals feeding on epilithic

- algae. *Can. J. Zool.*, **68**: 1896-1914.
- _____, 1994. Striking convergence in the mouthpart evolution of stream-living algae grazers. *J. Zool. Syst. Evol. Research*, **32**: 319-343.
- BAE, Y.J. and MCCAFFERTY, W.P., 1996. Ephemeroptera tusks and their evolution. In: *Current Directions in Research on Ephemeroptera*. CORKUM, L.D. and CIBOROWSKI, J.H. (eds.). Canadian Scholars' Press Inc., Toronto, 377-405.
- BRITO, I.M., CAMPOS, D.A., and BERTINI, R.J., 1984. Nota preliminar sobre os insetos da Formação Santana, Cretáceo Inferior da Chapada do Araripe. In: CONGRESSO BRASILEIRO DE GEOLOGIA, 32, Rio de Janeiro, 1984. *Anais.....*, Rio de Janeiro, SBG: 530-535.
- BROWN, D.S., 1961. The morphology and functioning of the mouthparts of *Chloeon dipterum* L. and *Baetis rhodani* (Pictet), (Insecta, Ephemeroptera). *Proceedings of the Zoological Society of London*, **136** (2): 147-176.
- CUMMINS, K.W., 1973. Trophic relations of aquatic insects. *Ann. Rev. Entomol.*, **18**: 183-206.
- EDMUNDS, G.F., ALLEN, R.K., and PETERS, W.L., 1963. An annotated key to the nymphs of the families and sub-families of mayflies (Ephemeroptera). *Univ. of Utah Biolog. Ser.*, **13** (1): 1-55.
- EDMUNDS, G.F., JENSEN, S.L. and BERNER, L., 1976. *The Mayflies of North and Central America*. Minneapolis. University of Minnesota Press. 330 p.
- FROEHLICH, C.G., 1964. The feeding apparatus of the nymph of *Arthroplea congener* Bengtsson (Ephemeroptera). *Opuscula Entomologica*, **29** (3): 188-208.
- HUBBARD, M.D., E. DOMINGUEZ and M.L. PESCADOR, 1992. Los Ephemeroptera de la República Argentina: un catálogo. *Rev. Soc. Ent. Argentina*, **50** (1-4): 201-240.
- ILLIES, J., 1968. Ordnung Ephemeroptera (Eintagsfliegen). *Handbuch der Zoologie*, Berlin, **4** (2) 2/5: 1-63.
- LABANDEIRA, C.C., 1997. Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. *Annual Review of Ecology and Systematics*, **28**: 153-193.
- LANDA, V. and SOLDÁN, T., 1985. Phylogeny and higher classification of the order Ephemeroptera: a discussion from the comparative anatomical point of view. *Studie csl. Akad. Ved.* **4**: 1-121.
- MARTINS-NETO, R.G., 1996. New mayflies (Insecta, Ephemeroptera) from the Santana Formation (Lower Cretaceous), Araripe Basin, northeastern Brazil. *Revista Española de Paleontología*, **11** (2), 177-192.
- MARTINS-NETO, R.G. and CALDAS E.B., 1990. Efêmeras escavadoras (Insecta, Ephemeroptera, Ephemeroidea) na Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil: descrição de três novos gêneros e três novas espécies (ninfas). In: SIMPÓSIO SOBRE A BACIA DO ARARIPE E BACIAS INTERIORES DO NORDESTE, 1, CRATO, 1990. Atas.... Rio Claro: 265-273.
- MAYSEY, J. G., 1990. Stratigraphy and depositional environment of the Crato Member (Santana Formation, Lower Cretaceous of N.E. Brazil). In: GRIMALDI, D. A. (ed.). *Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bulletin of the American Museum of Natural History*, **195**: 15-19.
- MCCAFFERTY, W.P., 1975. The burrowing mayflies of the United States (Ephemeroptera: Ephemeroidea). *Trans. Am. Ent. Soc.*, **101** (3): 447-503.
- _____, 1990. Ephemeroptera. In: GRIMALDI, D. A. (ed.). *Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bulletin of the American Museum of Natural History*, **195**: 20-50.

- McSHAFFREY, D. and McCafferty, W.P., 1986. Feeding behavior of *Stenacron interpunctatum* (Ephemeroptera: Heptageniidae). *Journal of the North American Benthological Society*, **7**: 87-99.
- _____, 1988. Feeding behavior of *Rhithrogena pellucida* (Ephemeroptera, Heptageniidae). *Journal of the North American Benthological Society*, **7** (2): 87-99.
- MERRITT, R.W. and CUMMINS, K.W., 1978. *An Introduction to the Aquatic Insects of North America*. Dubuque, Kendal/Hunt Publishers. 722 p.
- MORAES, J.F.S., SANTOS, J., and MASCARENHAS, J.C., 1976. *Projeto Santana*. Relatório final da etapa 1, Recife, DNPM/CPRM, (vol. 1), 269 p.
- POLEGATTO, C.M., 1998. *Morfologia Funcional do Aparelho Bucal de Ninfas de Farrodes sp. (Ephemeroptera, Leptophlebiidae)*. São Paulo, SP. Dissertação de Mestrado. Universidade de São Paulo - USP, 112 p.
- ROLDÁN-PÉREZ, G., 1988. *Guía para el estudio de los macroinvertebrados acuáticos del Departamento de Antioquia*. Bogotá. Editorial Presencia Ltda. 217 p.
- STRENGER, A., 1954. Zur Kopfmorphologie der Ephemeridenlarven. I, *Ecdyonurus* und *Rhithrogena*. *Österreichische Zoologische Zeitschrift*, **4**: 191-228.
- WILLIAMS, D.D. and FELTMATE, B.W., 1992. *Aquatic Insects*. University of Toronto. 358 p.

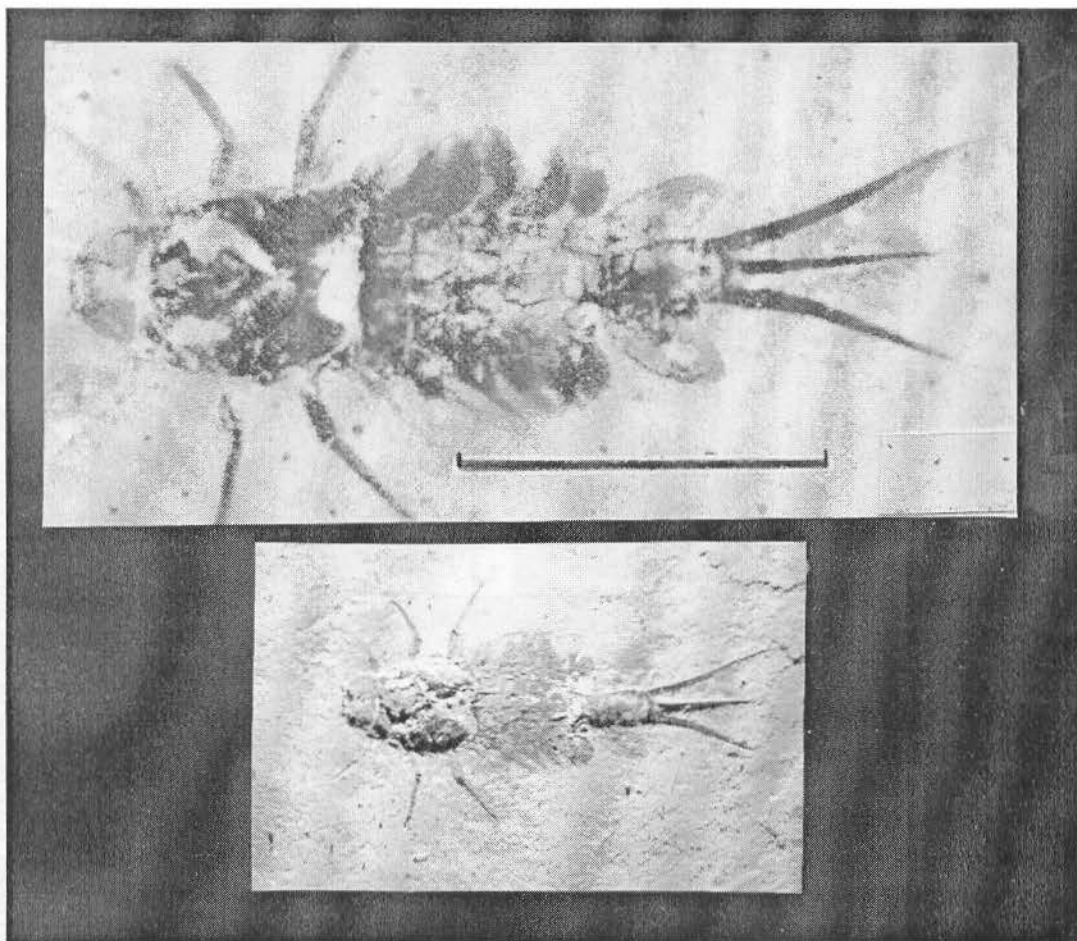


Figure 1 - *Cratogenites corradinae* Martins-Neto, 1996, holotype. Photo by the authors.

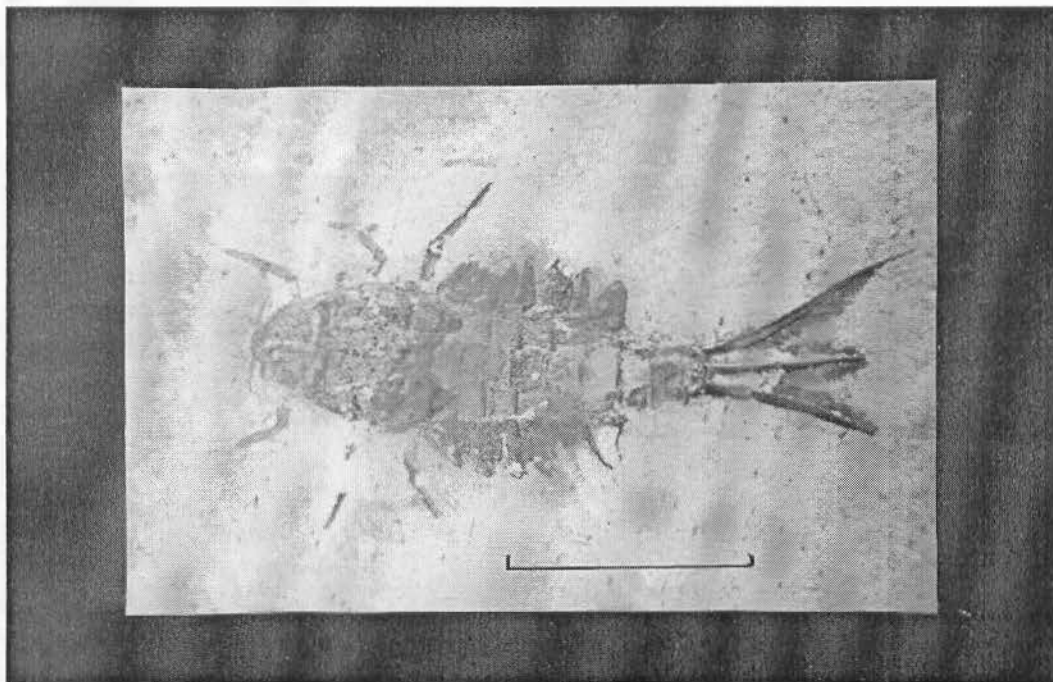


Figure 2 - *Paleobaetodes costalimai* Martins-Neto, 1996, holotype; left, photo by the authors; right, photo by Martins-Neto (1996); scale bar 5mm.

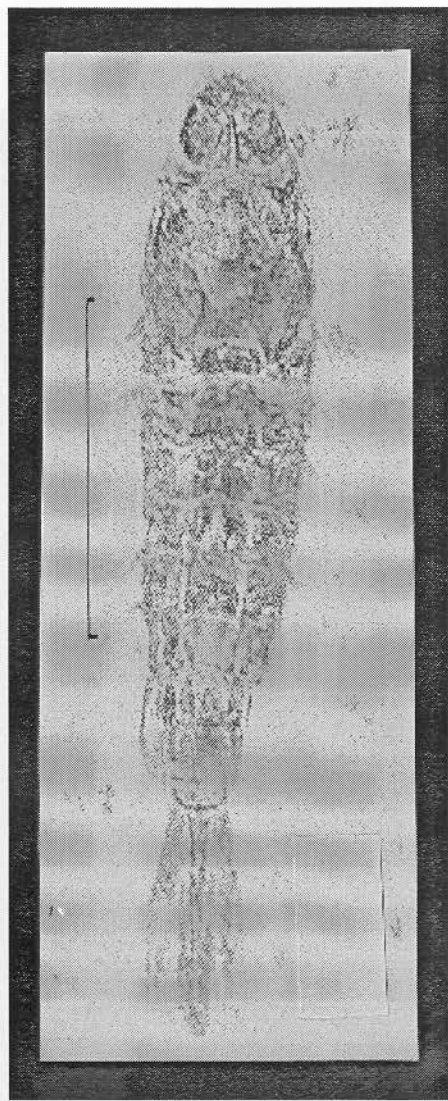


Figure 3 - *Paleobaetodes britoi* Martins-Neto, 1996, holotype. Photo by Martins-Neto (1996); scale bar 5mm.

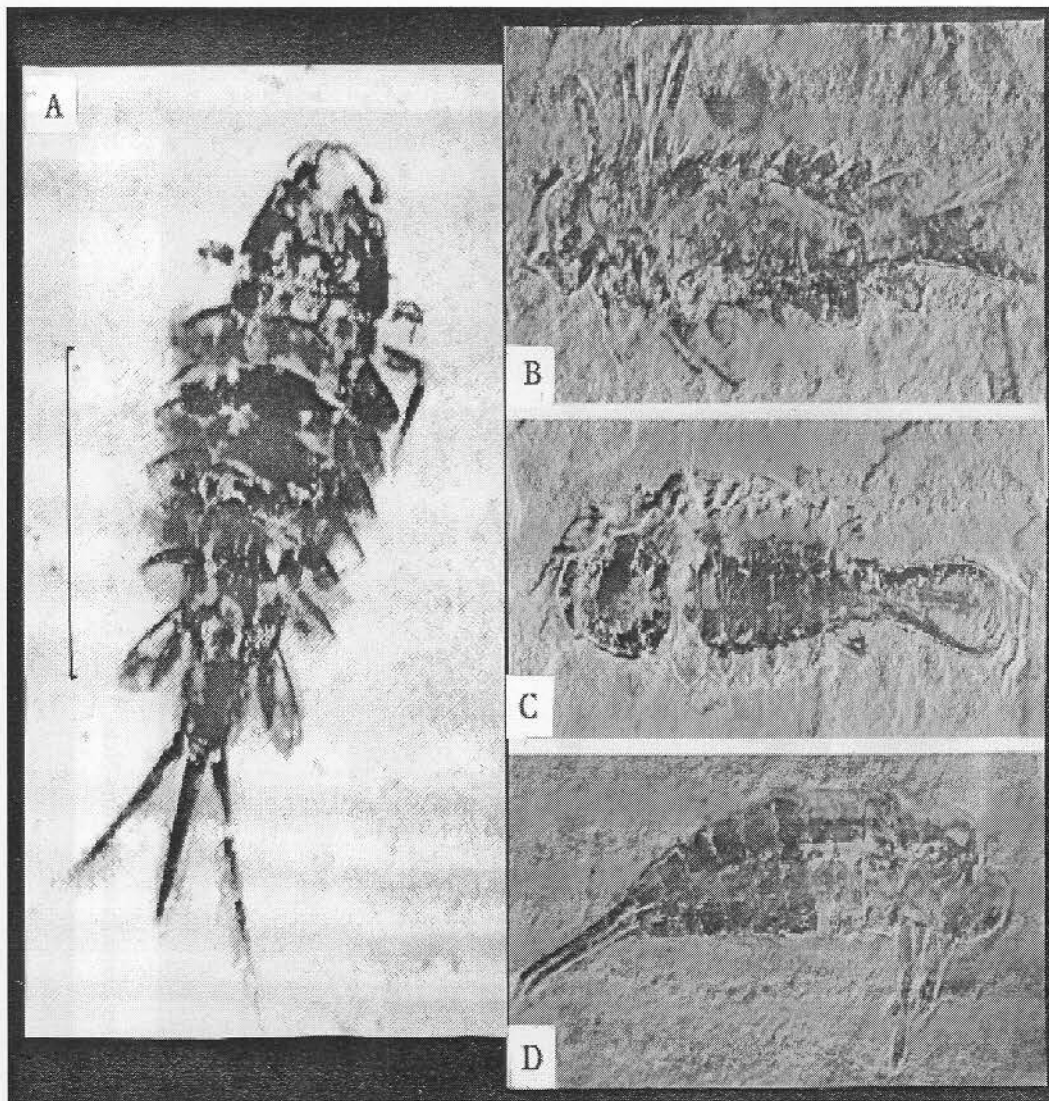


Figure 4 - *Protoligoneuria limai*, A. dorsal view, B e C. ventral view, D. lateral view, A. photo by Martins-Neto (1996), B-D; photos by McCafferty (1990); scale bar in A 5mm.



Figure 5 - *Siphogondwanus occidentalis*, photo by McCafferty (1990).



Figure 6 - *Cratoligoneuriella leonardii* Martins-Neto, 1996, holotype. Photo by Martins-Neto (1996); scale bar 5mm.

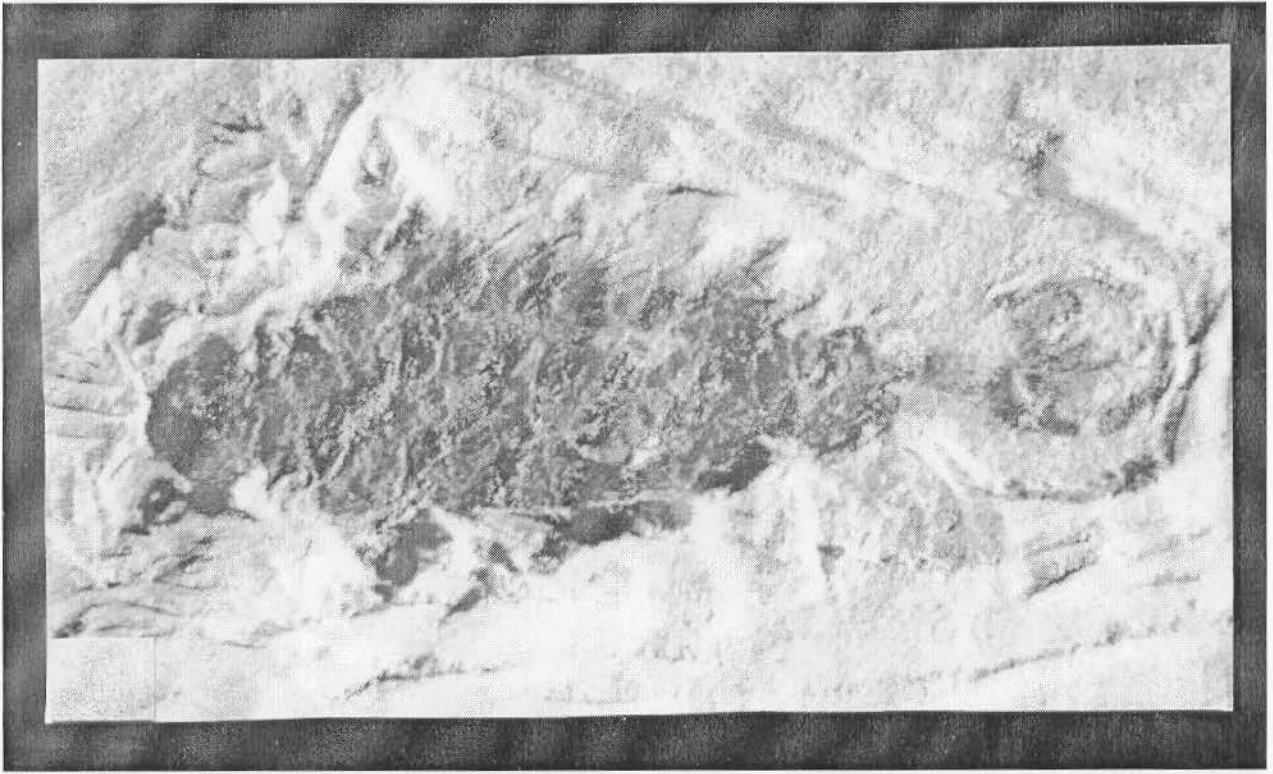


Figure 7 - *Colocrus indicum*, photo by McCafferty (1990).



Figure 8 - Ephemeroidea nymphs, A. *Cratonympha microcelata* (Ephemeridae), B. *Olindinella gracilis* (Pothamantide?), C. *Caririnympa mandibulata* (Polymitarcyidae); draws by Martins-Neto (in Martins-Neto & Caldas, 1990); scale bar 5mm.

Texto para a Fig. 9

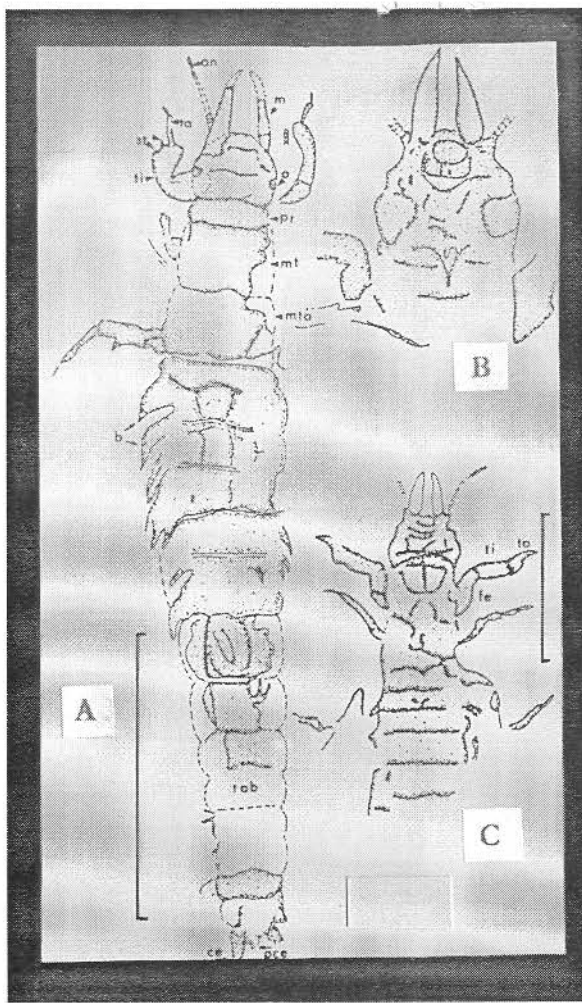


Figure 9 - Possible Leptophlebiidae, Atalophlebiinae nymph, photo by McCafferty (1990).

↳ texto para a Fig. 8

	Head shape	Size of the head	Structures of the mouthparts	Examples
Hypognathous				Baetidae Caenidae Siphonuridae Leptohyphidae
Prognathous				Leptophlebiidae Ephemeroidea Heptageniidae

Figure 10 - Model for the relationship between head- and mouthparts shape. In the hypognathous type, the head is oval or spherical, and the mouthparts are more generalized and sclerotized, without abundant bristles. By contrast, in the prognathous type, the head is flattened and broad, and the mouthparts are well specialized, with abundant bristles and with tooth-like projections. The draws does not show a specific mouthpart; they only are schematical.

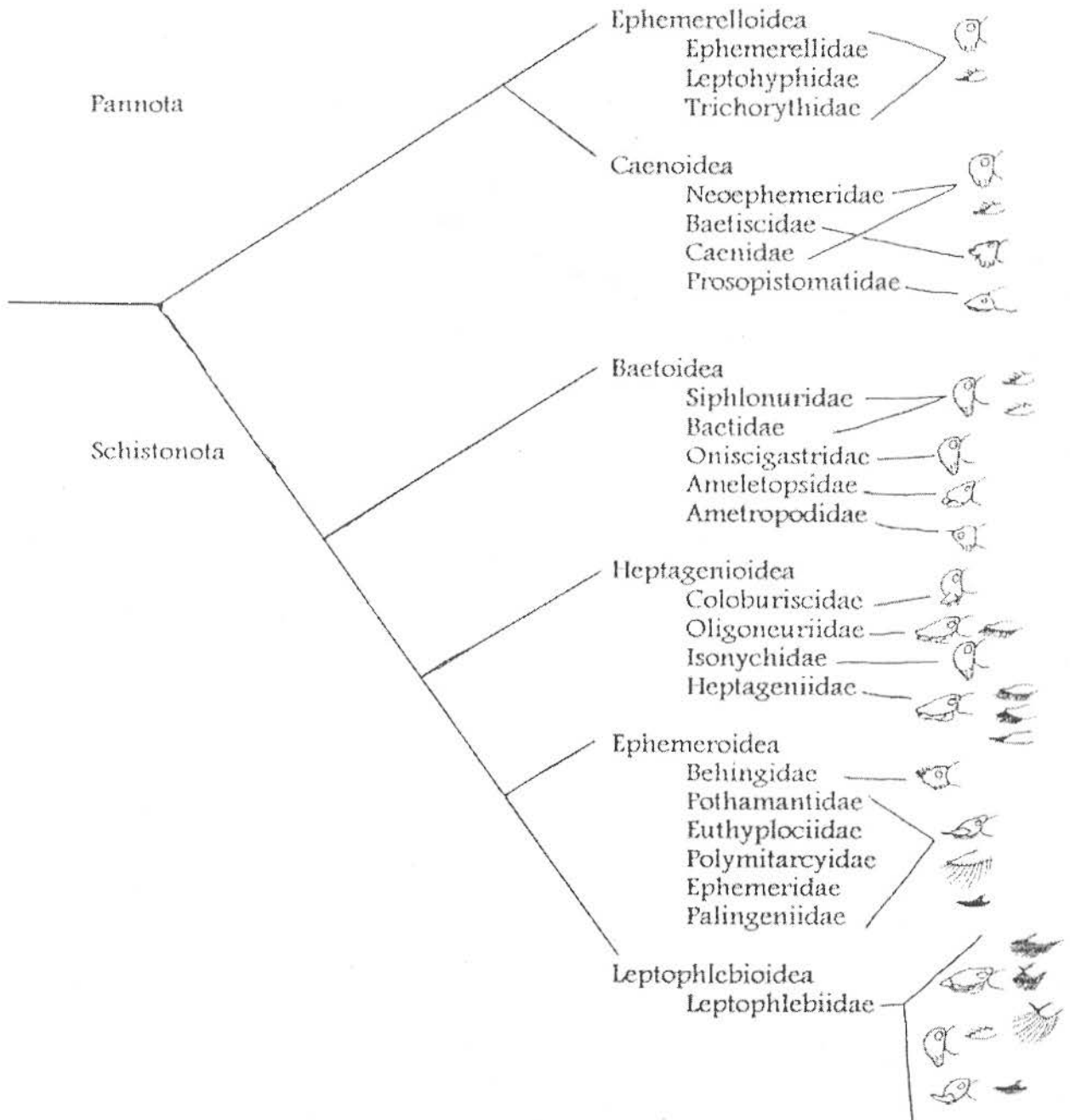


Figure 11 - Phylogenetic of Ephemeroptera and some characters of the head and the mouthparts. In this cladogram, by Landa and Soldán (1985), the schemes represent patterns of head and mouthparts, with simplified examples of bristles clusters and sclerotized projections. Regarding mouthparts, the more specialized mayflies are the Heptagenioidea, the Ephemeroidea, and the Leptophlebioidea, while the more basic one are the Ephemerelloidea, the Caenoidea, and the Baetoidea.