System and phylogeny of Pinnatitergaliae (Ephemeroptera)

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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/f1 = 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/fg1, Euthyplocia/fg1, Behningia/fg1 and Cryptoproctina (or Palingenia/f1 = Ephoron/g1). Cryptoproctina are divided to 2 holophyletic taxa – Palingenia/fg2 (incl. Pentagenia) and Polymitarcys/fg1 = Ephoron/g2 (incl. Campsaurus). Some authors united Euphotrophia/fg1 with Polymitarcys/fg1 = Ephoron/g2; actually characters which look as common for these two taxa, evolved independently.

Introduction
In the present paper, typified names of supraspecies 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/EPHEMEROPtera_/content_.htm).

Mayflies in widest sense constitute a taxon Panephemeroptera CRAMPTON, 1928, or Ephemeroptera sensu latissimo; hierarchical name: Ephemera/fg1 [f: Ephemeriniae LATREILLE, 1810; g: Ephemera LINNAEUS, 1758, typus E. vulgata LINNAEUS, 1758]. Panephemeroptera include Carboniferous insects related to mayflies (Triplosoba et al.) and Euphemeroptera. The taxon Euphemeroptera
KLUGE, 2000, or Ephemeroptera sensu lato (hierarchical name: Ephemera/fg2) includes Permian mayflies (Protereisema, 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/g1) and Bidentiseta KLUGE 1993 (hierarchical name: Ephemera/fg5). Bidentiseta are divided to Branchitectalae KLUGE, 1998 (hierarchical name: Heptagenia/f1=Oligoneuria/g1) and Furcatergaliae KLUGE, 1998 (hierarchical name: Ephemera/fg6) (non Furcatergalia KLUGE, 1989).

Phylogeny of Furcatertigalae 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) Caenotergalae KLUGE, 2000 [hierarchical name: Caenis/f1=Brachycercus/g1 (incl. Neoephemera)]; (3) Ephemera/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)](image)

**Status and general system of Pinnatitergaliae**

The taxon Pinnatitergaliae KLUGE, 2000 (or Ephemera/fg7), in its volume corresponds to "superfamily Epheremoidea" 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 tergaliae 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 tergaliae II-VI are also bilamellate and pectinate, but have opercular specialization. In its turn, Neoephemera/fg1 is attributed to Caenotergalae 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, MP₂ and CuA are curved and strongly divergent with MP₁; (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 suralar 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/fg2=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.

Some authors divide Pinnatitergaliae to 2 subordinate taxa – Behningia/fg1 (see below) and Scaphphodonta McCafferty, 1997. Scaphphodonta 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 Scaphphodonta, 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 Scaphphodonta, 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 Ephemerella/fg1, and this fact can not be explained by any of possible cladistic hypotheses (Kluge, 1997).

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

The taxon Euthyplocia/fg1 (incl. Campylocia, Polyplcicia, Proboscidiplocia, Ex euthyplocia) [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/fg(1), 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 tergial bases). In all other Pinnatitergaliae, tergialae 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/f1 = 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 prothorax; 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).

(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/fl=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.

(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 Ephemerfa/fg9, Ichthybotus, Potamanthus/fg1 and Euthyplocia/fg1 minima ULMER, 1916 [Euthyplocia] (determined presumably).
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/f1=Ephoron/g2 (incl. Campsurus).

Discussion

Some authors (Ulmer, 1920; McCafferty, 1991) united Euthyplocia/fg1 with Polymitarcys/f1 = Ephoron/g2 to the "family Polymitarcyidae". 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/g1 and Polymitarcys/f1 = Ephoron/g2 was based on the fact that the Afrotropical taxon Exeuthyplocia/fg1 (incl. Afroplocia) belongs to Euthyplocia/f1 and at the same time has burrowing larval specialization similar to that of Polymitarcys/f1 = 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/f1 = 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/f1 = 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/f1=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 Ephemeroidea" 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 curvation in other Pinnatitergaliae – Fig. 13); (2) larval hind tibia with a prominent inner-distal angle. Most probably, these two simple characters evolved independently in these groups.

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