

System and phylogeny of Pinnatitergaliae (Ephemeroptera)

NIKITA J. KLUGE

Russia, 199034, S-Petersburg, S-Petersburg State University, Biological Faculty, Department of Entomology
kluge@ent.bio.pu.ru

Abstract

The taxon Pinnatitergaliae (or Ephemera/fg7) is generally accepted, however its holophyly is questionable; possibly Pinnatitergaliae are paraphyletic and ancestral for Caenotergaliae (or Caenis/fl = Brachycercus/g1). Pinnatitergaliae are divided to 3 holophyletic taxa – Potamanthus/fg1, Euthyplocia/fg1, and Fossoriae (or Ephemera/fg8). The alternative division of Pinnatitergaliae to Behningia/fg1 and Scaphodonta is discussed. Fossoriae are divided to 4 holophyletic taxa – Ichthybotus/fg(1), Ephemera/fg9, Behningia/fg1 and Cryptoprosternata (or Palingenia/fl = Ephoron/g1). Cryptoprosternata are divided to 2 holophyletic taxa – Palingenia/f2=g1 (incl. *Pentagenia*) and Polymitarcys/fl=Ephoron/g2 (incl. *Campsurus*). Some authors united Euthyplocia/fg1 with Polymitarcys/fl=Ephoron/g2; actually characters which look as common for these two taxa, evolved independently.

Introduction

In the present paper, typified names of supra-species taxa are used in accordance with a non-ranking hierarchical nomenclature based on the International Code of Zoological Nomenclature (ICZN). Detailed principles of this nomenclature are explained in separate papers (Kluge, 1999a-c) and in the book on insect systematics (Kluge, 2000). The **hierarchical name** (nomen hierarchicum) consists of a generic name (i.e., an available name of genus-group in terms of the ICZN), a letter "f" or/and "g" separated from the generic name by an oblique stroke, and a number from 1 to more. If there is letter "f", the generic name is the oldest according to the rules for family-group; if there is letter "g", the generic name is the oldest among names of genus-group; if there is written "fg", the generic name is the oldest both for family-group and genus-group. Among taxa with hierarchical names based on the same generic name, that one is higher which number is lower; the highest taxon for which this generic name is the oldest, has number "1". Usage of hierarchical names allows to avoid absolute ranks (such as orders, suborders, superfamilies, families, subfamilies, tribes, genera, subgenera etc.), which often provoke disagreements among specialists, and at the same time to use all names regulated by the ICZN.

Besides typified hierarchical names, here are used traditional non-typified names; all of them are used as **circumscriptional (volumetric) names** (nomina circumscribentia); strict principles of the circumscriptional nomenclature are explained in the same publications.

General classification of mayflies is briefly given in a separate paper (Kluge, 1998) and in the book on insect systematics (Kluge, 2000). In detail it is given in Internet publication: a preliminary draft version in English was available since 1998 (<http://www.famu.edu/acad/research/mayfly/kluge/index.html>), completed and corrected text in Russian appeared in 2001 (http://www.bio.pu.ru/win/entomol/KLUGE/EPHEME_R_/content_.htm).

Mayflies in widest sense constitute a taxon **Panephemeroptera** CRAMPTON, 1928, or Ephemeroptera sensu latissimo; hierarchical name: **Ephemera/fg1** [f: Ephemerae LATREILLE, 1810; g: *Ephemera* LINNAEUS, 1758, typus *E. vulgata* LINNAEUS, 1758]. Panephemeroptera include Carboniferous insects related to mayflies (*Triplosoba et al.*) and Euephemeroptera. The taxon **Euephemeroptera**

KLUGE, 2000, or Ephemeroptera sensu lato (hierarchical name: **Ephemera/fg2**) includes Permian mayflies (*Protereisma*, *Phtharthus*, *et al.*) and Euplectoptera. The taxon **Euplectoptera** TILLYARD, 1932, or Ephemeroptera sensu stricto (hierarchical name: **Ephemera/fg3**) is divided to **Posteritorna** KLUGE *et al.*, 1995 (hierarchical name: **Baetisca/f1=Prosopistoma/g1**) and **Anteritorna** KLUGE 1993 (hierarchical name: **Ephemera/fg4**). Anteritorna are divided to **Tridentiseta** KLUGE *et al.*, 1995 (hierarchical name: **Baetis/fg1**) and **Bidentiseta** KLUGE 1993 (hierarchical name: **Ephemera/fg5**). Bidentiseta are divided to **Branchitergaliae** KLUGE, 1998 (hierarchical name: **Heptagenia/f1=Oligoneuria/g1**) and **Furcatergaliae** KLUGE, 1998

(hierarchical name: **Ephemera/fg6**) (non Furcatergalia KLUGE, 1989).

Phylogeny of Furcatergaliae is unclear, because taxa included here have such combination of characters, which does not allow to build any non-conflicting tree (Kluge, 1997). Preliminary, Furcatergaliae are divided to following 4 taxa of equal ranks: (1) **Pinnatitergaliae** KLUGE, 2000 [hierarchical name: **Ephemera/fg7**]; (2) **Caenotergaliae** KLUGE, 2000 [hierarchical name: **Caenis/f1=Brachycercus/g1** (incl. *Neoephemera*)]; (3) **Ephemerella/fg1** (incl. *Tricorythus*); and (4) **Leptophlebia/fg1** (incl. *Atalophlebia*). In the present paper, phylogeny of Pinnatitergaliae is discussed.

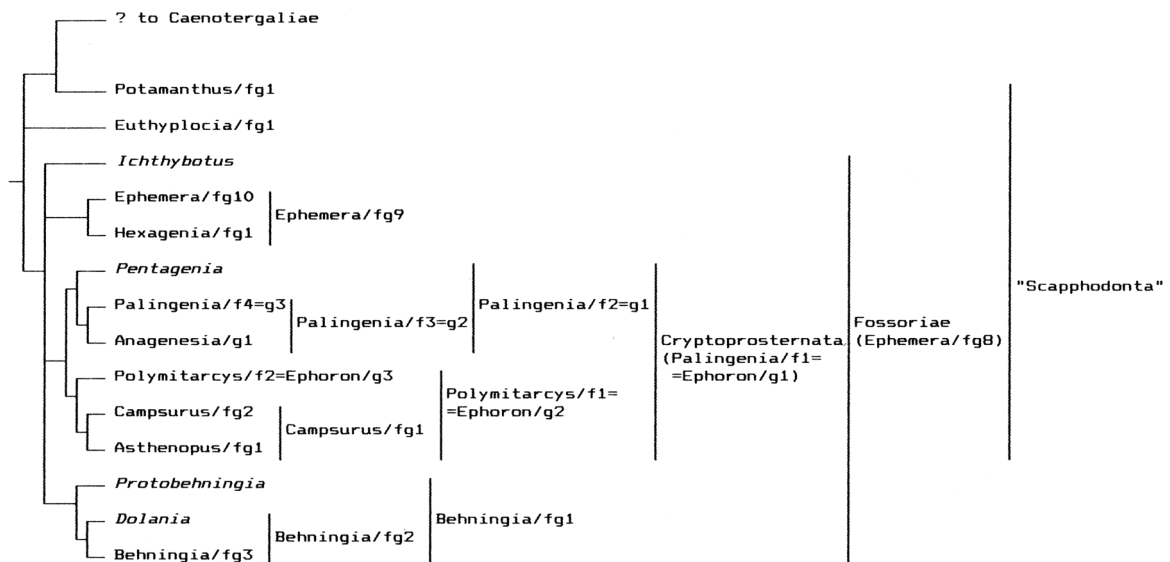


Fig. 1 - Phylogeny of Pinnatitergaliae (Ephemera/fg7)

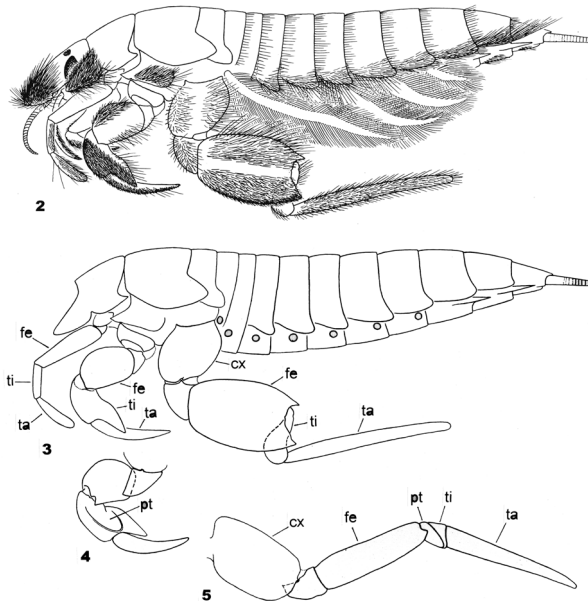
Status and general system of Pinnatitergaliae

The taxon **Pinnatitergaliae** KLUGE, 2000 (or **Ephemera/fg7**), in its volume corresponds to "superfamily Ephemeroidea" sensu Edmunds and Traver, 1954. This is a generally accepted taxon, however its holophyly is doubtful.

A single unique character of Pinnatitergaliae is shape of its tergalia of pairs II-VII, which are bifurcate and pectinate. However, probably this is not an autapomorphy, but a plesiomorphy if compared with *Neoephemera/fg1*, where tergalia II-VI are also bilamellate and pectinate, but have operculate specialization. In its turn, *Neoephemera/fg1* is attributed to Caenotergaliae on the base of unique apomorphies (Kluge, 1997; Wang *et al.*, 1997). Other peculiar characters of Pinnatitergaliae are in common with *Neoephemera/fg1*: (1) in proximal part of fore

wing, MP_2 and CuA are curved and strongly divergent with MP_1 ; (2) imaginal and subimaginal mesonotal suture is strongly curved posteriorly by sides of median line (Kluge, 1997: Fig. 3:4-5: MNs) (the same also in *Leptophlebia/fg1* and *Tetramerotarsata*); (3) imaginal and subimaginal lateral scutal suture goes from suralare posteromedially, being nearly straight (*ibid.*: LSS) (in other mayflies its posterior end is curved laterally – Kluge, 1997: Fig. 3:3); (4) subimaginal lateropostnotal crest begins from anterior margin of postsubalar sclerite and goes in ventral direction by margin of subalar cavity (Kluge, 1997: Fig.3:1: LPNC) (in other mayflies lateropostnotal crest begins from postsubalar sclerite at a distance from its anterior margin and goes at a distance from margin of subalar cavity, thus subimaginal sclerotization of lateropostnotum

has an axe-like shape – Kluge, 1997: Fig. 3:2). Probably all these characters were present in the common ancestor of Pinnatitergaliae + Caenotergaliae, but were secondarily lost in Caenoptera (i.e., Caenis/f2=Brachycercus/g2). Besides this, Pinnatitergaliae are characterized by presence of a collar on larval pronotum (Kluge, 1997: Fig. 2), this character being in common with all Caenotergaliae.

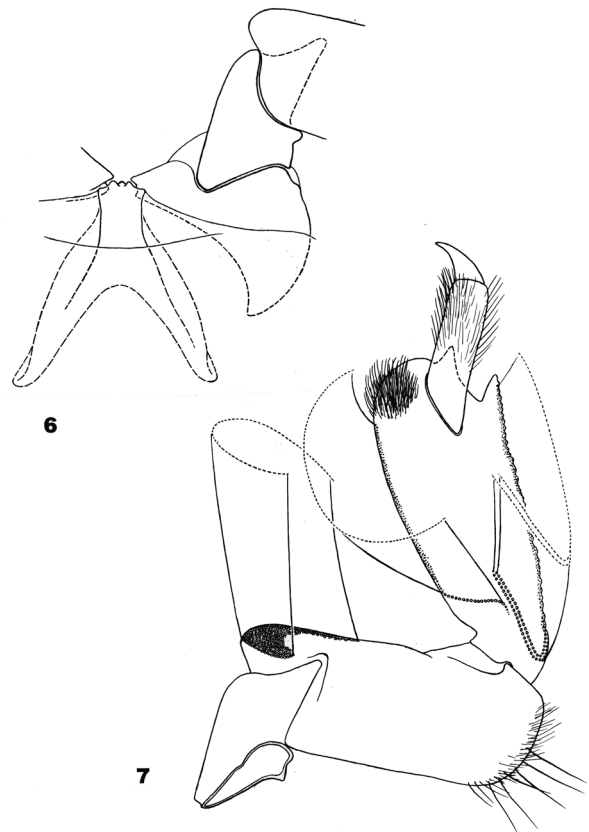


Figs. 2-5 - Behningia/fg2: 2 - Behningia/fg3 *tshernovae* EDMUNDS & TRAVER, 1959 [*Behningia*], young larva, lateral view; 3 - the same, without head, tergaliae and setation; 4 - the same, median view of middle leg; 5 - Behningia/fg2 *Dolania/g1 americana* EDMUNDS & TRAVER, 1959 [*Dolania*], hind leg. Abbreviations: cx - coxa; fe - femur; pt - patella; ta - tarsus; ti - tibia or telotibia.

Some authors divide Pinnatitergaliae to 2 subordinate taxa – **Behningia/fg1** (see below) and **Scapphodonta** McCAFFERTY, 1997. Scapphodonts have following unique characters: (1) presence of mandibular tusks; (2) presence of pectinate setae on inner side of larval hind femur and tibia; (3) non-pectinate tergaliae of pair I. An assumption that these characters are autapomorphies of Scapphodonts, contradicts to the assumption about holophyly of Fossoriae (see below). Probably ancestors of Behningia/fg1 had normal burrowing larvae with mandibular tusks, pectinate setae on hind legs and rudimentary non-pectinate tergaliae of pair I. Because of their high specialization, larval Behningia/fg1 lost mandibular tusks, initial burrowing specialization of fore legs and pectinate setae on hind legs. Such secondary loss of all these features seems

possible; assuming that Caenotergaliae originated from Pinnatitergaliae, we have to agree that loss of all these features took place in ancestors of Caenotergaliae as well. Tergaliae I in Behningia/fg1 are pectinate unilamellate and strongly differ from tergaliae II-VII (which are pectinate bilamellate, being typical for Pinnatitergaliae). In various taxa of Scapphodonts, first tergaliae, being always non-pectinate, have quite various structure: they can be bilamellate, unilamellate, or (in Potamanthus/fg1) in a form of 2-segmented stick. The last form is in common with Caenotergaliae and Ephemera/fg1, and this fact can not be explained by any of possible cladistic hypotheses (Kluge, 1997).

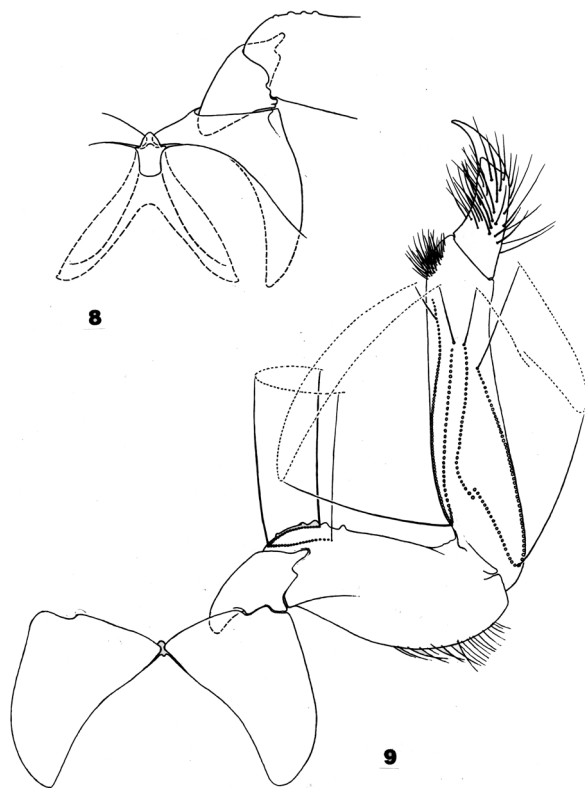
Instead of division to Behningia/fg1 and Scapphodonts, Pinnatitergaliae should be divided to three holophyletic taxa – Potamanthus/fg1, Euthyplocia/fg1 and Fossoriae (Fig. 1).



Figs. 6, 7 - Palingenia/f2=g1 *Pentagenia* sp.: 6 - bases of fore legs of larva, view from behind; 7 - fore leg of larva, front view (instead of dense long setae on mandible, are shown only their bases and general length).

The taxon **Potamanthus/fg1** (incl. *Rhoenanthus*) [f: Potamanthines ALBARDA in SELYS-LONGCHAMPS, 1888; g: *Potamanthus* PICTET, 1843, typus *Ephemera lutea*

LINNAEUS, 1764] corresponds to the "family Potamanthidae" in modern classifications and to the "tribe Potamanthini" or the "subfamily Potamanthinae" in classifications of first half of the 20th century. It has the following autapomorphy: on fore wing anal vein is bifurcate (while in other mayflies from the anal vein can arise only hind branches, which are distinctly different from the anal vein itself). Other peculiar characters of Potamanthus/fg1 are in common with Caenotergaliae and Ephemerella/fg1: (1) in larva, on dorsal side of fore femur, a transverse row of setae can be developed; (2) tergalia of 1st pair has a form of two-segmented stick-like rudiment, covered with setae and attached in anterior part of lateral margin of the segment (instead of its hind margin, as other tergaliae do); (3) egg with 2 polar caps and several anchors; each anchor consists of a knob and a skein of threads, which surround this knob in a form of regular ring (such caps and anchors are present in many Ephemerella/fg1, and caps – also in some Caenotergaliae). Other characters of Potamanthus/fg1 are either plesiomorphies or non-unique apomorphies.



Figs. 8, 9 - Polymitarcys/f2=Ephoron/g3 *nigridorsum* TSHERNOVA, 1934 [*Eopolymitarcys*]: 8 – bases of fore legs of larva, view from behind; 9 – fore leg of larva, front view (instead of dense long setae on femur and tibia, are shown only their bases and general length).

The taxon **Euthyplocia/fg1** (incl. *Campylocia*, *Polyplocia*, *Probosciodoplocia*, *Exeuthyplocia*) [f: Euthyplociinae LESTAGE, 1921; g: *Euthyplocia* EATON, 1871, typus *Palingenia hecuba* HAGEN, 1861] corresponds to the "family Euthyplociidae" or the "subfamily Euthyplociinae" in various modern classifications. It is characterized by following autapomorphies: (1) larval clypeus is projected forwards as a shelf above base of labrum (Fig. 15) (a unique apomorphy); (2) mandibular tusks are covered by dense irregular long slender setae; on inner side of tusk these setae are directed nearly perpendicular to the tusk, and probably are used for filtering (unique apomorphy); (3) larval fore tibia on inner-apical corner with a pointed projection (similar projection is found only in some mayflies not belonging to Pinnatitergaliae); (4) on fore wing, the bifurcation of MA (initially located in middle of wing) is turned proximally (non-unique apomorphy; among Pinnatitergaliae the same in *Behningia/fg1*, *Anagenesia/g1* and *Polymitarcys/f1=Ephoron/g2*); (5) gonostylus with no more than one distal segment (instead of two segments initial for Ephemeroptera) (non-unique apomorphy). Other characters of *Euthyplocia/fg1* are either plesiomorphies or non-unique apomorphies.

Both in *Potamanthus/fg1* and *Euthyplocia/fg1*, larva (which has the collar on pronotum – see above), has also a collar on mesonotum – a concave band at anterior margin, separated from the rest part of mesonotum by a transverse crest (Kluge, 1997: Fig. 2); the same in *Caenotergaliae* and *Ephemerella/fg1*.

The rest of Pinnatitergaliae constitute a holophyletic taxon Fossoriae. Phylogenetic relationship among *Potamanthus/fg1*, *Euthyplocia/fg1* and Fossoriae is unclear.

Status and general system of Fossoriae

The taxon **Fossoriae** KLUGE, 2000 (hierarchical name: **Ephemera/fg8**) is holophyletic, that is proved by following autapomorphies.

(1) Larval legs are initially specialized as burrowing (only in *Behningia/fg2* this burrowing specialization is secondarily lost); in all cases, there is retained a following apomorphy in femora structure, initially connected with the burrowing specialization. On femora of fore and middle legs, anterior side (which in other mayflies is directed more or less dorsally) is concave, bare, most time directed inside, while posterior side (which in other mayflies is directed more or less ventrally) is

convex, setose, most time directed outward; femur of hind leg, on the contrary, has anterior side convex, setose and most time directed outside, and posterior side concave, bare, most time directed inside. This difference in femora structure is present not only in representatives of Fossoriae, which use their legs for burrowing, but also in *Behningia/fg2*, which legs have gotten secondarily quite different specialization; in *Behningia/fg2* the opposite curvations of middle and hind femora are retained in spite of the fact that deeply specialized middle and hind legs have similar function (Figs. 2-5). In all other mayfly larvae, the outer (as usual, most convex and most setose) side of femur on all legs is their anterior (dorsal) side.

(2) Larval frons forms a shelf-like projection with flat dorsal surface, which hangs over clypeus and mandibular bases (Figs. 12-14). Sometimes frontal projection is poorly expressed or not expressed. Similar projection independently appeared in some other mayflies (particularly, in *Drunella/g1*).

(3) Tergaliae (which have shape typical for Pinnatitergaliae) in rest are directed dorsally-medially-posteriorly (with exception for *Behningia/fg2*, in which because of development of lateral tergal projections, tergaliae appear to be situated on ventral side).

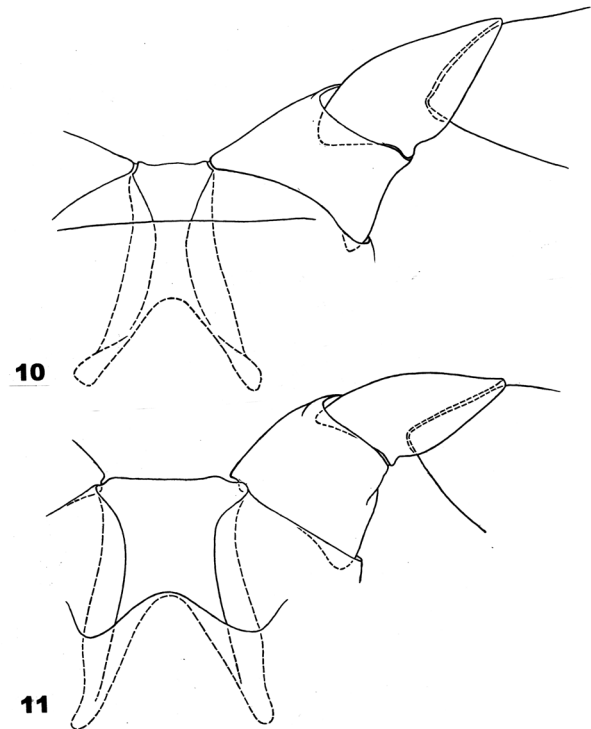
Fossoriae are divided to *Ichthybotus/fg1*, *Ephemera/fg9*, *Behningia/fg1* and *Cryptoprosternata*; phylogenetic relationship among them is unclear.

The taxon ***Ichthybotus/fg1*** [f: *Ichthybotidae* DEMOULIN, 1957; g: *Ichthybotus* EATON, 1899, typus *Ephemera hudsoni* McLACHLAN, 1894] corresponds to the "genus *Ichthybotus*", the "subfamily *Ichthybotinae*" and the "family *Ichthybotidae*"; it includes two New Zealand species only.

The taxon ***Ephemera/fg9*** (incl. *Hexagenia*) is holophyletic, that is proved by following unique autapomorphy. Bases of tergaliae of pair VII are strongly shifted anteriorly being located at equal distances from posterior and anterior margins of segment VII (this character can be used as diagnostic not only for larvae, but for winged stages as well, because they have visible traces of tergaliae bases). In all other Pinnatitergaliae, tergaliae at least of pairs II-VII are attached to posterior part of segment, as well as in majority of mayflies. *Ephemera/fg9* is divided to two holophyletic taxa ***Ephemera/fg10*** (incl. *Afromera*) and ***Hexagenia/fg1*** (incl. *Eatonica*).

The taxon ***Behningia/fg1*** (incl. *Protobehningia*) [f: *Behningiidae* MOTAS &

BACESCO, 1937; g: *Behningia* LESTAGE, 1930, typus *B. ulmeri* LESTAGE, 1930] corresponds to the "family *Behningiidae*" and the "superfamily *Behningioidea*". This evidently holophyletic taxon is characterized by a lot of unique autapomorphies (Peters and Gillies, 1991, *et al.*). It is divided to *Protobehningia* and ***Behningia/fg2*** (incl. *Dolania*).



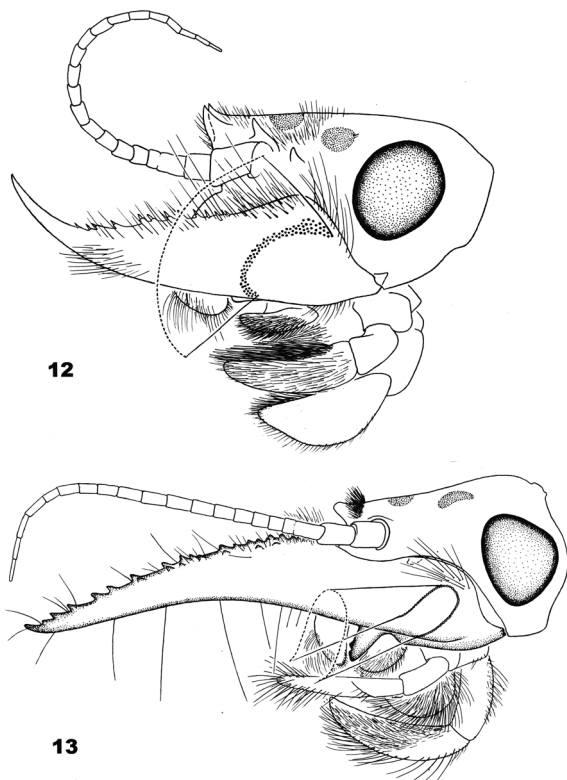
Figs. 10, 11 - Base of fore legs of larva, view from behind: 10 - *Ephemera/fg9 Hexagenia/fg3 limbata* SERVILLE, 1829 [*Ephemera*]; 11 - *Ephemera/fg10 vulgata* LINNAEUS, 1758 [*Ephemera*].

Status and system of *Cryptoprosternata*

The taxon ***Cryptoprosternata*** KLUGE, 2000 has a hierarchical name ***Palingenia/fl*** = ***Ephoron/g1*** [f: *Palingenines* ALBARDA in SELYS-LONGCHAMPS, 1888; g: *Ephoron* WILLIAMSON, 1802, typus *E. leucon* WILLIAMSON, 1802]. In its volume it formally corresponds to the "genus *Palingenia*" sensu Burmeister, 1839 and the "subfamily *Palingenines*" sensu Selys-Longchamps, 1888 (while these authors listed only representatives of European fauna, and their opinion on systematic position of non-European mayflies is unknown). *Cryptoprosternata* is a holophyletic taxon, that is proved by following unique autapomorphies.

(1) Larval, subimaginal and imaginal prosternum is narrowed, bases of fore coxae are brought together; larval fore coxae are contiguous

or nearly contiguous in one point where they are articulated with the prosternum; a part of the prosternum behind coxae bases is dipped into the body, thus furca represents a fork-like hollow formation, opened outside by a small unpaired opening exactly behind the place of connection of leg coxae (Figs. 6-9). At the same time, furcae of mesothorax and metathorax are not modified (i.e. each consists of a pair of widely separated apophyses). In other Ephemeroptera median coxal condyli are widely separated (Figs. 10, 11).

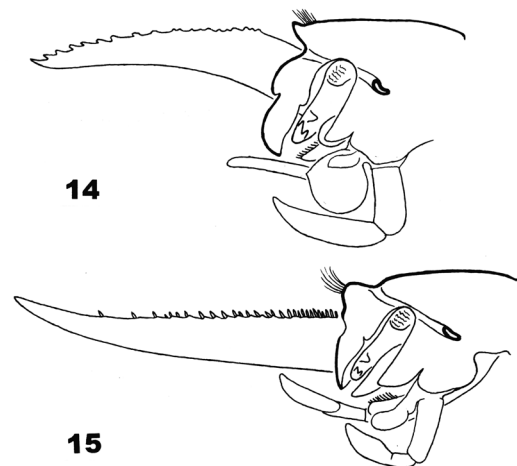


Figs. 12, 13 - Head of larva, laterally: 12 - *Palingenia/f3=g2 Anagenesia/g2 paradoxa* BULDOVSKY, 1935 [*Anagenesia*]; 13 - *Polymitarcys/f2=Ephoron/g3 nigradorsum* [*Eopolymitarcys*]. Instead of dense long setae on mandible, are shown only their bases and general length.

(2) In larva, on fore leg [specialized as burrowing - see Fossoriae (1)] inner side of femur is proximally convex; distal edge of trochanter, which bears a condylus, wedges itself into anterior side of the femur (Figs. 6-9). In other mayflies inner side of femur is straight, and trochanter is longest not on anterior, but on its inner side (Figs. 10-11).

(3) Larval mandibles and fore legs have the following regularly situated long setae. (A) Ventral side of mandible with an arched row of setae, this row is directed by its convex side

laterally-dorsally; in *Polymitarcys/f1=Ephoron/g2* this is a U-shape row (Fig. 13), in *Palingenia/f2 = g1* this is a widely arched stripe of irregularly situated setae (Fig. 12). (B) The proximal convexity of inner side of fore femur [see (2)] with a horseshoe-shaped row of setae: curvature of this row is situated at extreme femur base, and two its arms are directed distally; in *Polymitarcys/f1=Ephoron/g2* this row is regular (Fig. 9), and in *Palingenia/f2=g1* it has a form of stripe (Fig. 7). (C) Anterior (dorsal) side of fore tibia has at least a proximal oblique row of setae; in *Polymitarcys/f1=Ephoron/g2* this row is regular, both its ends are strongly curved distally and continue as two regular longitudinal rows (Fig. 9); in *Palingenia/f2=g1* this row is double and has no continuations (Fig. 7). (D) Inner side of fore tibia has a regular row of setae strongly differing in its shape in *Polymitarcys/f1 = Ephoron/g2* and *Palingenia/f2=g1* (Figs. 7, 9). At least the presence of the rows (B) and (C) is unique among all mayflies.



Figs. 14,15 - Median longitudinal section of larval head: 14 - *Polymitarcys/f2 = Ephoron/g3 nigradorsum* [*Eopolymitarcys*]; 15 - *Euthyplocia/fg1 minima* ULMER, 1916 [*Euthyplocia*] (determined presumably).

(4) Maxillary and labial palps are 2-segmented; palps of both pairs with 1st segment shortened, and 2nd segment (initial 2+3rd) thickened, of a simple shape - oval, oval-conic, banana-shaped, etc. (Figs. 12, 13). Correspondingly, labial palp has no muscle in second segment. In contrast to Cryptoprosternata, in majority of other Pinnatitergaliae - in *Ephemer/f9*, *Ichthybotus*, *Potamanthus/fg1* and *Euthyplocia/fg1* - maxillary palp is long and slender, and labial palp often has widened third segment; if second and third segments of labial palp are fused, they retain

general composite shape and sometimes muscle of second segment.

(5) Imaginal and subimaginal paracercus is reduced at least in male; in *Pentagenia* and *Polymitarcys/f2=Ephoron/g3* paracercus is developed in female, while in *Palingenia/f3=g2* and *Campsurus/fg1* it is reduced in both sexes (non-unique apomorphy).

Cryptoprosternata are divided to 2 holophyletic taxa – ***Palingenia/f2=g1*** (incl. *Pentagenia*) and ***Polymitarcys/fl=Ephoron/g2*** (incl. *Campsurus*).

Discussion

Some authors (Ulmer, 1920; McCafferty, 1991) united *Euthyplocia/fg1* with *Polymitarcys/fl = Ephoron/g2* to the "family Polymitarciidae". All common features of these taxa are connected with short-living specialization of winged stages; the same features independently evolved in some other mayfly groups – *Behningia/fg1*, *Anagenesia/g1*, *Oligoneuria/f3 = g4*, *et al.* Besides this, the idea about relationship of *Euthyplocia/fg1* and *Polymitarcys/fl = Ephoron/g2* was based on the fact that the Afrotropical taxon ***Exeuthyplocia/fg1*** (incl. *Afroplocia*) belongs to *Euthyplocia/fg1* and at the same time has burrowing larval specialization similar to that of *Polymitarcys/fl = Ephoron/g2*. Actually, the similarity between larvae of these taxa is a result of independent specialization. Particularly, similar projection in front of head in *Exeuthyplocia/fg1* is formed by clypeus [see above, *Euthyplocia/fg1* (1)] thus it is located ventrad of anterior tentorial pits (Fig. 15), while in *Polymitarcys/fl = Ephoron/g2* it is formed by frons [see above, *Fossoriae* (2)] and is located dorsad of the anterior tentorial pits (Fig. 14). Middle leg of *Exeuthyplocia/fg1* has femur shortened, sharply widened and somewhat curved in such a manner, that the middle leg can be directed anteriorly, like in *Polymitarcys/fl = Ephoron/g2* [see above, *Fossoriae* (1)]; but in contrast to *Fossoriae*, middle leg of *Exeuthyplocia/fg1* retains dense setation on initially anterior (dorsal) side (which is directed anteriorly-inside), and has no dense setation on initially posterior (ventral) side (which is directed posteriorly-outside).

Assuming that the burrowing specialization appeared in course of evolution of *Euthyplocia/fg1* (incl. *Exeuthyplocia*), and than was inherited by *Polymitarcys/fl=Ephoron/g2* from *Exeuthyplocia/fg1*, one has to regard *Euthyplocia/fg1* to be a paraphyletic taxon

(McCafferty, 1991); this assumption contradicts to the presence of unique autapomorphies of *Euthyplocia/fg1* (see above).

It was also suggested to unite *Ephemera/fg9* (incl. *Hexagenia*) with *Palingenia/f2=g1* to a "family Ephemerae" sensu McCafferty, 1991. Assumption about holophyly of this taxon contradicts to the idea about holophyly of Cryptoprosternata. The only common characters of *Ephemera/fg9* and *Palingenia/f2=g1* are the following: (1) mandibular tusks are curved laterally-dorsally (Fig. 12) (instead of medial or medial-vental curvature in other Pinnatitergalia – Fig. 13); (2) larval hind tibia with a prominent inner-distal angle. Most probably, these two simple characters evolved independently in these groups.

Acknowledgement

This work was supported by Russian federal grant "Universities of Russia – Fundamental Science" (UR 07.01.056).

References

- Edmunds G.F., Jr., Traver J.R., 1954. An outline of a reclassification of the Ephemeroptera. Proc. Entomol. Soc. Washington, 56:236-240.
- Kluge N.J., 1997. A paradoxical problem in the phylogeny of Furcatergalia (Ephemeroptera). In: Landolt P., Sartori M. (eds). Ephemeroptera & Plecoptera: Biology – Ecology - Systematics. Fribourg: MTL. pp. 520-526.
- Kluge N.J., 1998. Phylogeny and higher classification of Ephemeroptera. Zoosystematica Rossica, 7(2):255-269.
- Kluge N.J., 1999a. [A system of alternative nomenclatures of the supraspecific taxa]. Entomol. Obozrenie, 78(1):224-243 (in Russian).
- Kluge N.J., 1999b. A system of alternative nomenclatures of supra-species taxa. Linnaean and post-Linnaean principles of systematics. – Entomological Review, 79(2): 106-110 [authorized translation from Entomol. Obozrenie, 78(1):224-243].
- Kluge N.J., 1999c. Mito en sistematica y principios de nomenclatura zoológica / Myths in systematics and principles of zoological nomenclature. – In: Melic A., de Haro J.J., Mendes M., Ribera I. (eds.) Evolution y Filogenia de Arthropoda. Bol. Soc. Entomol. Aragonesa, 26:347-377.
- Kluge N.J., 2000. [Modern systematics of insects. Part I. Principles of systematics of living organisms and general system of insects with classification of primary wingless and paleopterous insects]. – S.-Petersburg, "Lan", 2000: 332 pp. (in Russian).
- McCafferty W.P., 1991. Toward a Phylogenetic Classification of the Ephemeroptera (Insecta): A

- Comentary on Systematics. *Ann. Entomol. Soc. Amer.*, 84: 343-360.
- Peters W.L., Gillies M.T., 1991. The male imago of *Protobehningia Tshernova* from Thailand (Ephemeroptera, Behningiidae). In: J. Alba-Tercedor J., Sanchez-Ortega A. (eds.). *Overview and strategies of Ephemeroptera and Plecoptera*. Florida, Sandhill Crane Press, pp. 207-216.
- Ulmer G., 1920. Übersicht über die Gattungen der Ephemeropteren, nebst Bemerkungen über eizelne Arten. *Stettiner Entomol. Zeitung*, 81:97-144.
- Wang T.-Q., McCafferty W.P., Bae Y.J., 1997. Sister relationships of the Neoephemeridae and Caenidae (Ephemeroptera: Pannota). *Entomol. News*, 108(1):52-56.