

Phylogeny and higher classification of Ephemeroptera

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The order Ephemeroptera is divided into Permopleoptera and Eupleoptera; Eupleoptera are divided into two holophyletic taxa – Posteritorna and Anteritorna; Anteritorna are divided into Tridentiseta (which is possibly a paraphyletic group) and a holophyletic taxon Bidentiseta; Bidentiseta are divided into Branchitergaliae and Furcatergaliae. Characters of these taxa are described and discussed, together with characters of higher taxa in Ephemeroptera suggested by other authors.

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INTRODUCTION

This paper represents a report made at the VII International Conference on Ephemeroptera in 1992 in Orono, Mine, USA (Kluge, 1992a), and the manuscript was submitted to the Proceedings of the Conference. Because of a confusion, the paper was not published in the Proceedings which appeared in 1995. In spite of that, the paper was cited as a published one (Kluge et al, 1995), and the names of new taxa introduced in this paper were used (Kluge, 1992b, 1993a, 1993b; Kluge et al., 1995). Here this paper is given with some later corrections.

McCafferty & Edmunds (1979) divided all recent Ephemeroptera into two suborders, Schistonota and Pannota. Kluge (1989) suggested another division of recent Ephemeroptera into two suborders, Costatergalia and Furcatergalia. McCafferty (1991) divided recent Ephemeroptera into three suborders: Pisciforma, Setisura and Rectracheata. In all these three classifications, one of the suborders (Schistonota, Costatergalia and Pisciforma) is wittingly paraphyletic, while the others (Pannota, Furcatergalia, Setisura and Rectracheata) were regarded to be holophyletic. In these three successive classifications, the volume of the paraphyletic taxon decreased, while the volume of holophyletic taxa increased. This corresponds to the general direction in which all classification of organisms changes.

In each of the three classifications, the families Baetiscidae and Prosopistomatidae

were united with some other taxa into a suborder which was regarded as holophyletic (Pannota, Furcatergalia, or Rectracheata). But earlier an opposite idea was expressed, according to which Baetiscidae and Prosopistomatidae separated early from other Ephemeroptera and inherited their unusual fore wing venation with unforked *CuA* from the Paleozoic Mithodotidae (belonging to the extinct suborder Permopleoptera), while other recent mayflies originated from another Palaeozoic family of the suborder Permopleoptera – Prottereismatidae (Edmunds & Traver, 1954a; etc.).

In the present paper, a new version of mayfly phylogeny and a new classification of Ephemeroptera are suggested. It has been already published briefly in some papers (Kluge, 1992a, 1992b, 1993b; Kluge et al., 1995). This classification is given below.

TAXONOMIC PART

Ephemeroptera Hyatt & Arms, 1891

The order is divided into (1) Permopleoptera and (2) Eupleoptera.

1. **Permopleoptera** Tillyard, 1932

An extinct (Permian – Triassic) taxon, characterized by homonomous wings and some other plesiomorphies. A paraphyletic taxon ancestral to Eupleoptera.

2. Euplectoptera Tillyard, 1932

Characterized by heteronomous wings: hind wing not exceeds 1/2 of fore wing length; in flight, anterior margin of hind wing coupled with posterior margin of fore wing. This may be an autapomorphy or a result of convergence (see below). Correspondingly, this taxon may be holophyletic or polyphyletic.

Age: Jurassic – Recent.

Euplectoptera are divided into (2.1) Posteritorna and (2.2) Anteritorna.

2.1. Posteritorna Kluge et al., 1995

This group corresponds in its content to:

- Larves cryptobranches: Lestage, 1917: 236;
- Prosopistominae sensu Lameere, 1917: 74;
- Prosopistomatoidea sensu Edmunds & Traver, 1954b: 240;
- Baetiscoidea sensu Peters & Hubbard, 1989: 115;
- Posteritorna: Kluge, 1992a: 10 (publication for temporary usage);
- Posteritorna: Kluge, 1992b: 24 (publication for educational usage);
- Posteritorna Kluge et al., 1995: 105.

Diagnosis. Tornus of fore wing behind apex of *CuP* (for the phylogenetic significance of this character see discussion below). In larval maxilla, number of dentisetae indefinite, more than 3 (see discussion below). In addition, a number of autapomorphies listed in discussion below.

A holophyletic taxon.

Posteritorna include Baetiscidae (with a single genus *Baetisca*) and Prosopistomatiidae (with a single genus *Prosopistoma*).

2.2. Anteritorna Kluge, 1993

This group corresponds in its content to:

- Larves nudibranches: Lestage, 1917: 244;
- Anteritorna: Kluge, 1992a: 10 (publication for temporary usage);
- Anteritorna: Kluge, 1992b: 24 (publication for educational usage);
- Anteritorna Kluge, 1993b: 35.

Diagnosis. Tornus of fore wing between apices of veins *CuA* and *CuP* (about phylogenetic significance of this character see discussion below). Larval maxilla with number of dentisetae determined, not more than 3 (see discussion below).

A holophyletic taxon.

Anteritorna are divided into (2.2.1) Tridentiseta and (2.2.2) Bidentiseta.

2.2.1. Tridentiseta Kluge et al., 1995

This group corresponds in its content to:

- Pisciforma sensu Kluge et al., 1995: 105 (non Pisciforma McCafferty, 1991);
- Tridentiseta Kluge et al., 1995: 105.

Diagnosis. Larval maxilla with 3 (or fewer) dentisetae (see discussion below).

Probably a paraphyletic taxon, as one of its groups (which one, is unknown) may be a sister group for Bidentiseta.

Tridentiseta are divided into Tetramerotarsata Kluge, 1997 and a paraphyletic group described as superfamily Siphonuroidea sensu Kluge et al., 1995.

2.2.2. Bidentiseta Kluge, 1993

This group corresponds in its content to:

- Bidentiseta Kluge, 1993a: 41; Kluge et al., 1995: 105.

Diagnosis. Larval maxilla with 2 (or fewer) dentisetae (see discussion below).

A holophyletic taxon.

Bidentiseta are divided into (2.2.2.1) Branchitergaliae and (2.2.2.2) Furcatergaliae.

2.2.2.1. Branchitergaliae taxon nov.

This group corresponds in its content to:

- Setisura sensu Kluge, 1993a: 41; Kluge et al., 1995: 105 (non Setisura McCafferty, 1991).

A holophyletic taxon. See apomorphies discussed below.

Branchitergaliae are divided into the group Eusetisura **taxon nov.** (which includes Isonychiidae sensu Landa, 1973, Coloburiscidae sensu Landa, 1973 and Oligoneuriidae sensu Edmunds & Traver, 1954b) and the superfamily Heptagenioidea sensu Kluge et al., 1995 (which includes *Pseudiron*, *Arthroplea* and Heptageniidae sensu Landa, 1969a).

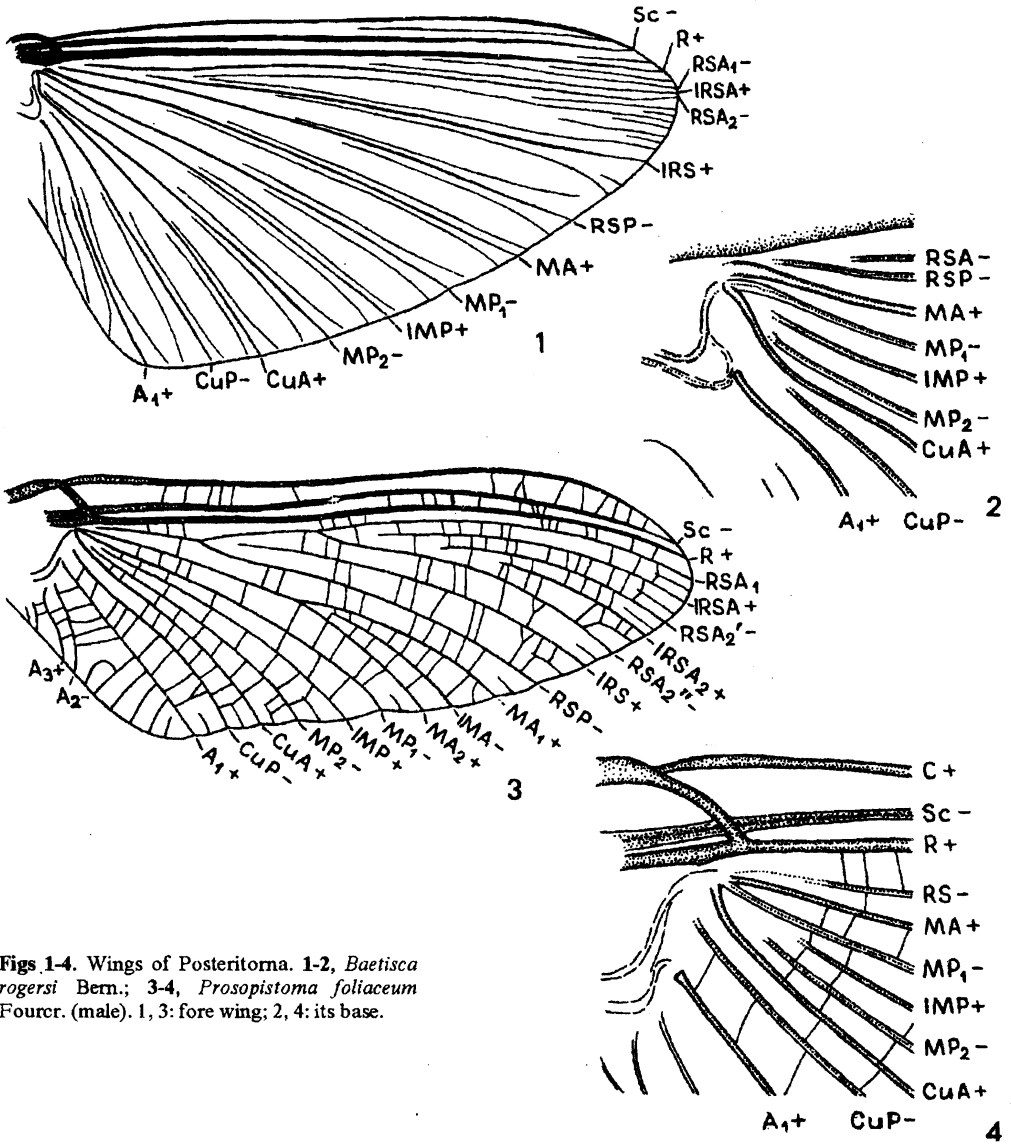
2.2.2.2. Furcatergaliae taxon nov.

This group corresponds in its content to:

- Furcatergalia sensu Kluge, 1993a: 41; 1993b: 41; Kluge et al., 1995: 105 (non Furcatergalia Kluge, 1989).

A holophyletic taxon. See apomorphies discussed below.

Furcatergaliae are divided into Ephemeroidea sensu Edmunds & Traver, 1954b,



Figs 1-4. Wings of Posteritorna. 1-2, *Baetisca rogersi* Bern.; 3-4, *Prosopistoma foliaceum* Fourcr. (male). 1, 3: fore wing; 2, 4: its base.

Caenoidea sensu Edmunds & Traver, 1954b, Ephemerelloidea sensu Koss, 1973 and Lep-tophlebiidae.

DISCUSSION

Posteritorna and Anteritorna

In Posteritorna, tornus (the hind angle) of the fore wing is situated distinctly behind *CuP*, usually behind *A1* (which is also known

as *PCu*); *CuA* and *CuP* run nearly parallel to each other, without branches or intercalaries between them (Figs 1, 3). In Anteritorna, tornus is situated between *CuA* and *CuP*, these veins are strongly divergent, with branches of *CuA* or intercalaries between them (only in *Ametropodidae* *CuP* and *A1* terminate very close to the tornus).

There are different views on the homology of veins of *Baetisca* (Demoulin, 1969; Edmunds & Traver, 1954a) and *Prosopistoma* (Gillies, 1954, 1956). The homologization ac-

cepted here is based on comparison of bases of concave and convex veins (Figs 1-4).

The difference in position of tornus in Posteritorna and Anteritorna is independent of the size of hind wings, as Anteritorna include species with hind wings well developed, or rudimentary, or completely absent. In the cases when the hind wing is rudimentary or absent, the tornus of fore wing is usually shifted proximally, becomes obtuse or is lost, but it never changes its position relatively to the terminations of the longitudinal veins, being in Anteritorna always between *CuA* and *CuP*. The difference in position of tornus in Posteritorna and Anteritorna can be explained by independent origin of these taxa from Permopleoptera which had homonomous wings without tornus. In Posteritorna and Anteritorna, the hind wings have been shortened independently, and in consequence of this, their fore wings got tornus independently twice, at two different places.

The division of all recent mayflies into Posteritorna and Anteritorna suggested here corresponds to the classification by Lameere (1917), who divided all recent mayflies into two families, Prosopistomatidae (with tribes Baetiscini and Prosopistomatini) and Ephemeridae (which had the same content as Anteritorna). On the other hand, now it is clear that the systematic position of the Mesozoic subfamily Hexagenitinae was determined by Lameere incorrectly: he used wrong homologization of their veins based on the incomplete fossils and placed Hexagenitinae in his Prosopistomatidae. Later studies showed that Hexagenitidae have venation typical of Anteritorna (Tshernova, 1961; etc.).

The here suggested contraposition of Posteritorna to all other recent mayflies is based on the single character (position of tornus), but it does not contradict all other known characters (see discussion below) and thus seems to be true.

Monophyly of Posteritorna

In some classifications, both families included here in Posteritorna, Baetiscidae and Prosopistomatidae, were regarded as related and were united in the superfamily Baetiscoidea (= Prosopistomatoidea) (Edmunds & Traver, 1954a, 1954b; Edmunds, 1962; Edmunds, Allen & Peters, 1963; Riek, 1973; McCafferty & Edmunds, 1979; Kluge, 1989). But in other classifications, *Baetisca* and

Prosopistoma were regarded as not related and were placed in different taxa. Eaton (1883-1888) placed *Baetisca* in his "Series I" of "Group III" (together with *Siphonurus* and others) and placed *Prosopistoma* in "Series III" of "Group II" (together with *Caenis* and *Tricorythus*). Demoulin (1958, 1961) placed Baetiscidae in Oligoneurioidea and Prosopistomatidae in Ephemerelloidea; later (Demoulin, 1969), he regarded Baetiscidae to be related with Oniscigastridae, and Prosopistomatidae with Ametropodidae. Tshernova (1970, 1980) placed Baetiscidae in Ephemerelloidea, and Prosopistomatidae in Caenoidea. McCafferty (1991) placed Baetiscidae in a separate superfamily Baetiscoidea, and Prosopistomatidae in Caenoidea (together with Caenidae and Ephemerellidae).

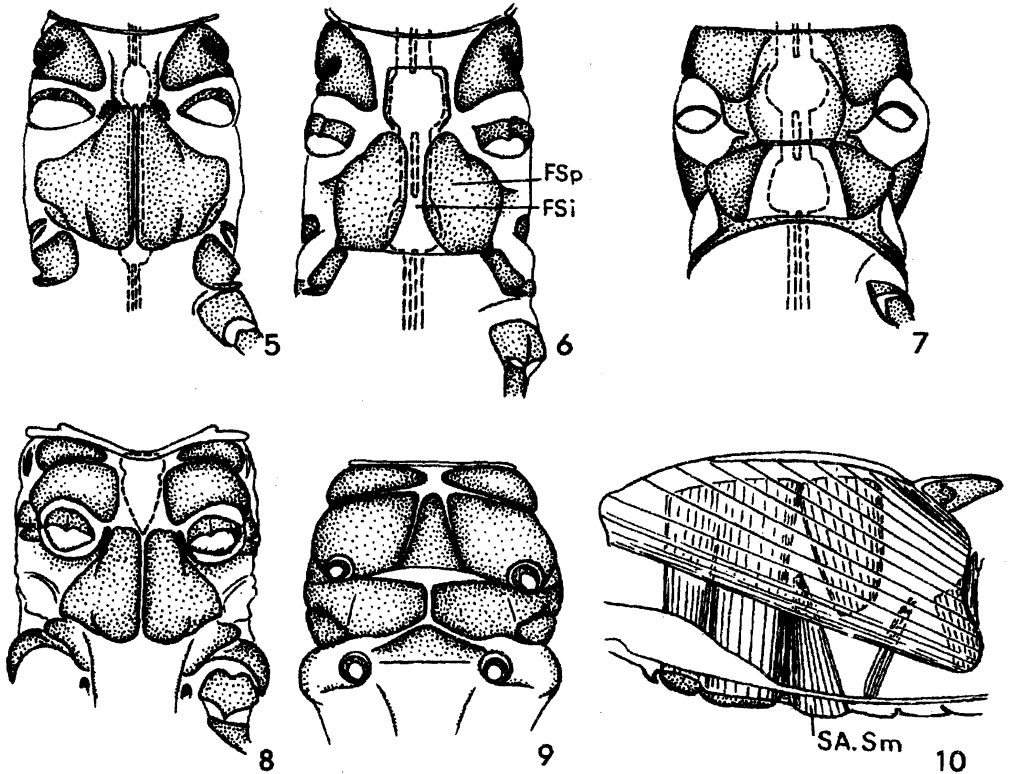
The monophyly of the Posteritorna, which include *Baetisca* and *Prosopistoma*, can be proved by the following synapomorphies:

(1) Tornus is behind *CuP* (Figs 1, 3) (see discussion above).

(2) While wing venation of *Baetisca* and *Prosopistoma* is quite different (Figs 1, 3), their vein bases are similar (Figs 2, 4): the stem of *MA+RS* reduced, so *RS*, *MA*, *MP₁* and *CuA* arise from the same point. *MP₂* independent from *MP₁* and begins close to its base. *CuA* and *MP₁* diverging more strongly than *MP₁* and *MA*. *CuP* independent from *CuA* and its base nearer to *CuA* than to *A₁*. In all other taxa of Ephemeroptera, combinations of characters are different.

(3) All nerve ganglia of the thorax and abdomen fused into a single synganglion situated in basisternum of mesothorax (Fig. 8) and furcasternal protuberances of mesothorax in imago contiguous, without median impression between them (Figs 8, 9). In all other Ephemeroptera, at least thoracic ganglia are not fused together (Figs 5-7); in the cases when metathoracic ganglion is more or less brought nearer to mesothoracic ganglion, metathoracic ganglion is situated between bases of subalar-sternal muscles (SA.Sm), so externally furcasternal protuberances (FSp) (which contain bases of SA.Sm) are separated by median longitudinal furcasternal impression (FSi) (Figs 6, 7). (For description of thorax structure see Kluge, 1994a).

(4) Structure of larval thorax highly specialized and unique. Pro- and mesonotum completely fused together, strongly enlarged (covering abdominal terga I-VII), with ventral portions (named epipleura) and with



Figs 5-10. Pterothorax structure. 5, *Potamanthus luteus* (L.), ventral view of pterothorax (nerve system shown by interrupted line); 6, *Leucorhoenanthus maximus* (Joly), the same; 7, *Caenis macrura* Steph., the same; 8, *Baetisca rogersi* Bern., the same; 9, *Prosopistoma foliaceum* Fourcr., male, the same; 10, *P. foliaceum*, longitudinal section. *FSi*, furcasternal longitudinal impression; *FSp*, furcasternal protuberance; *SA.Sm*, subalar-sternal muscle.

emargination on hind margin. Thoracic sternae have a pair of lateral longitudinal ridges (Eaton, 1883-1888: Pl. 43, 52).

(5) Structure of tergaliae (for explanation of this term see Kluge, 1989, 1996a) unique and highly specialized, nearly identical in *Baetisca* and *Prosopistoma*: pair I is the longest, with straight outer margin and fringed inner margin; pair II operculate, quadrangular, prominent; pairs III-V with fringed margins; pair VI elongate, widened and rounded apically, not fringed; pair VII absent (Lafon, 1953: Pl. II; Pescador & Peters, 1974: Figs 16, 20). This structure of tergaliae has some similarity with that in Caenoidea (sensu Edmunds & Traver, 1954b) which also have operculate quadrangular tergaliae of the pair II, fringed margins of tergaliae of the pairs III-V, and reduced pair VII; but in contrast to Posteritorna, in Caenoidea the pair I is rudimentary and the

pair VI has the same structure as the pairs III-V. Operculate tergaliae arose independently in several other unrelated mayfly groups: Oniscigastridae, Leptohiphinae, some Ephemerellidae, some Leptophlebiidae, but in these groups they have a differing structure.

(6) Bases of hind pairs of tergaliae (especially of the pair VI) are turned anteromedially; abdominal segment VI enlarged, its hind margin is elevated in its median part; a pair of oblique dorsal ridges run from anterior-lateral angles to this elevation (Pescador & Peters, 1974: Fig. 20). In addition to *Baetisca* and *Prosopistoma*, such form of abdominal segment VI is found only in *Coryphorus* of Tricorythidae (Peters, 1981).

(7) While structure of mouthparts in *Baetisca* and *Prosopistoma* is different, both groups have a synapomorphy in the structure of labium: lateral portions of submen-

tum enlarged and turned forward. This character is not unique and arose independently in several unrelated mayfly taxa.

About common characters of *Baetisca*, *Prosopistoma* and some other taxa, see discussion below.

Structure of larval maxillae in Ephemeroptera and division of Anteritorna into Tridentiseta and Bidentiseta

The newly examined structure of the maxillae allows some relationships in Anteritorna to be clarified.

The integral distal segment of the maxilla (which is usually regarded to be a result of fusion of galea and lacinia) has quite diverse form and structure in differently specialized mayfly larvae, but nearly in all cases it has the following common features. On its inner-apical (medio-apical) corner, the maxilla bears a transverse row of immobile denticles, usually three in number, which can be named *maxillary canines*. Two rows of setae run from canines towards the base of maxilla along its inner (median) margin: a medio-dorsal and a medio-ventral row; between these rows a light (possibly weakly sclerotized) narrow area is situated (Figs 11-25). It is interesting to note that a similar structure have the maxillae of larvae and imagoes of Odonata, while other insects usually have a single median row of stout setae on their lacinia. In Ephemeroptera, the initial number of maxillary canines is three, this number is preserved in most of mayflies, and only in several taxa the number of canines can be less than three: two, one, or canines can be absent; sometimes canines bear additional denticles.

Some setae in the medio-ventral and, especially, in the medio-dorsal row may be thickened and specialized. A term *dentisetae* is suggested for the distinctly thickened and specialized setae of the medio-dorsal row (Kluge, 1994b, 1996b; Kluge et al., 1995).

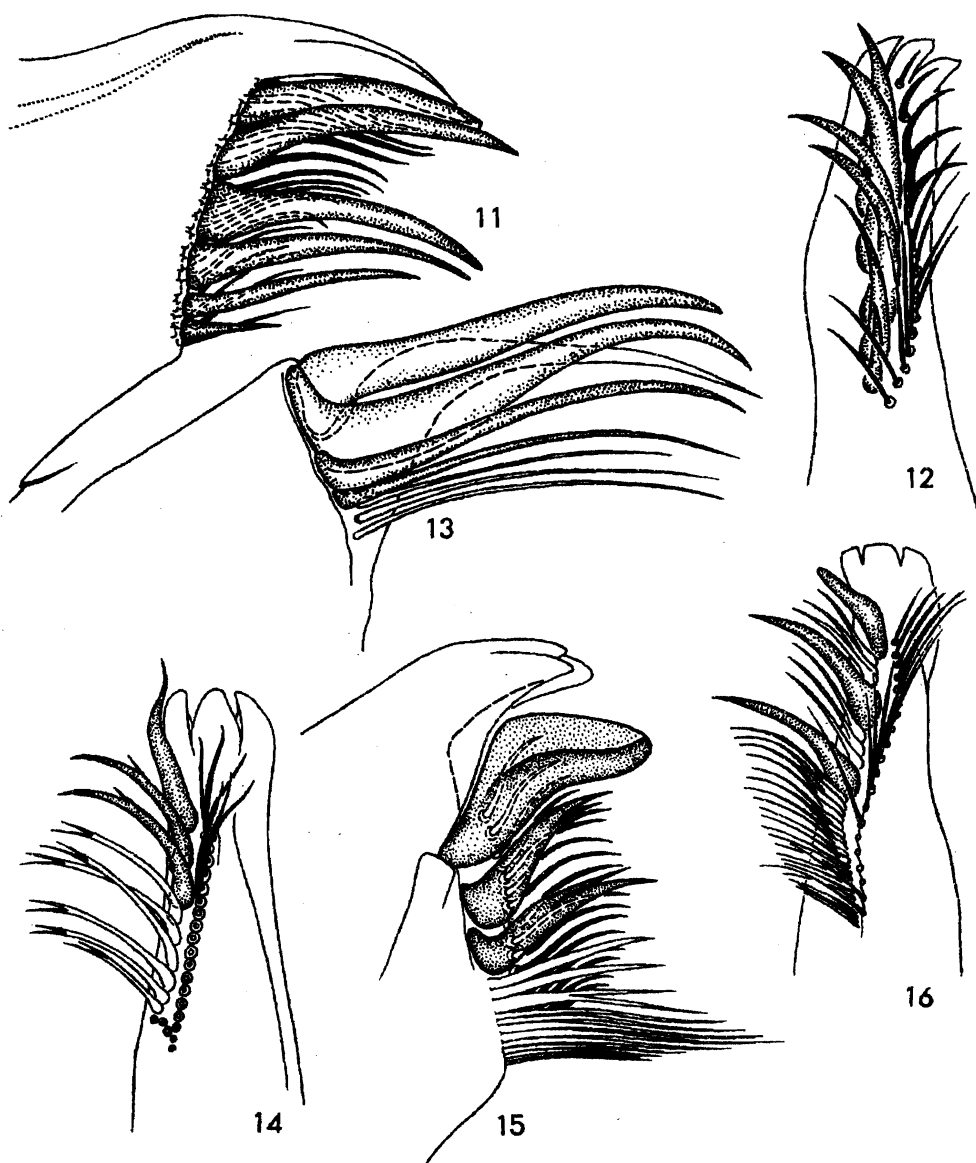
In the most primitive state, the number of dentisetae is indefinite and the thickest dentisetae are situated in the distal part of the row, while the thinner ones in its proximal part. Such structure is present in *Baetisca* (Figs 11, 12): in the examined specimens of *Baetisca carolina*, the number of dentisetae varies from 6 to 8. *Prosopistoma* has a highly specialized carnivorous mouth apparatus; maxillae are highly specialized, with a single long acute canine and few very long acute

dentisetae pressed against it (in Fig. 13 they are shown artificially moved apart from each other).

In Anteritorna, the number of dentisetae is definite, and dentisetae differ distinctly from other setae of the same medio-dorsal row. In Tridentiseta, the initial number of dentisetae is three, usually the thickest dentiseteta is the most distal one. In Bidentiseta, the initial number of dentisetae is two, usually the thickest dentiseteta is the proximal one. Both in Tridentiseta and in Bidentiseta, there are some specialized taxa which have the number of dentisetae less than the initial one.

Structure of maxillae in various Tridentiseta

In Siphonuridae sensu Kluge et al., 1995 (Fig. 16), Dipteromimidae, Metretopodidae, Ametropodidae, Oniscigastriidae (Kluge et al., 1995: Fig. 39) and Tetramerotarsata (Figs 14, 15; Kluge, 1997a: Fig. 3), three dentisetae are present; among them, in *Ametropus* the number of maxillary canines is reduced to two, in others all three canines are preserved. In some Tetramerotarsata, namely in *Cloeon* sensu Kluge & Novikova, 1992 (Fig. 14) and *Callibaetis*, the dentisetae may be slender and only slightly thicker than the setae proximal to them. In *Baetopus* s. l. (including *Raptobaetopus*) which have the mouth apparatus specialized for predatory habits, the setae proximal to the dentisetae are absent. In some other Tetramerotarsata (*Baetis* sensu Novikova & Kluge, 1987, *Cloedes*, *Afroptilum*), the most distal dentiseteta is extremely stout and can be pressed against the canines (Fig. 15). In the same way the most distal dentiseteta is modified in Nesameletidae (Kluge et al., 1995: Figs 47, 48), but in contrast to Tetramerotarsata, the two other dentisetetae are very weak and situated on a common plate. In *Rallidens*, all three dentisetetae are weak (Kluge et al., 1995: Fig. 53). In Ameletidae, maxillae are highly specialized for filtering, their canines are absent, and only a single small dentiseteta is present (Kluge et al., 1995: Figs 20, 21). In Acanthametropodidae, maxillae are highly specialized for predatory habits, their dentisetetae are very stout and completely fused with the corpus of maxilla, thus they look like canines; the number of canines and dentisetetae is reduced (Kluge et al., 1995: Figs 23, 28). The maxillary structure of Ameletidae and Acanthametropodidae does not allow reconstruction of the number of dentisetetae



Figs 11-16. Apex of left maxilla of Posteritorna and Tridentiseta. **11-12,** *Baetisca carolina* Trav.; **13,** *Prosopistoma* sp.; **14,** *Cloeon dipterum* (L.); **15,** *Baetis vernus* Curt.; **16,** *Siphonurus aestivalis* Etn. 11, 13, 15, dorsal view; 12, 14, 16, median view. Dentisetae shown by dots, setae of medio-ventral row shown by black.

of their ancestors, but it is quite probable that their ancestors had three dentisetae, as other Tridentiseta.

The position of Ameletopsidae (which are attributed to Siphonuroidea sensu Kluge et al., 1995) is not clear. The larvae of all Ameletopsidae are carnivorous with identical highly specialized structure of maxillae: canines are absent, and apex of maxilla bears a

horseshoe-shaped row of five long, stout, acute, mobile appendages (Kluge et al., 1995: Figs 59, 60). If these appendages are dentisetae, their number is larger than in Tridentiseta and Bidentiseta, that leads to conclusion that Ameletopsidae probably are not related to other Anteritorna and can be placed in a separate taxon. Such conclusion is supported by the fact that Ameletopsidae

are the only group in Euplectoptera in which larvae have mobile tarsal segments, that is a very archaic character. On the other hand, the five maxillary appendages of Ameletopsidae develop not as true setae (Kluge et al., 1995), so they cannot be dentisetae, but are new formations. In this case, their structure says nothing about relationships of Ameletopsidae, and this family may belong to Tridentiseta.

Structure of maxillae in various Branchitergaliae

In each of the main phylogenetic branches of Branchitergaliae, two dentisetae are present, at least in the primitive groups.

Among Eusetisura, in *Isonychia* and Oligoneuriidae maxillae have only two canines; canines of Coloburiscidae are secondarily serrate, so their number is unclear. In *Isonychia* s. str., the distal dentiseta is rudimentary, very poorly visible (Fig. 17); in *Isonychia* (*Prionoides*) *georgiae* McD., it is absent. In Oligoneuriidae s. str., both dentisetae are present; they are nearly as slender as setae proximal to them, but differ from these setae in the structure of their bases (Fig. 18). In Coloburiscidae, in contrast to all other Bidentiseta, the number of dentisetae is variable: in the same species it can be two or three (specimens with two and three dentisetae are found among *Murphyella needhami* Lest. and *Coloburiscoides* sp.; in 8 examined specimens of *Coloburiscus humeralis* (Walk.), two dentisetae are found). Probably such indefinite number of dentisetae arose in Coloburiscidae secondarily.

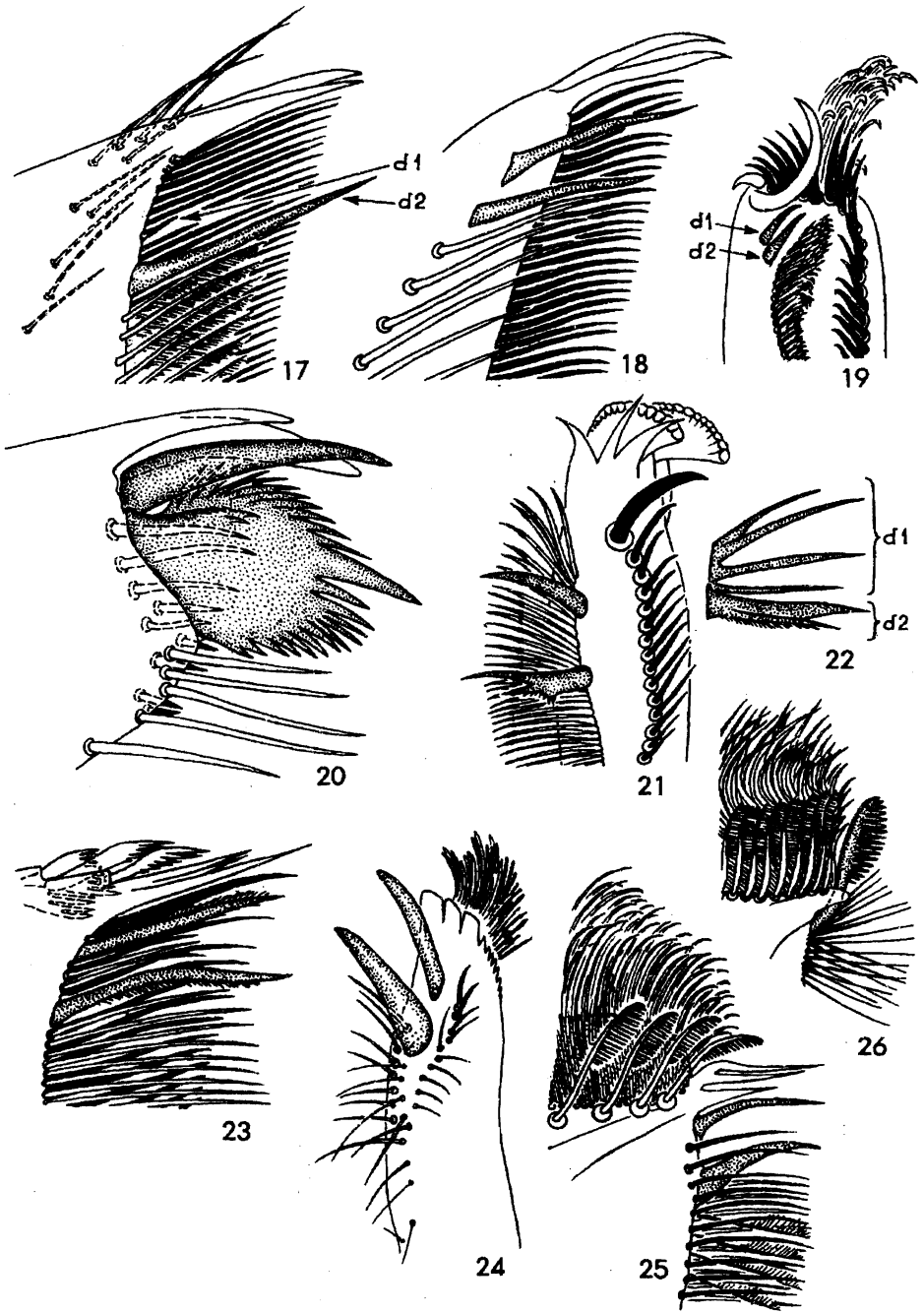
In all Heptagenioidea, two dentisetae are present. In *Pseudiron*, maxillae are specialized for predatory habits, with unusually large proximal dentiseta and with two canines only, so the distal dentiseta looks like a third canine (Fig. 20). In *Arthroplea*, the apex of the maxilla bears a single canine; in *Arthroplea bipunctata* McD., two dentisetae are distinctly larger than other setae of the medio-dorsal row, but in *A. congener* Bgtn. dentisetae are indistinguishable among setae of this row. In most of the Heptageniidae sensu Landa, 1969a, maxillae have three slender weak canines (except for *Epeorus* sensu Edmunds, Jensen & Berner, 1976 which has three canines strongly enlarged and stout, and *Cinygma* which has a single slender canine – Fig. 19). All examined Heptageniidae have two dentisetae, but their

dentisetae can be slender and poorly visible among long dense setae of the medio-dorsal and the medio-ventral row. Often the most distal seta of the medio-ventral row is as stout as dentisetae, so it seems that there are three dentisetae, while only two true dentisetae (i.e. dentisetae of the medio-dorsal row) are present (Figs 21, 23). In some cases it is very difficult to count dentisetae. In *Rhithrogena* s. str., both dentisetae are often pressed to one another and look like one dentiseta. In all *Ecdyonurus* sensu Kluge, 1988, the proximal dentiseta is bifurcate (Figs 21, 22); in the subgenera *Ecdyonurus* and *Afghanurus* sensu Kluge, 1997b, the distal dentiseta is simple (Fig. 21); in the subgenera *Notacanthurus*, *Electrogena* and *Cinygmina*, the distal dentiseta is divided into several branches (Fig. 22). In *Cinygma*, both dentisetae are rudimentary, much shorter than setae of medio-dorsal and medio-ventral row (Fig. 19).

Structure of maxillae in various Furcatergaliae

Like in Branchitergaliae, in each of the main phylogenetic branches of Furcatergaliae two dentisetae are present, at least in the primitive representatives.

In Ephemeroidea sensu Edmunds & Traver, 1954b, three canines and two dentisetae are retained in the most primitive groups, but lost in some derived taxa. All three canines and both dentisetae are developed in Potamanthidae (Fig. 24), Euthyplociidae (here canines are well developed in *Euthyplocia*, but rudimentary in *Exeuthyplocia*) and *Ichthybotus*. Among Ephemeridae sensu nov. (i. e. including *Hexagenia* and excluding *Ichthybotus* and *Pentagenia*), all three canines and both dentisetae are well developed in *Ephemerella*, but the distal dentiseta is vestigial and only two canines are present in Hexageniinae (*Hexagenia limbata* Guern. and *Eatonigenia chiae* Dang examined). Among Behningiidae, in *Protobehningia* two canines are present and dentisetae are absent (Elpers & Tomka, 1994: Fig. 2); in *Behningia* and *Dolania* only one canine and only one dentiseta are present (Elpers & Tomka, 1994: Fig. 15b). In Palingeniidae sensu McCafferty & Edmunds, 1976 (both in *Pentagenia* and Palingeniinae), the maxilla has only one canine and only one dentiseta. Among Polymitarciidae, all three canines and two dentisetae are retained in



Figs 17-26. Apex of maxilla of Bidentisetia. 17, *Isonychia ussurica* Bajk., left maxilla, dorsal view; 18, *Oligoneuriella pallida* (Hag.), the same; 19, *Cinygma lyriformis* McD., left maxilla, median view; 20, *Pseudiron meridionalis* Trav., left maxilla, dorsal view; 21, *Ecdyonurus* sp. n. (gr. *venosus*), left maxilla, median view; 22, *E. abracadabrus* Kluge, dentisetae separately, dorsal view; 23, *Heptagenia (Kageronia) fuscogrisea* (Retz.), left maxilla, dorsal view; 24, *Potamanthus luteus* (L.), left maxilla, median view; 25, *Leptophlebia marginata* (L.), right maxilla, ventral view; 26, *Choroterpes (Euthraulus) sumbarensis* Kluge, the same. Dentisetae are shown by dots, setae of medio-ventral row are shown by black; d1, d2, distal and proximal dentisetae.

the primitive genus *Ephoron*; in *Campsurus*, both dentisetae are retained, but there are only two canines; in *Povilla*, all three canines are retained, but dentisetae are completely lost.

In all Caenoidea sensu Edmunds & Traver, 1954b, all three canines and both dentisetae are developed.

The same is true for most of Ephemeroidea sensu Koss, 1973, except for some highly specialized groups. Particularly, in *Uracanthella* and *Cincticostella* which have specialized filtering maxillae, canines are lost (but both dentisetae are retained). In *Diceromyzon*, maxillae are highly specialized, scraping, with a single vestigial dentisetula. In *Tricorythus*, maxillae are so highly specialized, that they have lost all canines, dentisetae, medio-dorsal and medio-ventral rows of setae.

In the most primitive group of the Leptophlebiidae, i. e. Leptophlebiinae sensu Kluge, 1994b, maxillae bear slender rudiments of three canines and two dentisetae (Fig. 25; Kluge, 1994: Fig. 7). In Habrophlebiinae and Atalophlebiinae, canines are lost (Kluge, 1994b: Figs 8, 9); in Atalophlebiinae, the distal dentisetula is also lost (Fig. 26); in some Atalophlebiinae (*Traverella* and others), all dentisetae are lost.

The foregoing account shows that the number of dentisetae is very conservative, and their reduction takes place only in rare cases.

Holophyly of Branchitergaliae

Branchitergaliae have the following apomorphies:

(1) Tergaliae have an additional ventral (hind) fibrillose portion. Only in few representatives (in *Arthroplea*, in some species of *Cinygmula*, etc.), this portion is secondarily lost. This apomorphy is not unique: in addition to Branchitergaliae, such a fibrillose portion is present in *Rallidens* and some Ameletopsidae (*Chilopter* and *Mirawara*).

(2) Maxillae with a ventral row of setae parallel to the inner margin. This row is developed in *Isonychia* (Fig. 17), *Arthroplea*, and Heptageniidae (only in *Ecdyonurus* sensu Kluge, 1988, it is transformed into an irregular field of setae – see Kluge, 1988, 1993a). In Oligoneuriidae s. str., this row is indistinct and turned laterally; in Coloburiscidae and *Pseudiron*, it is absent.

(3) Eggs have anchors (Fig. 31) each of which consists of a long cable twisted into a small cylindrical coil and a cap at the end of the cable; in twisted condition of the anchor, this cap covers the coil apically. Such anchors are found on eggs of various species of Heptageniidae, *Arthroplea*, *Isonychia*, Coloburiscidae. On eggs of Oligoneuriidae s. str., the anchors are also present, but they are rudimentary, very short, mushroom-like, and not coiled (Fig. 30). In other Ephemeroptera, anchors, when present, have a differing structure.

(4) In imago and subimago, the posterior arms of the prealar bridge of mesothorax (for explanation of this term, see Kluge, 1994) are shortened and do not reach the lateral margins of scutum (Figs 28, 29; compare with Fig. 27).

Holophyly of Furcatergaliae

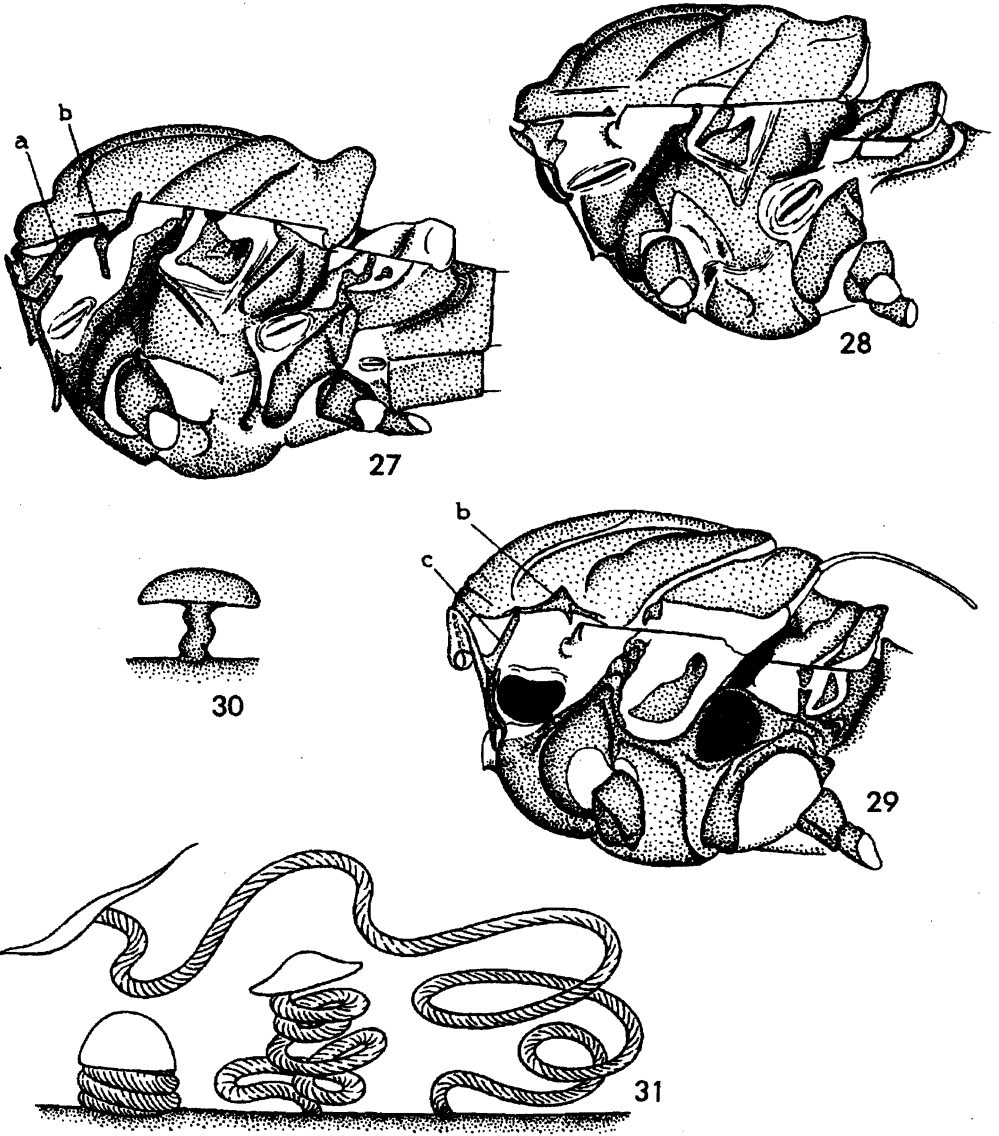
The taxon Furcatergaliae has the following apomorphies:

(1) In imagoes and subimagoes, first tarsal segment (which like in majority of other Ephemeroptera is immovably fused with tibia) is strongly shortened. Only in some specialized groups of Furcatergaliae, where legs are non-functional (in Behningiidae, Polymitarciidae, Palingeniidae), or all tarsal segments are strongly shortened (in *Caenis*), the first tarsal segment can be relatively long, that is probably a secondary elongation.

(2) In the hind wings (if they are present), *MA* is not forked. This apomorphy is not unique: independently from Furcatergaliae, loss of *MA* fork occurs in some other mayfly taxa (particularly, fork of *MA* is absent in both species of *Arthroplea* and in *Cinygma dimicki* McD., but is present in two other species of *Cinygma*).

(3) According to the investigation by Landa (1969), visceral tracheae in all Furcatergaliae are lost in the abdominal segment II, being developed only in the segments III-VIII or IV-VIII, while in other mayflies visceral tracheae are developed in all segments II-VIII. But actually the position and number of visceral tracheae is under individual variability, so future investigations are necessary to clarify whether this apomorphy is reliable.

In my previous paper (Kluge, 1989), it was stated that, in contrast to Costatergalia (a paraphyletic taxon which is now divided into



Figs 27-31. Details of structure of Branchitergaliae in comparison with *Siphonurus*. 27, *Siphonurus aestivalis* Etn., lateral view of pterothorax; 28, *Isonychia ignota* Walk., the same; 29, *Oligoneuriella* sp., the same; 30, vestigial anchor on egg surface of *Oligoneuriella* sp.; 31, anchors typical of Branchitergaliae. *a*, posterior arm of prealar bridge; *b*, joining of posterior arm of prealar bridge with scutum; *c*, secondary dorso-posterior arm of prealar bridge.

Tridentiseta and Branchitergaliae), Furcatergalia (a polyphyletic taxon which is now divided into Posteritorna and Furcatergaliae) have apomorphies in the structure of larval tergaliae (loss of the tergalial ribs) and larval caudal filaments (loss of the primary swimming hairs). But now I have found out that in some representatives of Furcatergaliae these apomorphies are absent, so

these are not apomorphies of Furcatergaliae as a whole. Short rudiments of the tergalial ribs are present in some Ephemeridae and Behningiidae; weak ribs are visible on tergaliae of some Tricorythidae. Ephemeridae, Palingeniidae and Behningiidae have primary swimming hairs (the hairs on the inner margins of cerci and the lateral margins of paracercus) which differ in their structure

from secondary swimming hairs on the lateral margins of cerci. Other Furcatergaliae have no swimming hairs, or have only secondary swimming hairs on both margins of cerci and paracercus.

Systematic position of *Baetisca* and *Prosopistoma*

Here *Baetisca* and *Prosopistoma* are placed in a separate taxon Posteritorna which is opposed to all other recent mayflies. This contradicts the former classifications, where Baetiscidae and Prosopistomatidae were united with Caenoidea and Ephemerelloidea into the taxon Pannota (McCafferty & Edmunds, 1979; McCafferty, 1991) or were united with Caenoidea, Ephemerelloidea, Ephemeroidea and Leptophlebioidea into the taxon Furcatergalia (Kluge, 1989). Actually, *Baetisca* and *Prosopistoma* have no apomorphies which are present in Furcatergaliae:

(1) In contrast to Furcatergaliae which have initially 2 maxillary dentisetae, *Baetisca* have a primitive structure of maxillae with indefinite number of dentisetae (Figs 11, 12). In highly specialized maxillae of *Prosopistoma*, the number of dentisetae is also more than two (Fig. 13).

(2) In contrast to Furcatergaliae, the first tarsal segments of imago in *Baetisca* are not shortened (they are longer than the next ones). Imaginal legs of *Prosopistoma* are non-functional, and their tarsal joints are indistinct.

(3) In imagoes of *Baetisca* and *Prosopistoma*, the ventral surface of mesothoracic episternum is completely divided by the paracoxal suture into anepisternum and katepisternum (Figs 8-9), while in Furcatergaliae the paracoxal suture usually terminates more laterally (Figs 5-7).

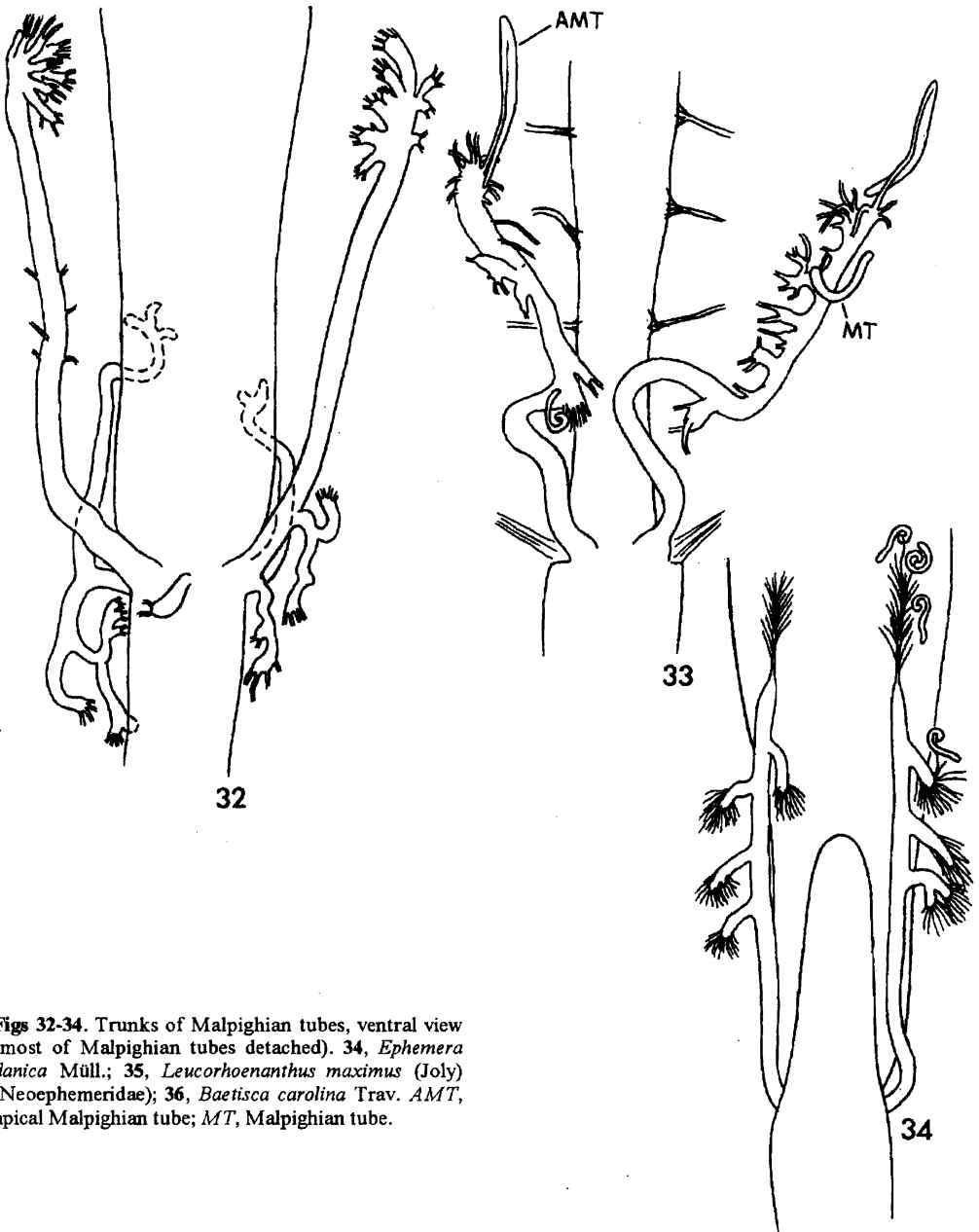
(4) In contrast to Furcatergaliae, larval visceral tracheae of *Baetisca* and *Prosopistoma* are developed in all abdominal segments II-VIII (according to Landa, 1969).

Other characters of Furcatergaliae (non-forked MA of hind wing, reduction of ribs of larval tergalia, development of secondary setae on lateral margins of larval cerci) are present in *Baetisca* and *Prosopistoma*, but these characters are present also in some taxa of Tridentiseta and Branchitergalia, so they do not prove relationship of Posteritorna and Furcatergaliae.

McCafferty & Edmunds (1979) placed Baetiscidae and Prosopistomatidae in the suborder Pannota based on the structure of larval mesonotum which is fused with the median margins of fore wing buds. But such a fusion occurs independently from Pannota in Oligineuriidae, Coloburiscidae, and the genus *Pseudopannota* (Baetidae), so this character is not sufficient to prove a relationship between Baetiscoidea and the rest of Pannota.

In contrast to other taxa included in Pannota (Caenoidea sensu Edmunds & Traver, 1954b and Ephemerelloidea sensu Koss, 1973), Posteritorna retained the primary swimming setae on the caudal filaments of the larva: both in *Baetisca* and *Prosopistoma*, the setae on the median sides of cerci and lateral sides of paracercus (the primary ones) differ in their structure from the setae on the lateral sides of cerci (the secondary ones).

Landa (1969) described a similarity in the structure of larval Malpighian tubes between *Baetisca* and Neoephemeridae, and between *Prosopistoma* and Caenidae. Landa's classification of types of Malpighian tubes is based on the number of trunks and presence of branches of these trunks. According to his investigations, various Neoephemeridae and *Baetisca* have the type Fb β - 2 trunks, each with 3 non-branched processes; Caenidae and *Prosopistoma* have the type Fb α - 2 non-branched trunks; Potamanthidae, Ephemeridae and Polymitarciidae have the type Ea - 6 non-branched trunks; Behningiidae have the type B - 8 low buds; and so on. Actually, the number of trunks and their branches is strongly variable, it may differ in specimens of the same species and in the left and right halves of the same specimen. Most constant are the longest trunks, while short trunks and short branches can easily arise and disappear, varying individually. So, it is impossible to compare total numbers of trunks and branches in different taxa, it is possible only to compare position of the longest trunks. Larvae of *Baetisca*, *Prosopistoma*, Neoephemeridae, Caenidae, Ephemeridae, Potamanthidae, Behningiidae and *Isonychia* examined by me have 2 long lateral trunks directed anteriorly (Figs 32-34). These long trunks can bear at their anterior ends a pair of peculiar straight Malpighian tubes which are partly fused with their ducts (Fig. 33); an identical pair of peculiar Mal-



Figs 32-34. Trunks of Malpighian tubes, ventral view (most of Malpighian tubes detached). **34**, *Ephemera danica* Müll.; **35**, *Leucorhoenanthus maximus* (Joly) (Neophemeridae); **36**, *Baetisca carolina* Trav. AMT, apical Malpighian tube; MT, Malpighian tube.

pighian tubes directed anteriorly is found also in some mayflies which have no trunks: *Baetis* (Landa, 1968: Fig. 12 BR), *Ephemera*, *Tricorythodes*. So, the lateral paired position of Malpighian tubes is common to many groups of Ephemeroptera. Another structure of trunks of Malpighian tubes is found in all examined Heptageniidae: there are 4 long trunks directed anteriorly (a pair

of ventro-lateral and a pair of dorso-lateral trunks) and indefinite number of additional short trunks or buds (Kluge, 1993: Figs 1-19). Thus only three main types of Malpighian tubes are found in Ephemeroptera: absence of long trunks, one and two pairs of long trunks directed anteriorly. As *Baetisca*, *Prosopistoma*, Neophemeridae and Caeniidae have a widely distributed type of Mal-

pighian tubes (with two long trunks), structure of their Malpighian tubes does not allow discussion on their relationships.

Status of Rectracheata McCafferty, 1991

McCafferty (1991) established the suborder Rectracheata McCafferty, 1991 which united the taxon Furcatergalia Kluge, 1989 and the family Oniscigastridae (for which he established a separate infraorder Vetulata McCafferty, 1991). The only character which allowed the bringing together Vetulata and Furcatergalia was the presence of tracheal anastomoses in the abdominal segments IV-VII (Landa, 1969); in all other respects, Vetulata have nothing in common with Furcatergalia. In my opinion, this character is not sufficient to prove relationship of these taxa, because it can arise independently. For example, in *Chiloporter* well developed anastomoses in abdominal segments III-VIII are present, while in other Ameletopsidae tracheal anastomoses in the segments III-VII are absent (Landa, 1969). On this base Landa (1973) established for *Chiloporter* a separate family Chiloporteridae. But relationship between *Chiloporter* and other Ameletopsidae is evident, all of them have identical and quite unusual structure of mouth apparatus (see Kluge et al., 1995); because of this, other authors (including McCafferty, 1991) do not accept this family. According to Landa's description, the tracheal anastomoses of the abdominal segments II and III can be present or absent in some closely related taxa of Leptophlebiidae, Ephemerellidae and Tricorythidae; tracheal anastomoses of the abdominal segments VIII-IX are also strongly variable. It means that during mayfly evolution tracheal anastomoses can easily originate in the same abdominal segments independently in different lineages, so their presence is not sufficient to establish a taxon of high rank.

The larvae of Vetulata have three well developed maxillary dentisetae. It means that Vetulata could not derive from a common ancestor with Furcatergaliae separately from Branchitergaliae, as both Furcatergaliae and Branchitergaliae (and most probably their common ancestor as well) have only two dentisetae. It leads to conclusion, that Rectracheata is a polyphyletic taxon.

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