# PROBLEMS IN THE PHYLOGENY OF THE EPHEMEROPTERA

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## ABSTRACT

In the phylogenetic systematics of the Ephemeroptera several confusions arise due to the application of symplesiomorphic characters to establish sister groups. As a result of this methodology, paraphyletic lineages were occasionally defined. A striking example for such a situation is the separation of the Ephemeroptera into the sister group *Pannota* and *Schistonota*. The *Pannota* group is defined as a suborder by synapomorphic characters and is a monophyletic unit. The *Schistonota* group, on the other side, is based on symplesiomorphic characters. It is not the true sister group of the *Pannota* and consequently of paraphyletic origin.

Synapomorphic characters were established using published data of the internal anatomy of the larvae, the mouth parts of the larvae and imaginal external morphological features. To these, data of our results on the morphology of larval mouth parts were added. The achieved systematics is far from being complete. Our attempt was merely to focus on the Heptageniidae and especially on the systematics of the order at the highest hierarchic level.

## INTRODUCTION

In recent years many contributions have been published on the phylogeny and higher classification of Ephemeroptera. Landa and Soldán (1985) provide a concise review of the present topics. Although a great deal of useful characters concerning internal anatomy and external morphology were described, very few attempts, besides the work of Riek (1973), Kluge (1989), and Peters (1980), were taken to apply this data to modern ideas on phylogenetic systematics.

In the present paper we will apply data on useful characters to find the closed hereditary units of evolutionary species groups of Ephemeroptera. The evolutionary species concept (Wiley, 1978, 1981) is based on a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendency and historical fate. In this context, the origin of new species is based on the splitting of an existing species by allopatric, parapatric or sympatric speciation processes. The primary species may or not keep its existence during this process. In the evolutionary process closed hereditary groups are produced which contain

one or more evolutionary species and their common ancestor species. To find the phylogenetic relationships in the Ephemeroptera we follow a consequent search for the adelphotaxa relations of closed hereditary groups. To find the proper adelphotaxa relations we look for synapomorphic characters by carefully avoiding symplesiomorphic ones. In the present work we confine ourselves to the external morphology and internal anatomy although several other attempts were made in our laboratories to apply biochemical characters as well (Zurwerra *et al.*, 1986, 1987; Hefti and Tomka, 1989; Hefti *et al.*, 1988, 1989; Landolt, 1989; Studemann *et al.*,1989).

## ADELPHOTAXA OF THE FAMILIES OF THE EPHEMEROPTERA

The useful synapomorphic characters for the higher hierarchic level are presented in Table 1. In this table the characteristics corresponding to the internal anatomy are taken from Landa and Soldan (1985). The outer morphological characters if not otherwise stated were compiled for the larval and imaginal states from Edmunds *et al.* (1963, 1979) and for the eggs from Koss and Edmunds (1974). The useful characters on larval mouth parts are explained in Figs 4 to 8. Although we found that the posterior border of the abdominal tergites is decorated in the Baetoidea and Heptagenoidea (synapomorphy 1) we had not yet had the opportunity to cover a sufficient number of species in our investigations; there are possible convergencies to some Leptophlebiidae. Similarly we could not yet prove the absence of branches of dorsal trunks in the head of nymphs for the Ametropodidae and Metretopodidae (synapomorphy 1). Regarding synapomorphy 2 the ventral anastomosis of trachea in the Caenidae and Baetiscidae is reduced to thin branches. In any synapomorphic character convergencies may be found. The usefulness of a character is inversely proportional to the number of involved convergencies. The characters mentioned may be useful synapomorphies for very large hereditary units but their value must be proven on a correspondingly large number of species. We point out the further convergencies and uncertainities involved in the phylogenetic systematics proposed in Fig. 1. The proper adelphotaxa has not yet been found for the Siphlonuridae - Rallidentidae new family. The wing case of the nymph of *Murphyella*, Oligoneuriidae, shows a convergence to the *Pannota*. In *Chiloporter*, Ameletopsidae the ventral anastomoses of the tracheae show convergence to synapomorphy 2 (Table 1). The genus *Neurocaenis* represents a further developmental state with respect to synapomorphy 24 (Table 1). The structure of the mouth parts show a plesiomorphic character state for very different families like Siphlonuridae, Baetidae, Oniscigastridae, Neoephemeridae and Caenidae.

Further synapomorphic characters must be found on world wide material to come to conclusive results and also complete the present systematics for the family Oniscigastridae which is not included.

In the present phylogenetic systematics of Ephemeroptera the generic composition of the families are defined as by Landa and Soldan (1985) with the following exceptions:

Siphlonuridae:
- *Dipteromimus* McLachlan, 1875;
- *Edmundsius* Day, 1953;
- *Parameletus* Bengtsson, 1908;
- *Siphlonisca* Needham, 1909;
- *Siphlonurus* Eaton, 1868.

Rallidentidae, new family:
- *Ameletoides* Tillyard, 1933;
- *Ameletus* Eaton, 1885;
- *Metamonius* Eaton, 1885;
- *Metreletus* Demoulin, 1951;
- *Nesameletus* Tillyard, 1933;
- *Rallidens* Penniket, 1966.

Acanthametropodidae:
- *Acanthametropus* Tschernova, 1948;
- *Analetris* Edmunds, 1972;
- *Siphluriscus* Ulmer, 1920.

Metretopodidae:
- *Metretopus* Eaton, 1901;
- *Siphloplecton* Clemens, 1915;

Pseudironidae:
- *Pseudiron* McDunnough, 1901.

Heptageniidae:
- Heptageniinae Needham, 1901;
- Anepeorinae McCafferty and Provonsha 1988
- Spinadinae McCafferty and Provonsha 1988.

Arthropleidae:
- *Arthroplea* Bengtsson, 1909.

## ADELPHOTAXA OF THE GENERA OF THE HEPTAGENIIDAE

The synapomorphic characters in Table 2 were used to construct the four adelphotaxa of the Heptageniidae (Fig. 2). A subdivision of the "*Rhithrogena* group" into the adelphotaxa "*Rhithrogena*" (*Cinygmula, Rhithrogena, Paegniodes*) and "*Epeorus*" (*Bleptus, Ironodes, Epeorus*) was achieved solely by larval characters.

The synapomorphies for the genera of the Heptageniidae were established on material of world wide origin.

## ADELPHOTAXA OF THE GENUS *RHITHROGENA*

The synapomorphic characters in Table 3 were used to establish the adelphotaxa in the genus *Rhithrogena* (Fig. 3). Mainly material from Europe and some from the Neartic was used in this special study. Some of the

synapomorphies (Table 3; Figs 10, 11) have already been published for the "*lobata*" and "*laevigata*" groups (Zurwerra *et al.*, 1987). Special care was taken to find the synapomorphic character for the "*alpestris*" sub-group. The sclerotized emargination on the first abdominal sternite of the larvae was used by several authors to characterize *Rhithrogena* species. The inclination of the anterior margin of this sclerite was used to separate *Rhithrogena loyolaea* and related species from others. A thorough analysis (Fig. 9) shows no synapomorphy for any of the established groups. In the "*laevigata*" group but also in its adelphotaxa in the "*lobata*" group, we find distally and proximally inclined sclerite margin. The apomorphic state of this sclerite is: the full circumference is prominent. This character is then the synapomorphic one of the "*alpestris*" sub-group.

The aim of this preliminary contribution is to encourage students of Ephemeroptera to apply the modern concepts of phylogenetic systematics.

## ACKNOWLEDGMENTS

We would like to thank Prof. G. Lampel, Ch. Elpers, D. Hefti, Dr. P. Landolt and D. Studemann for their help in the elaboration of the manuscript. This work has been supported by the Swiss National Science Foundation (Grant nr. 3.506-0.86).

## REFERENCES

Edmunds, G. F., R. K. Allen and W. L. Peters (1963): An annotated key to the families and subfamiles of mayflies (Ephemeroptera). Univ. Utah Biol. Sci. Ser. 13 (1): 1-55.

Edmunds, G. F., S. L. Jensen, and L. Berner (1976): The mayfies of North and Central America. University of Minnesota Press, Minneapolis, 330 pp.

Hefti, D., U. H. Humpesch and I. Tomka (1988): An electrophoretic and morphological study of three *Ecdyonurus* species (Ephemeroptera: Heptageniidae) occuring in the British Isles. System. Entomol. 13: 161-170.

Hefti, D. and I. Tomka (1989): Comparative morphological and electrophoretic studies on *Afronurus zebratus* (Hagen, 1864) comb.n. and other European Heptageniidae (Ephemeroptera), including a key to the European genera of Heptageniidae. Aquatic Insects 11 (2), 115-124.

Hefti, D., I. Tomka and& A. Zurwerra (1991): Revision of the European species belonging to the *Ecdyonurus helveticus*-group (Heptageniidae). Present volume.

Koss, R. W. and G. F. Edmunds (1974): Ephemeroptera eggs and their contribution to phylogenetic studies of the order. Zool. J. Linn. Soc., 55 : 267-344.

Kluge, V. J. (1989). A question of the homologyof the tracheal gills and paranotal processi of the Mayflies larvae and wings of the insects with

reference to the taxonomy and phylogeny of the order Ephemeroptera. Dokladi na corok pervow, Nauka Press, Lenigrad, 3-76.

Landa, V. and T. Soldan (1985): Phylogeny and higher classification of the Ephemeroptera: a discussion from the comparative anatomical point of view. Ceskoslovenska Academie Ved, Studie CSAV 4: 1-121.

Landolt, P. (In press): An approach to the Application of Molecular Biological Methods to Solve Taxonomical and Phylogenetic Problems of the Ephemeroptera. Present volume.

McCafferty, W. P. and G. F. Edmunds (1979): The Higher Classification of the Ephemeroptera and its Evolutionary Basis. Ann. ent. Soc. Amer., 72: 5-12.

Peters, W. L. (1980): Phylogeny of the Leptophlebiidae (Ephemeroptera): an introduction. *In* Flannagan, J. F. and K. E. Marshall: Advances in Ephemeroptera Biology. Plenum Press, New York and London, 3: 33-41.

Riek, E. F. (1973): The classification of the Ephemeroptera. *In* Peters, W. L. and J. G. Peters. Proceedings of the First International Conference of Ephemeroptera. E. J. Brill, Leiden. pp. 160-178.

Studemann, D., P. Landolt and I. Tomka (In press): European Siphlonuridae (Ephemeroptera): a phylogenetic system for the four genera. Present volume.

Wiley, E. O. (1978): The evolutionary species concept reconsidered. Syst. Zool. 27: 17-26.

Wiley, E. O. (1981): The theory and practice of phylogenetic systematics. J. Wiley and Sons, New York.

Zurwerra, A., I. Tomka and G. Lampel (1986): Morphological and enzyme electrophoretic studies on the relationships of the European *Epeorus* species (Ephemeroptera, Heptageniidae). System. Entomol. 11: 255-266.

Zurwerra, A., M. Metzler and I. Tomka (1987): Biochemical systematics and evolution of the European Heptageniidae. Arch. Hydrobiol. 109. 481-510.

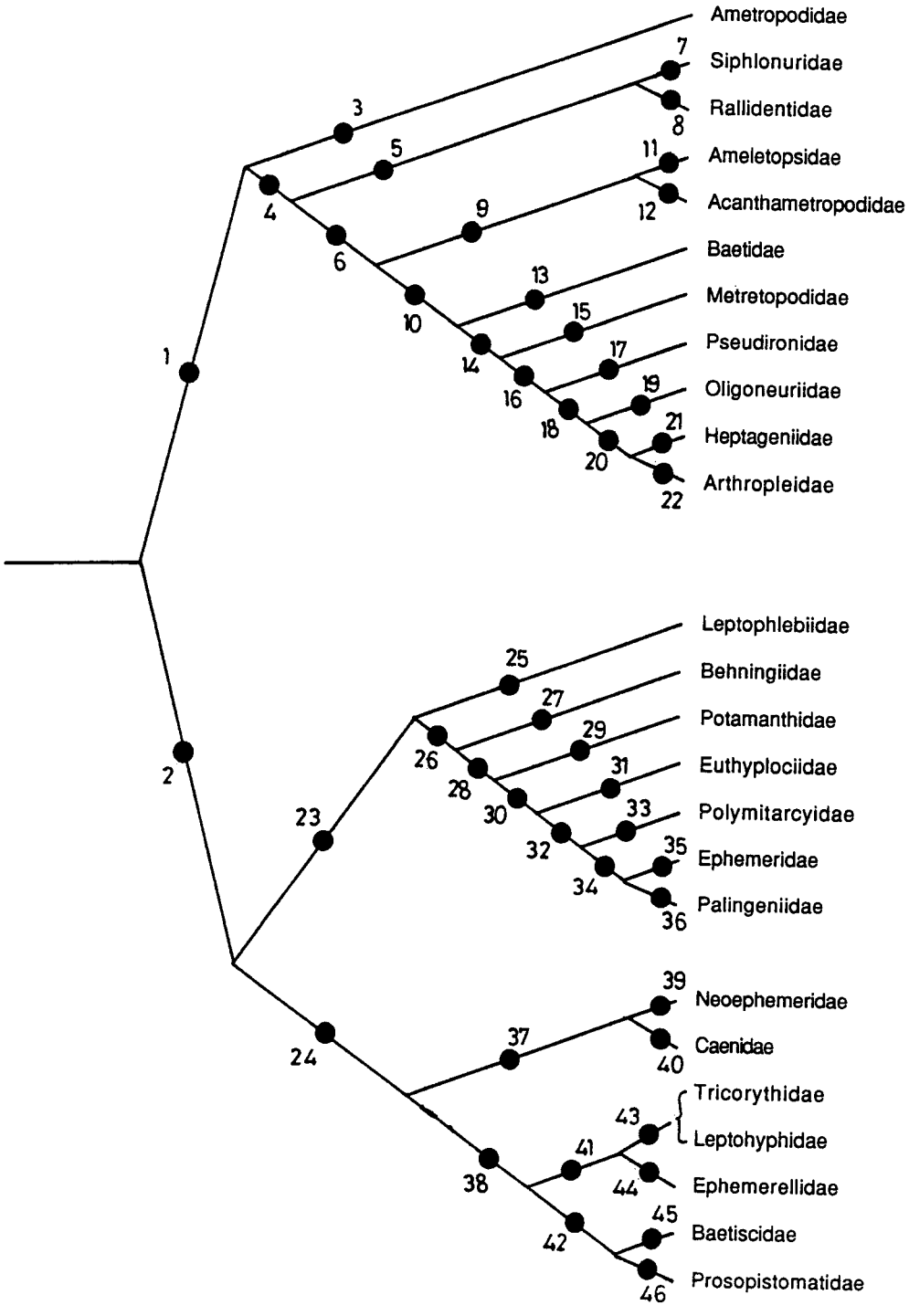


Fig. 1: Cladogram of Ephemeroptera families.

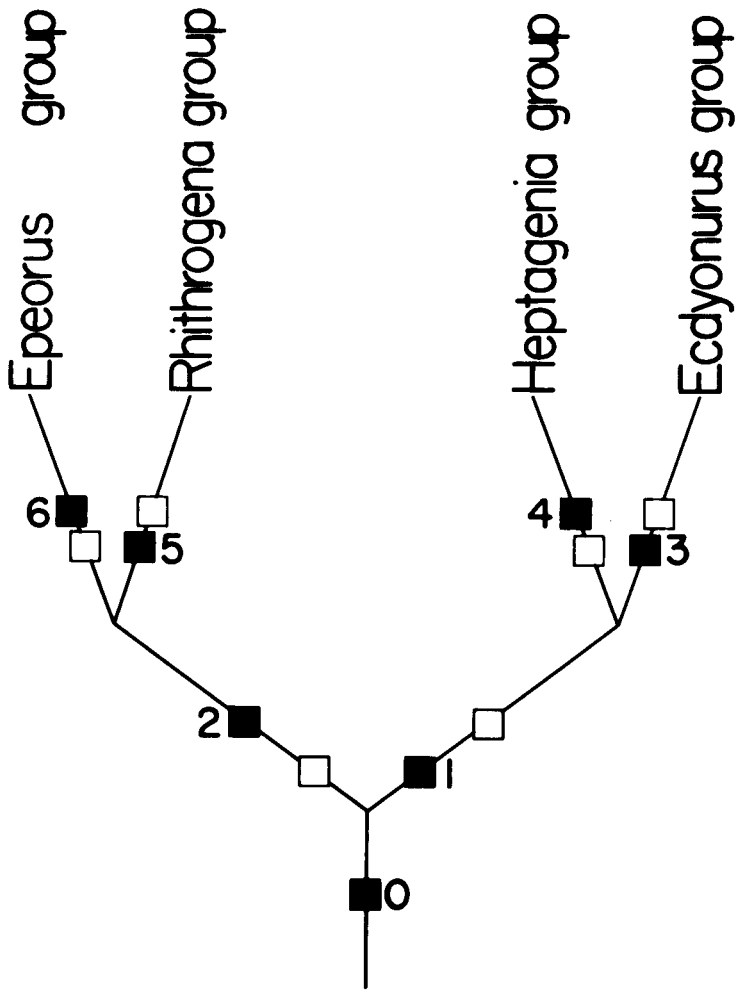


Fig. 2: Cladogram of genera of Heptageniinae.

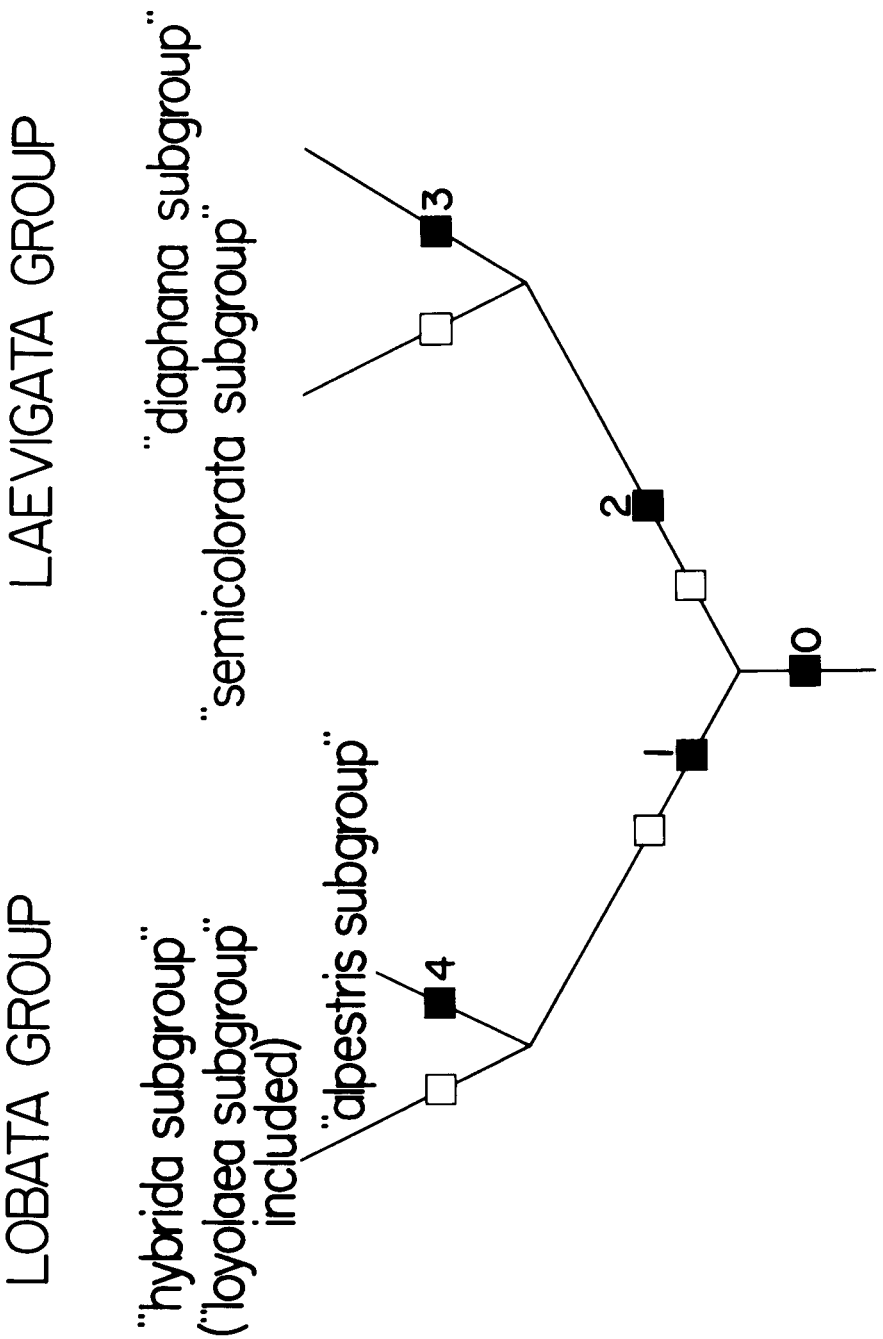


Fig. 3: Cladogram of *Rhithrogena*.

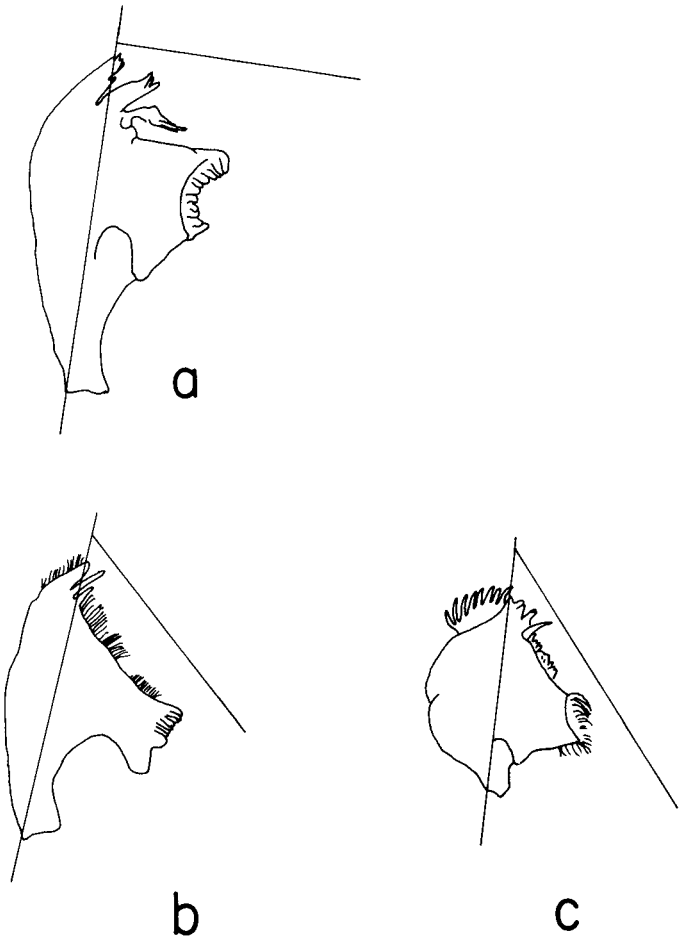


Fig. 4: Synapomorphic character 8 for families of the Ephemeroptera: structure of the mandible for *Siphlonurus* sp. (a), *Ameletus* sp. (b) and *Ralliidens* sp. (c).

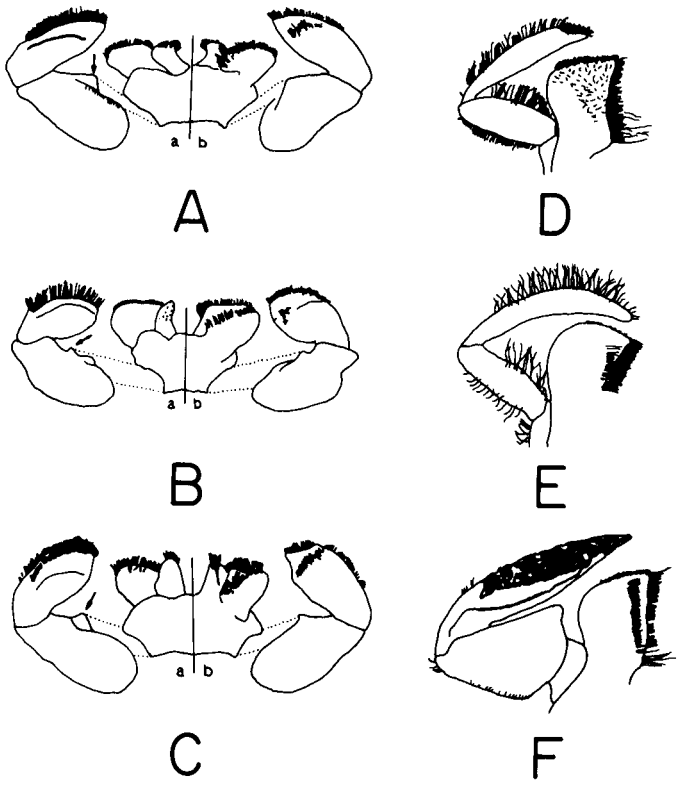


Fig. 5: Synapomorphic character 21 for the families of Ephemeroptera: labium (ventral view (a) and dorsal view (b)) of Heptageniinae first labial palpus with notch: *Ecdyonurus* sp. (A), *Heptagenia* sp. (B), *Rhithrogena* sp. (C); maxilla (ventral view): *Ecdyonurus* sp. (D), *Heptagenia* sp. (E), *Rhithrogena* sp. (F).

Fig. 6: Synapomorphic character 25 for families of Ephemeroptera: crown of galea-lacinia of Leptophlebiidae (*Leptophlebia* sp.).

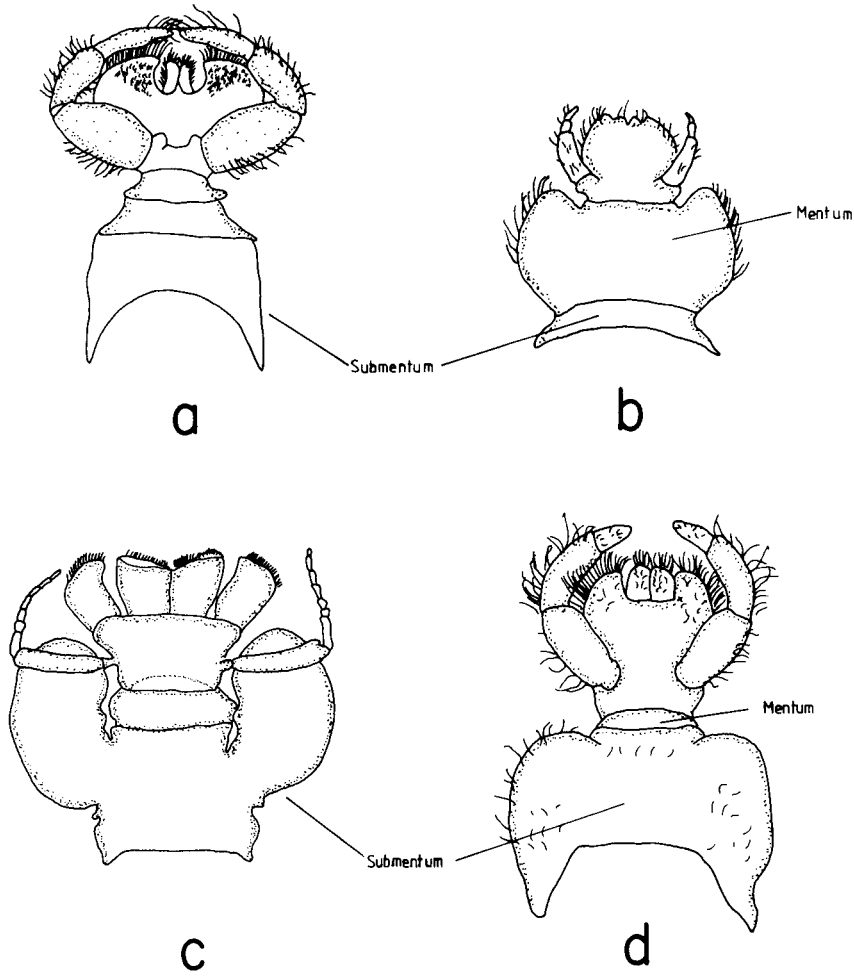


Fig. 7: Synapomorphic characters 29 and 38 for families of Ephemeroptera: labium of *Potamanthus* (a), *Tricorythodes* (b), *Chiloporter* (c) and *Ephemerella* (d).

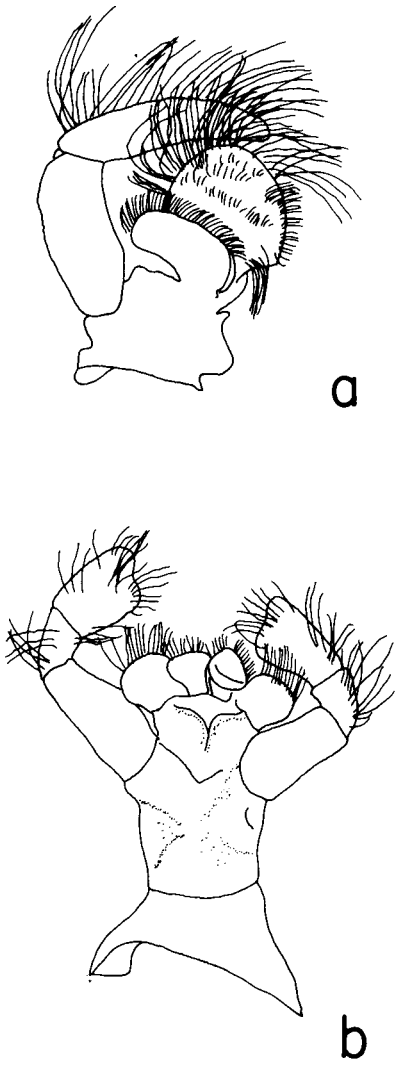


Fig. 8: Synapomorphic character 30 for the families of Ephemeroptera: labium of *Ephoron* sp. (a) and *Ephemera* sp. (b).

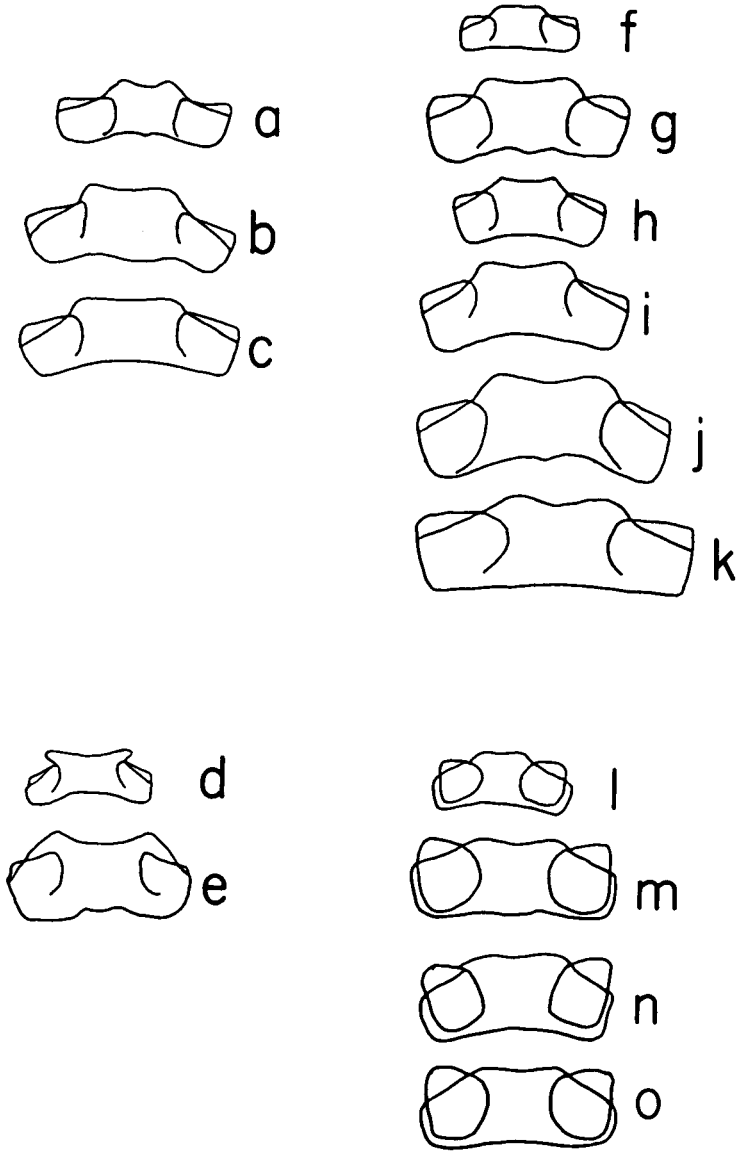


Fig. 9: *Rhithrogena* sp. abdominal sternite: *laevigata* group, *semicolorata* sub-group: *R.* sp. n. 1 (a), *R. dorieri* (b), *R. semicolorata* (c); *diaphana* sub-group: *R. savoiensis* (d), *R.* sp. n. 2 (e); *R. lobata* group, *hybrida* sub-group: *R. nivata* (f), *R. endenensis* (g), *R. strenua* (h), *R. loyolaea* (i), *R.* sp. n. 3 (j), *R. insularis* (k); synapomorphic character 4 on Fig. 3 *alpestris* sub-group: *R. kimminsi* (l), *R. alpestris* (m), *R. allobrogica* (n), *R. intermedia* (o).

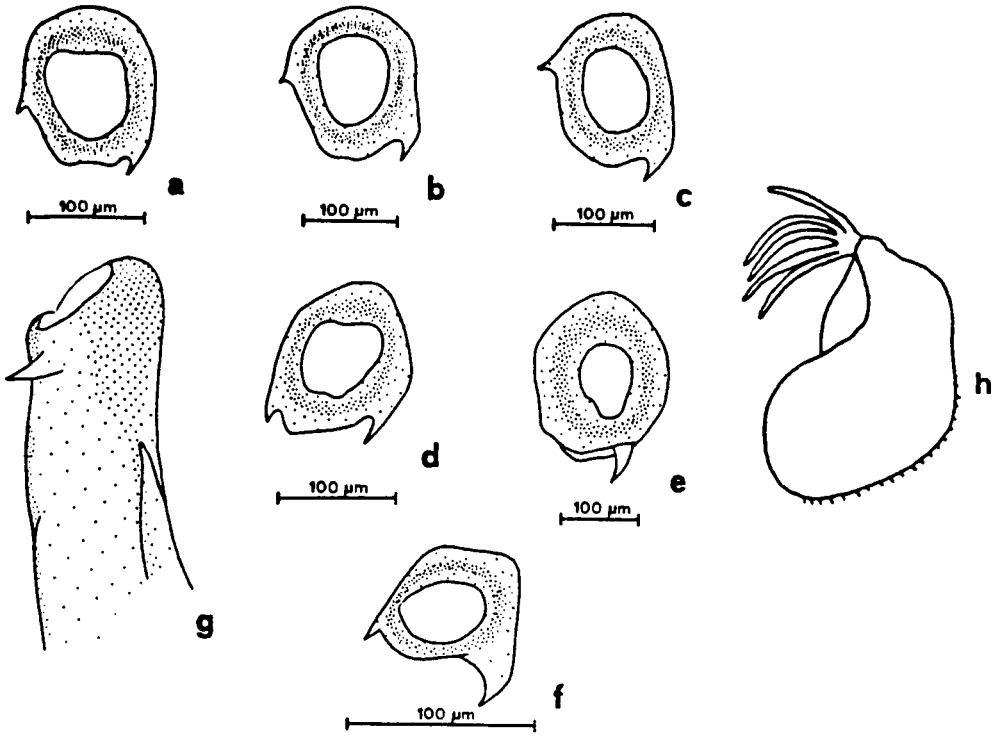


Fig. 10: Synapomorphic character 2 on Table 3 : (h) *Rhithrogena iridina* 7th. gill plate; symplesiomorphic character of the "*laevigata*" group: penis lobe in apical view of (a) *R.* sp. n. 5, (b) *R. iridina*, (c) *R. braaschi*, (d) *R. colmarsensis*, (e) *R. germanica*, (f) *R. savoiensis*; (g) lateral view of the penis lobe of *R. colmarsensis*.

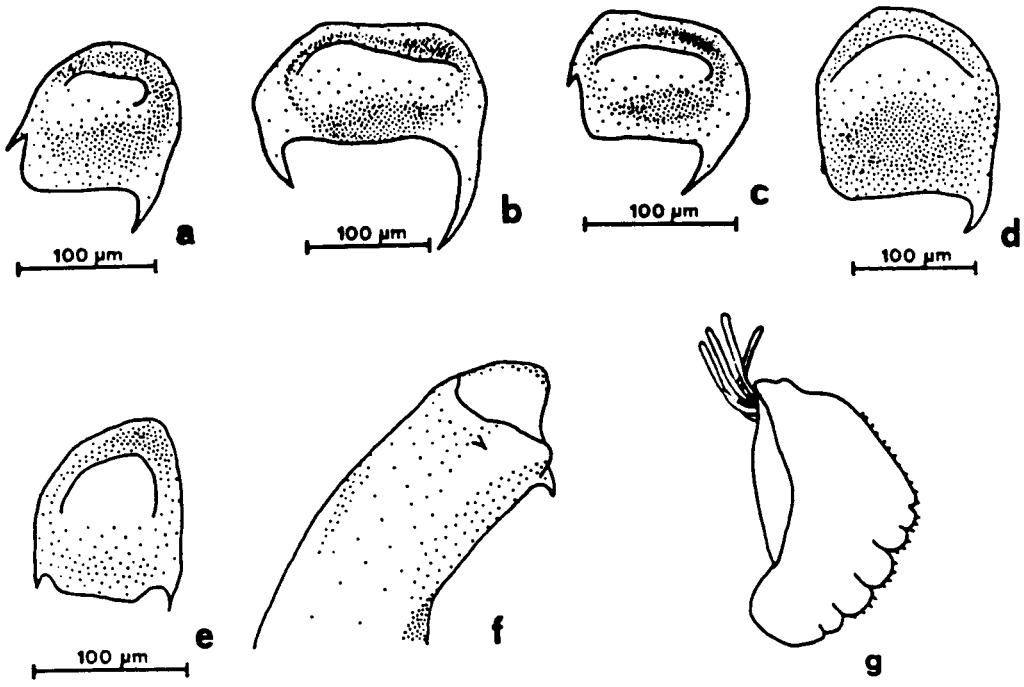


Fig. 11: Synapomorphic character 1 on Table 3 for the "*lobata*" group, penis lobe apical view of (a) *R. puthzi*, (b) *R. degrangei*, (c) *R. insularis*, (d) *R. loyolaea*, (e) *R. alpestris*; (f) latero-dorsal view of the penis lobe of R. alpestris; symplesiomorphic character of the "*lobata*" group : (g) *R. loyolaea* 7th. gill plate.

Table 1: Synapomorphic characters for the cladogram (Fig. 1) of Ephemeroptera families.

1. No branches of dorsal trunk of tracheae formed in the head (nymph).
2. Ventral anastomosis of tracheae in segments other than VIII and IX of the abdomen (nymph); characters of tracheal gills [tergalia defined by Kluge (1989)] as in furcatergalia [subordo Kluge (1989)].
3. Malpighian tubules bent, entering six unbranched long trunks (nymph); two distal segments of labial palpi forming a clamp (nymph); coxae with tracheal trunks (nymph).
4. Nerve ganglion of abdominal segment 1 merges with that of metathorax (nymph).
5. Not yet found.
6. No nerve ganglion in abdominal segment VIII (nymph).
7. Partial reduction of sclerotized band along fore margin of gills (nymph).
8. Border between incisors and molars on one side and the line connecting tip of first incisor and outer posterior corner of mandible on the other side enclose an angle less than 60 degrees (Fig. 4) (nymph).
9. Visceral tracheae only in abdominal segments II-VIII (nymph); tibiae shorter than tarsi on legs (nymph); posterior margin of stomodaeum bulbous forming a crop (nymph).
10. In fore wings paired intercalaries parallel with veins CuA and CuP (see 19 where this character is lost (imago).
11. Labial and maxillary palpi with more than ten segments (Fig. 7c) (nymph).
12. Hind wings at least half as long as fore wings (imago).
13. Antennae more than three times as long as width of head (nymph); last two gangalia in abdominal segment VII fused to an oval entity (nymph).
14. Labial palpi two segmented (nymph).
15. Fore tarsal claws bifid (nymph).
16. Nymph distinctly flattened, head prognathous; abdominal gills composed of plates and fibrilliform tufts (nymph).
17. Maxillary palpi four segmented (convergent to Prosopistomatidae); gill plates forked in a unique way: two appendages are not in one plane (nymph).
18. Paraglossae much larger than glossae (broader and longer) (nymph).
19. Maxillary gills present (nymph); tibia of fore legs with two rows of hairs (nymph); secondary loss of cubital intercalaries parallel with veins CuA and CuP (imagp).
20. Hind tarsi five segmented (imago).
21. Notch on basal segment of labial palpi (Fig. 5) (nymph).
22. Forceps with three short apical segments (imago); second segment of maxillary palpi elongated, not covered by head capsule and decorated with long and distinct hairs (nymph); secondary loss of fibriliform tufts from abdominalgills (nymph).
23. Paraglossae much larger than glossae, laterally broadened (nymphs).
24. Synapomorphic character of Pannota (*sensu* McCafferty and Edmunds, 1979: nymph).
25. Crown of the galea-lacinia covered with fine long hairs (nymph).

26. Abdominal ventral tracheae anastomose at least in segments III-IX (nymph).
27. Penes extended beyond forceps (imago).
28. Malpighian tubules spirally coiled, entering long branched trunks (nymph); outer lateral edge of mandibles with tusk or denticule (nymph).
29. Paraglossae don't form a separate segment (Fig. 7a) (convergent to Euthyplocia) (egg).
30. Gonads in ventro-lateral position (nymph).
31. Mandibular tusks with distinct long hairs (nymph).
32. Labial palpi with two segments (nymph).
33. Head with ten air sacks (nymph); labial palpi not in the plane of labium (Fig. 8a) (nymph).
34. Glossae basally fused (Fig. 8b) (nymph).
35. Pointed emargination of hind leys (nymph); mandibular tusks curved upward apically (nymph); vein A1 unforked, attached to hind margin of fore wings by three or more veinlets (imago).
36. Mandibular tusks with dorso-lateral keel (nymph).
37. Abdominal visceral tracheae present only in segments IV-VIII (nymph).
38. At least paraglossae and sometimes glossae don't form separate segments (Fig. 7b, d convergent to synapomorphy 29) (nymph).
39. Mesonotum with distinct rounded lobes at antero-lateral corners (nymph); thin branches of nerve tracheae join irregularly on median line of abdomen (nymph).
41. One single unit polar cap formed by non-coiled threads (egg).
42. All ganglia fused and accumulated in thorax (nymph).
43. Mentum larger than submentum or submentum lost (Fig. 7b) (nymph).
44. Genital forceps composed of three segments: basal segment thickest, apical segment thinest; length of medial segment at least five times that of basal one; length of basal and apical segments subequal; length and width of basal and apical segments subequal (imago).
45. Margin of hind wings with numerous long free intercalaries (imago).
46. Not yet found.

Table 2: Synapomorphic characters for cladogram of the genera of Heptageniinae.

0. Anterior margin of first segment of labial palpi with protuberance (Fig. 5: A, B, C) (nymph).
1. Outer edge on distal segment of maxillary palpi with long hairs (Fig. 5: D, E) (nymph).
2. Second segment of labial palpi borad with hooked pectinated spinules (Fig. 5: F) (nymph); outer edge of mandibles without hair (nymph).
3. Scattered hairs on ventral surface of galea-lacinia (Fig. 5: D) (nymph).
4. Distal segment of maxillary palpi bent (Fig. 5: E) (nymph).
5. Incisors on mandibles broad (nymph); distal segment of labial palpi enlarged, not covered by head capsule (nymph).
6. Two caudal filaments (nymph).

Table 3: Synapomorphic characters for cladogram in *Rhithrogena*.

0. Gills form a closed disk (nymph).
1. One-half of ejaculation opening bordered by sclerotized lobes (Fig. 11: a-f) (imago).
2. Margin of last gill plates not crenated (Fig. 10: h) (nymph).
3. First gill plates without plica (convergence to the "*alpestris* sub-group") (nymph).
4. Sclerotized plates on first abdominal sternite prominent at its full circumference (Fig. 9: l-o) (nymph); first gill plates without plica (convergence to the "*diaphana* sub-group") (nymph).