Chapter III

Ephemeroptera in wider and narrower senses

If only Recent representatives are to be discussed, the taxon Ephemeroptera (mayflies) looks distinctly outlined. However, there are known several fossil Palaeozoic forms which have relationship with Recent mayflies, but do not fall into the taxon Ephemeroptera if characterize it by structure of Recent representatives. These extinct forms together with Recent mayflies form a group which can be called Ephemeroptera in widest sense, or Panephemeroptera; it includes a subordinate taxon which also can be called Ephemeroptera, or Euephemeroptera; in its turn, Euephemeroptera include a subordinate taxon Ephemeroptera in narrowest sense, or Euplectoptera, to which all Recent mayflies belong. Phylogenetic relationships of these taxa are assumed as following:

† Protephemeroidea

† plesiomorphic Permoplectoptera

── Posteritorna

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└─ Branchitergaliae

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Furcatergaliae

Bidentiseta

Ameletoptera

Euplectoptera

Ephemeroptera

Below, following classification of mayflies is given:

{1} Panephemeroptera

or Ephemeroptera sensu latissimo, or Ephemera/fg1

(Figs 3–106)

Nomen hierarchicum: Ephemera/fg1 (incl. Triplosoba)

[f: Ephemerae Latreille 1810: 273; g: Ephemerinæ Linnaeus 1758: 546, typus E. vulgâta Linnaeus 1758 (design. Latreille 1810)].

Nomina circumscribentia univoca:

— Panephemeroptera Crampton 1928: 85;
— Ephemeroptera Crampton 1938: 170;

Nomina circumscribentia non-univoca (in circumscription matching also Euephemeroptera and Euplectoptera) – see below, Euplectoptera.

In circumscription exactly matches:

— ordo Ephemeroptera: Demoulin 1956b: 8;
— ordo Ephemerida: Rohdendorf 1977: 20;
— superordo Panephemeroptera Crampton 1928: 83;
— superordo Panephemeroptera, or Ephemeroptera Crampton 1938: 170;
— superordo Ephemeroptera: Martynov 1938: 32;
— superordo Ephemeropteraoididae Rohdendorf 1968: 61;
— superordo Ephemeroptera: Rasnitsyn 2002: 86;
— cohors Ephemeriformes: Rohdendorf 1977: 20;
— sectio Ephemerata: Boudreaux 1979: 196;
— subclassis Ephemeroidea: Handlirsch 1906: 37;

In circumscription non-univocally matches taxa listed below, under Euplectoptera.


Characters of unclear phylogenetic status.

(1) Wings are unable to fold on back: in rest are directed dorsally (Fig.8:A) or spread laterally (Fig. 14:A). The same in Odonatoptera Lameere 1900 (or Odonata Fabricius 1793 s. L., or Libellula/fg1) and Protorrhinchoptera Rohdendorf 1968 (or Dictyoneura/fg1), in contrast to Neoptera Martynov 1923.

(2) At least fore wing is costalized: veins Sc and RA go parallel to C nearly up to wing apex; RS
begins as a common stem (FIGS 7:C–D; 14:A–B). The same in Protorrhynchota and many others.

(3) Convex and concave veins are regularly alternating (FIGS 7:A–D, 14:A–B); there are concave RS, convex MA, concave MP, convex CuA, concave CuP and others (besides concave Sc and convex RA which are common for Pterygota). The same in Protorrhynchota; Odonatoptera have less number of regularly alternating veins; Neoptera have different composition of veins behind RA (FIG.7:E) Among Panephemeropera these veins can be lost only on vestigial hind wings of some Euplectoptera.

(4) Triad branching of veins provides regular alternating of convex and concave branches (FIGS 7: B–D, 14:A–B). Vein RS [concave – see (3)] forms a triad of concave RSA and RSp and convex iRS between them; RSA forms a triad of concave RSA1 and RSA2 and convex iRSA between them (the same in Odonatoptera, but in contrast to Protorrhynchota). MP [concave – see (3)] forms a triad of concave MP1 and MP2 and convex iMP. Euplectoptera have also triads formed by RSA2 and MA (FIGS 7: C, 14:B). Only in extremely specialized representatives of Euplectoptera some of these veins are lost.

Plesiomorphy of Panephemeropera. Paracercus is present, often long and multisegmented (FIGS 12, 14), sometimes reduced to a non-segmented vestige; presence of paracercus is a unique plesiomorphy among Pterygota.

Size. Fore wing length 2–40 mm.

Age and distribution. Carboniferous (see Protephemeroidea) — Recent; world-wide.

Panephemeropera are divided into Protephemeroidea and Euphemeroptera.

{1.1} Extinct taxon Protephemeroidea, or Triplosoba/fg(1) (Panephemeropera Protephemeroidea) (FIG. 14:A)

Nomen hierarchicum: Triplosoba/fg1 [f: Triplosobidae Handlirsch 1906: 312; g: Triplosoba Handlirsch 1906: 312, typus Blanchardia pulchella Bronniart 1893 (monotypy); syn. obj.: Blanchardia Bronniart 1893: 325 (non Blanchardia Castelnaud 1875)].

Nomina circumscribentia:
— Protephemeroidea Handlirsch 1906;
— Protephemereda Krausse & Wolff 1919;
— Protephemereda Crampton 1928;
— Protephemereda Hamilton 1972.

In circumscription matches:
— gen. Blanchardia Bronniart 1893: 325 (nom. praecocc.);
— gen. Triplosoba Handlirsch 1906: 312;
— subfam. Triplosobinae: Demoulin 1956b: 7;
— fam. Triplosobidae Handlirsch 1906: 312;
— superfam. Triplosoboidea: Demoulin 1956b: 7;
— ordo Protephemeroidea Handlirsch 1906: 311;
— ordo Protephemereda Krausse & Wolff 1919: 156;
— ordo Protephemereda Crampton 1928: 83;
— ordo Protephemereda Hamilton 1972: 146;

References. Brongniart 1893: ?; – Lameere 1917: ?;
– Carpenter 1963: ?.

Characters of unclear phylogenetic status.

(1) Wings of both pairs RS is basally fused with RA and independent from MA (FIG.14:A) (in contrast to Euphemeroptera).

(2) RSA2 is non-branched (probably on wings of both pairs, but for certain known for hind wings only – FIG.14:A) (in contrast to many Euphemeroptera).

(3) MA is non-branched (FIG.14:A) (in contrast to majority of Euphemeroptera).

Size. Fore wing length more than 21 mm.

Age. Carboniferous (France).

Species composition of Protephemeroidea. One species – pulchella Bronniart 1893 [Blanchardia], known as a single adult specimen.

Material examined: –.

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{1.2} Euphemeroptera, or Ephemeroptera sensu lato, or Ephemera/fg2 (Panephemeropera Euphemeroptera) (FIGS 3–13; 14:B–D; 15–106)

Nomen hierarchicum: Ephemera/fg2 (sine Triplosoba; incl. Phtharthus).

Nomen circumscribens univocum:

Nomina circumscribentia non-univoca (in circumscription matching also Panephemeropera and Euplectoptera) – see below, Euplectoptera. In circumscription exactly matches:
— subordo Ephemiderina: Tshernova 1980: 31;
— ordo Plectoptera: Handlirsch 1906: 37;
— ordo Ephemiderina: Handlirsch 1919: 63 [573];
— ordo Ephemiderida: Krausse & Wolff 1919: 157;


Characters of unclear phylogenetic status.

(1) Wings of both pairs have a costal brace – a short vein which goes from wing base between C and Sc, falls into Sc and at the same place is connec-
ted by a cross vein with RA. Unique character. For Proteptheroidea costal brace is not described. In Permoplectoptera costal brace is situated between C and Sc (Fig.14:B), but in Euplectoptera it is stout, convex anteriorly, and projects dorsal-anterial of C (Fig.6); in Discoglossata it is modified (Fig.42:A).

(2) Vein RS arises not from RA, but from MA (in contrast to Proteptheroidea); the common basal stem RS+MA can be either independent from RA (Fig.7:C), or basally fused with RA (particularly on hind wings of Euplectoptera – Fig.7:D), or secondary reduced (Fig.17:A). Non-unique character, the same in some other Pterygota.

(3) Vein RS2 (concave – see Paneptheroidea (4)) forms a triad of concave RSa2 and RSa2; and convex iMA between them (Fig.7:C). Unique character. This third triad of RS is present on wings of both pairs in Permoplectoptera (Fig.14:B) and fore wings of many Euplectoptera [but not on their hind wings – see Euplectoptera (1) below]. On fore wings of some Euplectoptera veins RSa2 and iRS2 secondarily become intercalaries or lost (see Index of characters [2.2.37]).

(4) On wings of both pairs MA [convex – see Paneptheroidea (3)] forms a triad of convex MA and MA1; and concave iMA between them (Fig.7:C–D). This branching of MA secondary disappears on vestigial hind wings of some Euplectoptera and on fore wings in some groups with especially modified venation (see Index of characters [2.2.43]). Usually furcation of MA is situated approximately in middle of wing, but sometimes it can be secondarily transferred proximally (on fore wings of some specialized Euplectoptera) or toward wing margin (on vestigial hind wings of some Euplectoptera).

(5) Larva is aquatic, initially with a peculiar swimming siphlonuroid specialization (Figs 9:A–B; 14:C–D; 28:A), abdomen is elongate and able to make undulate dorsoventral swimming movements; caudalii are not long (shorter than in imago), with primary swimming setae – i.e. each cercus has a row of setae on inner side, and paracercus has a pair of rows of setae of the same kind on its lateral sides; thanks to this, caudalii can function as a horizontal caudal fin. As larvae of other Paneptheroidea are unknown, it is unclear if this specialization is an autapomorphy of Euplectoptera or an autopomorphy of a larger taxon. In many Euplectoptera this swimming specialization is secondarily lost.

(6) Larva has tergalii on abdominal segments I–IX (Fig.14:D). As larvae of other Paneptheroidea are unknown for certain, it is unclear, if the presence of tergalii is a character of Euplectoptera or of a larger taxon; if proceed from the assumption that tergalii are serial homologues of wings, their presence is a plesiomorphy. In various Euplectoptera tergalii of these or that pairs are lost (see Index of characters [1.3.19]).

Size. Fore wing length 2–40 mm.

Age and distribution. Perm (see Permoplectoptera) – Recent; world-wide.

Euplectoptera are divided into Palaeozoic pleiomorphon Permoplectoptera and Mesozoic–Recent taxon Euplectoptera. Some fossil mayflies have uncertain systematic position (see Appendix: p.359).

\{1.2.1\} † Plesiomorphon Permoplectoptera, or Protereisma/f1=Phtharthus/g1 (Paneptheroidea Euplectoptera Permoplectoptera) (Figs 14:B–D)

Nomen hierarchicum: Protereisma/f1=Phtharthus/g1 [f: Protereismatidae (orig. Protereismidae) Lameere 1917; g: Phtharthus Handlirsch 1904a, typus Ph. rossicus Handlirsch 1904 (design. orig.; syn.subj. Ph. netshaevi Handlirsch 1904)].

Nomina circumscribentia:
— Protereismatidae Sellards 1907: 345;
— Permoplectoptera Tillyard 1932: 117.

In circumscription matches:
— fam. Protereismatidae Sellards 1907: 345;
— fam. Protereismidae Lameere 1917: 45;
— superfam. Protereismatoidea: Demoulin 1958: 6;
— subordo Permoplectoptera Tillyard 1932: 117;
— Permoplectoptera, or Protereisma/f1=Phtharthus/g1: Kluge 2000: 243.


Plesiomorphies of Permoplectoptera (in contrast to Euplectoptera). Wings are homonomous – i.e. hind wings have nearly the same size and venation as fore wings (Fig.14:B). At least in some representatives tergalii are present not only on abdominal segments I–VII, but on abdominal segments VIII–IX as well (Fig.14:D). For larva of americana [Kukalo-va], segmented tarsus and two claws are described, that resembles adult structure and differs from larval Euplectoptera (Kukalova 1968).

Size. Fore wing length 6–32 mm.

Age. From Early Permian to Late Jurassic (Europe and North America).

Classification of Permoplectoptera. Larvae and winged stages are associated for a single form only [see (A)]; other forms are described either as winged stages, or...
as larvae with uncertain characters. Thus, only artificial classification of Permoplectoptera can be used, with following groups distinguishable.

(A) On wings of both pairs CuA forms a triad; vein gemination is absent; Permian. Here belong: **Protereisma/g** [g: Protereisma Sellards 1907, typus P. permianum Sellards 1907 (design. orig.)]; **Protechma/g** [g: Protechma Sellards 1907: 349, typus P. acuminatum Sellards 1907 (design. orig.)]; **Prodomrites/g** [g: Prodomites Cockerell 1924: 136, typus Prodomus rectus Sellards 1907 (design. orig.)]; syn. obj.: **Prodomus Sellards 1907: 349** (non Perdomus Distant 1904); **Bantisca/g** [g: Bantisca Sellards 1907: 349, typus B. elongata Sellards 1907 (design. orig.)]; **Rekter/g** [g: Rekter Sellards 1907: 349, typus R. arcuatus Sellards 1907 (design. orig.)].

(B) On wings of both pairs CuA is non-branched; vein gemination is absent; Permian. Here belong: **Misthodotes/g** [f: Misthodotidae Tillyard 1932: 260, g: Misthodotes Sellards 1909: 151, typus Dromus obtusus Sellards 1907 (design. orig.)]; syn. obj.: **Dromeus Sellards 1907: 257** (non Dromeus Reiche 1854); **Eudoter/g** [f: Eudoteridae Demoulin 1954f: 553, g: Eudeter Tillyard 1936b: 443, typus E. delicatulus Tillyard 1936 (design. orig.)], regarded as a generic synonym of Misthodotes (Carpenter 1979: 237). Other species: biguttatus Tillyard 1932 **[Misthodotes]**, edmunds Carpenter 1979 **[Protereisma]**, insigne Tillyard 1932 **[Protereisma]**, latum Sellards 1907 **[Protereisma]**, minus Sellards 1907 **[Protereisma]**, sellardsi Tillyard 1932 **[Protereisma]**, uralicum Zalessky 1947 **[Protereisma]**.

(D) Poorly preserved winged insects.

(D.1) Permian. **Loxophlebia/g** [g: Loxophlebia Martinov 1928: 8, typus L. apicalis Martinov 1928 (design. orig.)]. Permian, known as distal fragment of a wing, regarded as a generic synonym of Protereisma (Rohdendorf 1957: 76). Other species: rossenrayensis Guthori 1967 **[Protereisma]**.


(E) Larvae with unknown wing venation.

(E.1) Permian. **Phthartus/g** [see above, Protereisma/l=Phthartus/g]. Originally the genus Phthartus was described basing on 3 specimens deposited in Kazan’ University – 2 syntypes of Ph. netshaevi Handlirsch 1914 (16–17 mm long) and holotype of Ph. rossicus Handlirsch 1904 (24 mm long); each specimen represents a reverse replica of dorsal side of body, lacks cuticle or pigmentation and locates at a bottom of an ovoid concavity on a separate stone. Lectotype of Ph. netshaevi (designated here) is a larger specimen (body 17 mm, caudalii 5 mm) (Fig.14:C). All three specimens are conspecific (Kluge & Sinitshenkova 2002). In the former descriptions and reconstruction by Handlirsch (1904, 1906–1908, 1925) it was stated that Phthartus had wing buds directed posteriorly, tergalii attached ventrally, stick-like and setose; caudalii covered by setae on all sides. Basing on these descriptions, some authors concluded that initial position of insect wings is posterior rather than lateral, that mayfly tergalii originated from ventral limbs, and that most primitive recent mayflies are Pinnatitergaliae, whose larval cerci have setae on both sides. Re-examination of the fossils revealed the following: in all three specimens wing buds are not preserved at all (that is strange, because moso- and metanota of all three specimens are well-preserved, each with distinct posterior scutal protuberances and scutellum characteristic for a wing-bearing segment); tergalii are attached not ventrally, but to posterior-lateral angles of segment, and probably are lamellate and rugose (so as look being stick-like and pectinate); caudalii have primary swimming setation only (Kluge & Studemann & Landolt & Gonser 1995; Kluge & Sinitshenkova 2002). On the place where a replic of the head should be, each specimen has a sharp impression of an unusual form.

Other Permian larvae are: **Jarmila/g** [f: Jarmilidae Demoulin 1970b: 7; g: Jarmila Demoulin 1970b: 7, typus...
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\[ \text{J. elongata} \text{ Demoulin 1970 (design. orig.)} \]


\[ \text{E.2} \text{ Triassic. Mesoplectopteron/fg} \text{ [F: Mesoplectopterinae Demoulin 1955g: 345; g: Mesoplectopteron Handlirsch 1918, typus M. longipes Handlirsch 1918: 112 (design. orig.)].} \]

\[ \text{Material examined: netshevi [Phtharthus] and rossicus [Ph.];} \]

\[ \text{or} \text{ Behningia Chen 1958.} \]

\[ \text{Ephemeroptera sensu stricto, or} \text{ Ephemeroptera/fg3} \text{ (Panephemeroptera Euphemeroptera Euplectoptera) (Figs 3–13; 15–106).} \]

\[ \text{Nomen hierarchicum: Ephemera/fg3 (sine Phtharthus; incl. Prosopistoma).} \]

\[ \text{Nomen circumscriptum univocum:} \]

\[ \text{Ephemeroptera Tillyard 1932: 267 (non Euplectoptera Fischer 1853).} \]

\[ \text{Nomina circumscribentia non-univoca (in circumscription matching also Panephemeroptera and Euphemeroptera):} \]

\[ \text{– Anisoptera} \text{ Stephens 1835: 53;} \]

\[ \text{– Plecoptera} \text{ Packard 1886: 808;} \]

\[ \text{– Ephemeroptera} \text{ Hyatt & Arms 1891: 13;} \]

\[ \text{– Plectoptera adelphica} \text{ Crampton 1916: 305;} \]

\[ \text{– Archipterygota} \text{ Börner 1909: 121;} \]

\[ \text{– Prometabola} \text{ Chen 1958.} \]

\[ \text{In circumscription exactly matches:} \]

\[ \text{– subordo Euplecoptera Tillyard 1932: 267;} \]

\[ \text{– Euplecoptera, or Ephemera/fg3} \text{ Kluge 2000: 245.} \]

\[ \text{In circumscription non-univocally matches following taxa} \]

\[ \text{– each of which also matches Euphemeroptera and Panephemeroptera):} \]

\[ \text{– gen. Ephemera Linnaeus 1758: 546;} \]

\[ \text{– natio Ephemeraeades: Billberg 1820: 97;} \]

\[ \text{– tribus Ephemeredes: Leach 1815: 137;} \]

\[ \text{– fam. Ephemereidae Laterreille 1810: 273;} \]

\[ \text{– fam. Ephemeronia: Burmeister 1829: 20;} \]

\[ \text{– fam. Ephemeroptera: Stephens 1835: 54;} \]

\[ \text{– sectio Anisoptera Stephens 1835: 53;} \]

\[ \text{– subordo Ephemera: Packard 1883: 192;} \]

\[ \text{–ordo Ephemera: Haeckel 1866;} \]

\[ \text{–ordo Ephemeroidea: Brauer 1885: 353;} \]

\[ \text{–ordo Plectoptera Packard 1886: 808;} \]

\[ \text{–ordo Ephemeroptera Hyatt & Arms 1891: 13;} \]

\[ \text{–ordo Agnatha: auct. (non Agnathes Cuvier 1798);} \]

\[ \text{– sectio Plectopteradelphia Crampton 1916: 305;} \]

\[ \text{– supersectio Archipterygota Börner 1909: 121;} \]

\[ \text{–cohors Prometabola Chen 1958.} \]

\[ \text{References.} \text{ Tillyard 1932: @*;} \]

\[ \text{– Tshernova 1962b: @*;} \]

\[ \text{– Kluge 2000: @*.} \]

\[ \text{Characters of unclear phylogenetic status.} \]

\[ \text{(1) Anteromotoric: hind wings are diminished, coupled with fore ones and modified in following manner: hind wing veins RA, RS and MA have a common stem [instead of the stem RS+MA separated from RA on fore wing – see Euphemeroptera (2)]; RS forms a single triad [instead of three successive triads of fore wing – see Euphemeroptera (3)], thus hind wing has maximum three simple triads alternating as concave and convex – RS, MA and MP (FIG.7:D). Hind wing length is subequal or less than a half of fore wing length. At flight hind and fore wings of each side couple because costal margin of hind wing is bent dorsally and basitomal margin of fore wing is bent ventrally. Thus, a functional diptery is present. In connection with this, fore wing is triangular, with tornus expressed (the same independently appeared in other anteromotoric Pterygota). As tornus of fore wing has different position in different Euplectoptera [see Posteritorna (1) and Anteritorna (1) below], its independent origin can be assumed, as well as independent shortening of hind wing. In various taxa among Euplectoptera hind wings undergone further reduction up to complete disappearance (see Index of characters [2.2.59]).} \]

\[ \text{(2) Tergalii [see Euphemeroptera (4)] of abdominal segments VIII–IX are lost, thus tergali are present only on segments I–VII or only on some of them. Pattern of this character is not quite clear, as larvae of many Permoplectoptera are unknown.} \]

\[ \text{Size.} \text{ Fore wing length 2–40 mm.} \]

\[ \text{Age and distribution.} \text{ From Jurassic (see Euse-} \]

\[ \text{tiura INCERTAE SEDIS, Fossoriae INC. SED. and} \]

\[ \text{Anteritorna INC. SED.) – till Recent; world-wide.} \]

\[ \text{Some Triassic fossils were attributed to Euplectopteran genera Mesoneta, Mesobaetis and Archaeo-} \]

\[ \text{beňingia without enough ground (see below, "Other species of Euphemeroptera INCERTAE SEDIS" and "Euarthropoda INCERTAE SEDIS", pp. 360, 361). Reliable fossils of Triassic Euplectoptera are unknown.} \]

\[ \text{Euplectoptera are divided into Posteritorna (Chapter IV) and Anteritorna (Chapters V–VII: p.71). Some fossil mayflies have uncertain systematic position (see Appendix: p.356).} \]
Figure 14. Palaeozoic mayflies.

A – Triplosoba/fg* pulchella [Blanchardia], reconstruction of adult (based on description by Carpenter 1963).

B – Protereisma/fg latum [Protereisma], hind wing (based on figure and photograph by Carpenter 1933).

C – lectotypus of Phtharthus netshaevi, larva.

D – Protereisma/fg americana [Kukalova], reconstruction of larva (based on photograph of holotype in Kukalova 1968 and Carpenter 1979 and description by Carpenter 1979).