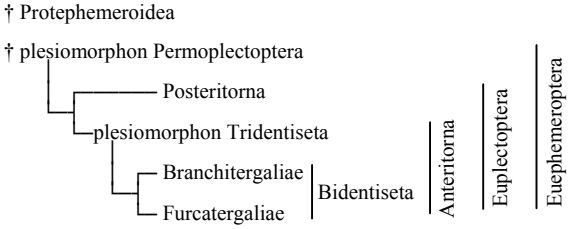
SPECIAL PART

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:



Below, following classification of mayflies is given:

{1} Panephemeroptera, or Ephemeroptera s.l., or Ephemera/fg1
{1.1} Protephemeroidea, or Triplosoba/fg1
{1.2} Euephemeroptera, or Ephemeroptera s.l., or Ephemera/fg2
{1.2.1} Permoplectoptera, or Protereisma/f1=Phtharthus/g1
{1.2.2} Euplectoptera, or Ephemeroptera s.str., or Ephemera/fg3

{1} **Panephemeroptera** or **Ephemeroptera** sensu latissimo, or **Ephemera/fg1**

(Figs 3–106)

Nomen hierarchicum: **Ephemera/fg1** (incl. *Triplosoba*) [f: Ephemerinae Latreille 1810: 273; g: *Ephemera* Linnaeus 1758: 546, typus *E. vulgata* Linnaeus 1758 (design. Latreille 1810)].
Nomina circumscribentia univoca:
— **Panephemeroptera** Crampton 1928: 85;
— **Ephemeropteria** Crampton 1938: 170;
— **Ephemeropteroidea** Rohdendorf 1968: 61.
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 Ephemeropteria Crampton 1938: 170;
— superordo Ephemeroptera: Martynov 1938: 32;
— superordo Ephemeropteroidea Rohdendorf 1968: 61;
— superordo Ephemeridea: Rasnitsyn 2002: 86;
— cohors Ephemeriformes: Rohdendorf 1977: 20;
— sectio Ephemerata: Boudreaux 1979: 196;
— subclassis Ephemeroidea: Handlirsch 1906: 37;
— Panephemeroptera, or Ephemera/fg1: Kluge 2000: 241.
In circumscription non-univocally matches taxa listed below, under Euplectoptera.

References. Martynov 1938: ⊕*; – Tshernova 1962b: ⊕*; – Kluge 2000: ⊕*; – Rasnitsyn 2002: ⊕*.

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 Protorrhynchota 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 Panephemeroptera 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 RSa_1 and RSa_2 and convex iRSa between them (the same in Odonatoptera, but in contrast to Protorrhynchota). MP [concave – see (3)] forms a triad of concave MP_1 and MP_2 and convex iMP. Euplectoptera have also triads formed by RSa_2 and MA (FIGS 7: C, 14:B). Only in extremely specialized representatives of Euplectoptera some of these veins are lost.

Plesiomorphy of Panephemeroptera. 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.

Panephemeroptera are divided into Protephemeroidea and Euephemeroptera.

{1.1} Extinct taxon **Protephemeroidea**, or **Triplosoba/fg(1)**

(Panephemeroptera Protephemeroidea)

(Fig. 14:A)

Nomen hierarchicum: **Triplosoba/fg(1)** [f: Triplosobidae Handlirsch 1906: 312; g: *Triplosoba* Handlirsch 1906: 312, typus *Blanchardia pulchella* Brongniart 1893 (monotypy); syn. obj.: ***Blanchardia*** Brongniart 1893: 325 (non *Blanchardia* Castelnau 1875)].

Nomina circumscribentia:
— **Protephemeroidea** Handlirsch 1906;
— **Protephemerida** Krausse & Wolff 1919;
— **Protephemeroptera** Crampton 1928;
— **Protephemerodea** Hamilton 1972.

In circumscription matches:
— gen. *Blanchardia* Brongniart 1893: 325 (nom. praeocc.);
— gen. *Triplosoba* Handlirsch 1906: 312;
— subfam. Triplosobinae: Demoulin 1956b: 7;
— fam. Troplosobidae Handlirsch 1906: 312;
— superfam. Triplosoboidea: Demoulin 1956b: 7;
— ordo Protephemeroidea Handlirsch 1906: 311;
— ordo Protephemerida Krausse & Wolff 1919: 156;
— ordo Protephemeroptera Crampton 1928: 83;
— ordo Protephemerodea Hamilton 1972: 146;
— Protephemeroidea, or Triplosoba/fg1: Kluge 2000: 242.

Monospecific taxon.

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

Characters of unclear phylogenetic status.

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

(2) RSa_2 is non-branched (probably on wings of both pairs, but for certain known for hind wings only – FIG.14:A) (in contrast to many Euephemeroptera).

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

Size. Fore wing length more than 21 mm.

Age. Carboniferous (France).

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

Material examined: –.

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{1.2} **Euephemeroptera**, or **Ephemeroptera** sensu lato, or **Ephemera/fg2**

(Panephemeroptera Euephemeroptera)

(Figs 3–13; 14:B–D; 15–106)

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

Nomen circumscribens univocum:
— **Euephemeroptera** Kluge 2000: 242.

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

In circumscription exactly matches:
— subordo Ephemerina: Tshernova 1980: 31;
— ordo Plectoptera: Handlirsch 1906: 37;
— ordo Ephemerida: Handlirsch 1919: 63 [573];
— ordo Ephemeroptera: Krausse & Wolff 1919: 157;
— Euephemeroptera, or Ephemera/fg2: Kluge 2000: 242.

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

References. Tshernova 1962b: ⊕*; – Carpenter 1963: ♂ ⊕*; – Kluge 2000: ♂ ⊕*; – Kluge & Sinitshenkova 2002: ♂ ⊕*.

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 Protephemeroidea 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 dorsad-anteriad 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 Protephemeroidea); 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 RSa_2 [concave – see Panephemeroptera (4)] forms a triad of concave RSa_2' and RSa_2'' and convex $iRSa_2$ 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 RSa_2' and $iRSa_2$ secondarily become intercalaries or lost (see Index of characters [2.2.37]).

(4) On wings of both pairs MA [convex – see Panephemeroptera (3)] forms a triad of convex MA_1 and MA_2 and concave iMA between them (FIG.7:C–D). This branching of MA secondary disappears on vestigial hind winds 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 flipper. As larvae of other Panephemeroptera are unknown, it is unclear if this specialization is an autapomorphy of Euephemeroptera or an autapomorphy 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 Panephemeroptera are unknown for certain, it is unclear, if the presence of tergalii is a character of Euephemeroptera or of a larger taxon; if proceed from the assumption that tergalii are serial homologues of wings, their presence is a plesiomorphy. In various Euephemeroptera 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. Permian (see Permoplectoptera) – Recent; world-wide.

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

{1.2.1} † Plesimorphon **Permoplectoptera**, or **Protereisma/f1=Phtharthus/g1**

(Panephemeroptera Euephemeroptera 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:

— **Protereismephemeridae** Sellards 1907: 345;

— **Permoplectoptera** Tillyard 1932: 117.

In circumscription matches:

— fam. Protereismephemeridae 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.

References. Sellards 1907: ⊕; – Tillyard 1932: ⊕; – Carpenter 1933: ⊕; – Kukalova 1968: ⦸; – Tshernova 1970: ⊕; – Carpenter 1979: ⦸ ⊕.

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* [*Kukalova*], 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/fg** [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.)]; **Prodromites/g** [g: *Prodromites* Cockerell 1924: 136, typus *Prodromus rectus* Sellards 1907 (design. orig.); syn. obj.: ***Prodromus*** Sellards 1907: 349 (non *Prodromus* 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.); syn. obj.: ***Recter*** Sellards 1909: 151]; **Pinctodia/g** [g: *Pinctodia* Sellards 1907: 352, typus *P. curta* Sellards 1907 (design. orig.)]; **Mecus/g** [g: *Mecus* Sellards 1909: 151, typus *Scopus gracilis* Sellards 1907 (design. orig.); syn. obj.: ***Scopus*** Sellards 1907: 352 (non *Scopus* Brisson 1760; nec Oken 1809; nec Scudder 1882)] (all these names are regarded as generic synonyms by Tillyard 1932: 244); **Kukalova/fg** [f: Kukalovidae Demoulin 1970b: 6; g: *Kukalova* Demoulin 1970b: 6, typus *K. americana* Demoulin 1970 (design. orig.)], known as larvae with well-preserved venation on wing buds (Carpenter 1979). Other species: *directum* Carpenter 1979 [*Protereisma*], *insigne* Tillyard 1932 [*Protereisma*], *latum* Sellards 1907 [*Protereisma*], *minus* Sellards 1907 [*Protereisma*], *sellardsi* Tillyard 1932 [*Protereisma*], *uralicum* Zalessky 1947 [*Protereisma*].

(B) On wings of both pairs CuA is non-branched; vein gemination is absent; Permian. Here belong: **Misthodotes/fg** [f: Misthodotidae Tillyard 1932: 260; g: *Misthodotes* Sellards 1909: 151, typus *Dromeus obtusus* Sellards 1907 (design. orig.); syn. obj.: ***Dromeus*** Sellards 1907: 257 (non *Dromeus* Reiche 1854)]; **Eudoter/fg** [f: Eudoteridae Demoulin 1954f: 553; g: *Eudoter* 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*], *edmundsi* Carpenter 1979 [*Misthodotes*], *ovalis* Tillyard 1932 [*Misthodotes*], *sharovi* Tshernova 1965 [*Misthodotes*], *stapfi* Kinzelbach & Lutz 1984 [*Misthodotes*], *zalesskyi* Tshernova 1965 [*Misthodotes*]. Adults of *sharovi* [*M.*] have mayfly features (wing venation of *Misthodotes*-type and three caudalii), but at the same time have unusually elongate mouth apparatus of unclear structure resembling that of Protorrhynchota.

(C) At least on hind wing CuA forms a triad, CuP is sinuous, and veins geminate forming pairs $RSp+MA_1$ and $iMP+MP_2$; Permian. This is **Palingeniopsis/fg** [f: Palingeniopsidae Martynov 1938: 35; g: *Palingeniopsis* Martynov 1932: 10, typus *P. praecox* Martynov 1932 (design. orig.)]. This taxon known as a single wing, was regarded to be related with *Palingenia* and some other Recent taxa which also have CuP curvation and vein gemination (Martynov 1932, Demoulin 1958, Tshernova 1980). Actually such kind of gemination occurs in non-related taxa (see Index of characters [2.2.41] and [2.2.44]); CuP of *Palingeniopsis* is curved in opposite direction than in Fimbriatotergaliae.

(D) Poorly preserved winged insects.

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

(D.2) Jurassic. **Mesephemera/fg** [f: Mesephemeridae Lameere 1917: 47; g: *Mesephemera* Handlirsch 1906: 600, typus *Ephemera procera* Hagen 1862 (design. Hubbard 1981: 69)]; redescribed by Demoulin 1955i. Other formal species (according to Demoulin 1955i): *lithophilus* Germar 1842 [*Tineites*], *palaeon* Weyenbergh 1874 [*Anomalon*], *prisca* Germar 1839 [*Sciaria*], *speciosa* Oppenheim 1888 [*Ephemera*] nom. praeocc., *weyenberghi* Handlirsch 1906 [*Mesephemera*].

(E) Larvae with unknown wing venation.

(E.1) Permian. **Phtharthus/g** [see above, Protereisma/f1=Phtharthus/g1]. Originally the genus *Phtharthus* was described basing on 3 specimens deposted in Kazan' University – 2 syntypes of *Ph. netshaevi* Handlirsch 1904 (16-17 mm long) and holotype of Ph. rossicus Handlirsch 1904 (24 mm long); each specimen represents a reverse replic 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 *Phtharthus* 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 postrior 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 look as 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/fg** [f: Jarmilidae Demoulin 1970b: 7; g: Jarmila Demoulin 1970b: 7, typus

J. elongata Demoulin 1970 (design. orig.)]; **Oboriphlebia/fg** [f: Oboriphlebiidae Hubbard & Kukalova-Peck 1980: 29; g: *Oboriphlebia* Hubbard & Kukalova-Peck 1980: 29, typus *Kukalova moravica* Demoulin 1970 (design. orig.)]. Other species: *tertia* Hubbard & Kukalova-Peck 1980 [*Oboriphlebia*], *quarta* Hubbard & Kukalova-Peck 1980 [*Oboriphlebia*], *quinta* Hubbard & Kukalova-Peck 1980 [*Oboriphlebia*]. Other specimen: larval paratype of *sharovi* Tshernova 1965 [*Misthodotes*], possibly conspecific with the type specimens of *Phtharthus*.

(E.2) Triassic. **Mesoplectopteron/fg** [f: Mesoplectopterinae Demoulin 1955g: 345; g: *Mesoplectopteron* Handlirsch 1918, typus *M. longipes* Handlirsch 1918: 112 (design. orig.)].

Material examined: *netshaevi* [*Phtharthus*] and *rossicus* [*Ph.*]): ♉ (Kazan. Univ.); *sharovi* [*Misthodotes*]: ⊕ (Paleontol. Inst.); larva ascribed to *sharovi* [*M.*]: ♉ (Paleontol. Inst.); *zalesskyi* [*M.*]: ⊕ (Paleontol. Inst.).

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{1.2.2} **Euplectoptera**, or **Ephemeroptera** sensu srticto, or **Ephemera/fg3**

(Panephemeroptera Euephemeroptera Euplectoptera)

(Figs 3–13; 15–106)

Nomen hierarchicum: **Ephemera/fg3** (sine *Phtharthus*; incl. *Prosopistoma*).

Nomen circumscribens univocum:

— **Euplectoptera** Tillyard 1932: 267 (non Euplectoptera Fischer 1853).

Nomina circumscribentia non-univoca (in circumscription matching also Panephemeroptera and Euephemeroptera):

— **Anisoptera** Stephens 1835: 53;
— **Plectoptera** Packard 1886: 808;
— **Ephemeroptera** Hyatt & Arms 1891: 13;
— **Plectopteradelphia** Crampton 1916: 305;
— **Archipterygota** Börner 1909: 121;
— **Prometabola** Chen 1958.

In circumscription exactly matches:

— subordo Euplectoptera Tillyard 1932: 267;
— Euplectoptera, or Ephemera/fg3: Kluge 2000: 245.

In circumscription non-univocally matches following taxa (each of which also matches Euephemeroptera and Panephemeroptera):

— gen. *Ephemera* Linnaeus 1758: 546;
— natio Ephemeraedes: Billberg 1820: 97;
— tribus Ephemerides: Leach 1815: 137;
— fam. Ephemerinae Latreille 1810: 273;
— fam. Ephemerina: Burmeister 1829: 20;
— fam. Ephemeridae: Stephens 1835: 54;
— sectio Anisoptera Stephens 1835: 53;
— subordo Ephemerina: Packard 1883: 192;
— ordo Ephemerida: Haeckel 1866;
— ordo Ephemeridae: Brauer 1885: 353;
— ordo Plectoptera Packard 1886: 808;
— ordo Ephemeroptera Hyatt & Arms 1891: 13;
— ordo Agnatha: auct. (non Agnathes Cuvier 1798);
— sectio Plectopteradelphia Crampton 1916: 305;
— supersectio Archipterygota Börner 1909: 121;
— cohors Prometabola Chen 1958.

References. Tillyard 1932: ⊕*; – Tshernova 1962b: ⊕*; – Kluge 2000: ⊕*.

Characters of unclear phylogenetic status.

(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 Euephemeroptera (2)]; RS forms a single triad [instead of three successive triads of fore wing – see Euephemeroptera (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 basitornal 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]).

(2) Tergalii [see Euephemeroptera (4)] of abdominal segments VIII–IX are lost, thus tergalii 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.

Size. Fore wing length 2–40 mm.

Age and distribution. From Jurassic (see Eusetisura INCERTAE SEDIS, Fossoriae INC. SED. and Anteritorna INC. SED.) — till Recent; world-wide. Some Triassic fossils were attributed to Euplectopteran genera *Mesoneta*, *Mesobaetis* and *Archaeobehningia* without enough ground (see below, "Other species of Euephemeroptera INCERTAE SEDIS" and "Euarthropoda INCERTAE SEDIS", pp. 360, 361). Reliable fossils of Triassic Euplectoptera are unknown.

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).

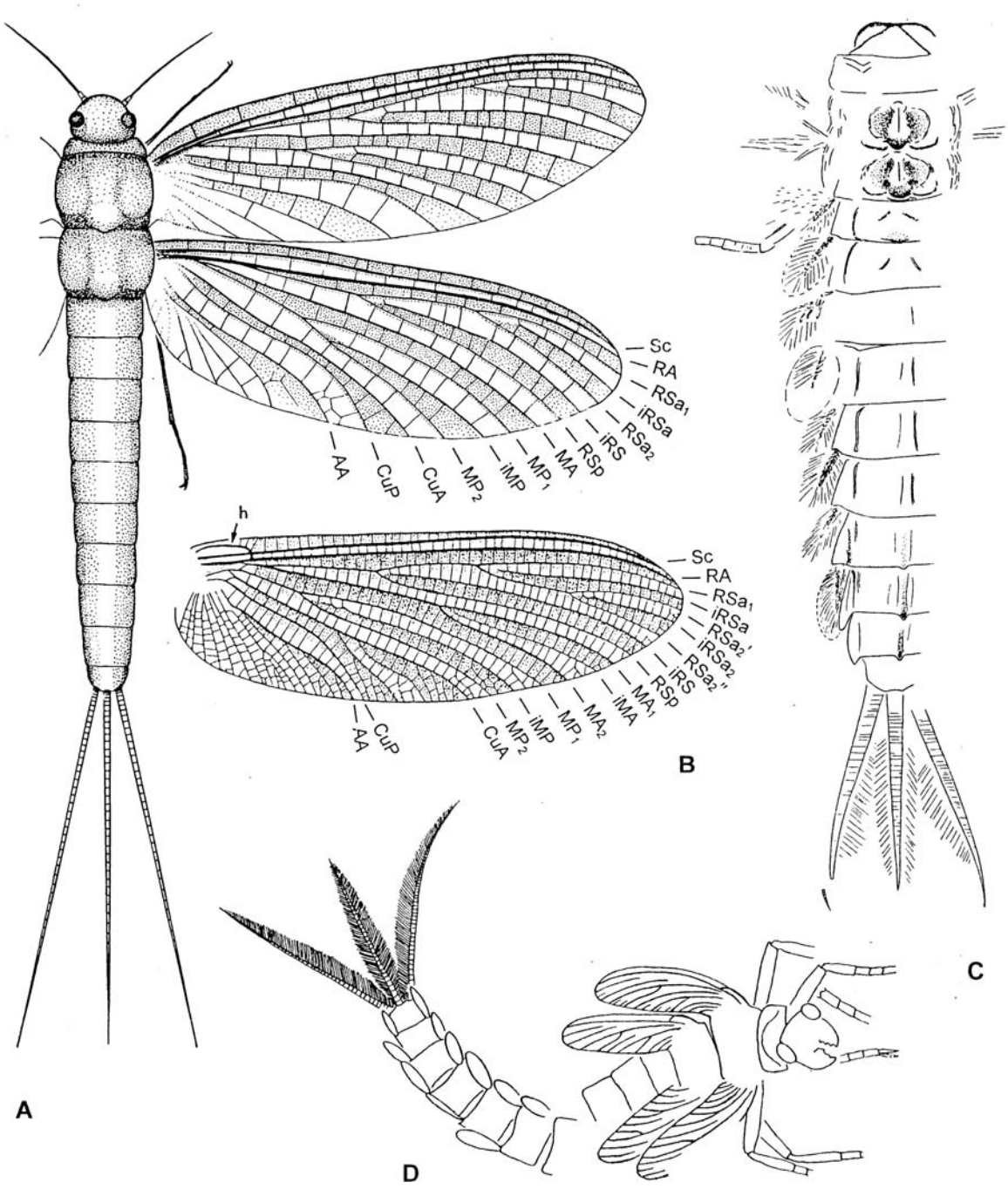

Figure 14. Palaeozoic mayflies.

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