

TREATISE ON INVERTEBRATE PALEONTOLOGY

*Prepared under Sponsorship of
The Geological Society of America, Inc.*

The Paleontological Society

The Palaeontographical Society

SEPM (The Sedimentological Society)

The Palaeontological Association

RAYMOND C. MOORE
Founder

ROGER L. KAESLER
Editor

ELIZABETH BROSIUS, JACK KEIM, JANE PRIESNER
Assistant Editors

Part R ARTHROPODA 4

Volume 3: Superclass Hexapoda

By F. M. CARPENTER

THE GEOLOGICAL SOCIETY OF AMERICA, INC.
and
THE UNIVERSITY OF KANSAS
BOULDER, COLORADO, and LAWRENCE, KANSAS
1992

tera, Diaphanopteroidea, Ephemeroptera, Protodonata, and Odonata. With the single exception of the Odonata, all of these are known as far back as the Late Carboniferous.

Order EPHEMEROPTERA

Hyatt & Arms, 1890

[Ephemeroptera HYATT & ARMS, 1890, p. 69] [=Protephemeroidea HANDLIRSCH, 1906b, p. 311; Aphelophlebia PIERCE, 1945, p. 4] [Several names have been proposed for this order. Ephemeroptera is the term consistently used now by specialists in the order.]

Delicate insects with short, filiform antennae; mouthparts vestigial in existing families, mandibulate and functional in Paleozoic families; compound eyes large, 3 ocelli present; abdomen slender, terminating in a pair of long, segmented cerci and usually with a long, median caudal process; legs usually weak in recent species, the mesothoracic and metathoracic pairs often much reduced, but all legs well developed in Paleozoic families; wings very delicate, with a complete set of all main veins in addition to intercalary veins (indicated by an I prefix) and crossveins; base of costal area supported in some families by a stout crossvein or a series of crossveins (costal brace; see Figs. 14,4a and 15,a); in all recent and Tertiary species, as well as those from the Mesozoic, hind wings much smaller than fore pair and in some genera completely absent; in known Paleozoic species, pairs of wings similar in size and venation; digestive tract modified to form aerostatic organ; reproductive ducts paired in both sexes. Nymphs aquatic, occurring in ponds and streams, usually with at least 7 pairs of abdominal tracheal gills; cerci and median caudal process present; mostly herbivorous. Postembryonic development slow, with 20 or more ecdyses and a single molt from winged subimago to imago. *U. Carb.—Holo.*

The Ephemeroptera is a relatively small order of about 2,000 species. Although basically primitive, the recent members are highly adapted to living in aquatic environments in the nymphal stages and to a very brief imaginal life. The nymphal gills are unusually large compared with those of other aquatic insects

and are capable of rapid movements, aiding the circulation of water. Nymphal development is slow, taking at least a few months and commonly as long as three years. In contrast, most imagoes live for only a few hours to a few days. The process of mating is hastened by swarming.

The earliest record of the Ephemeroptera is a single imago of *Triplosoba pulchella* (BRONGNIART) from the Upper Carboniferous of Commentry, France, but representatives of five extinct families, including nymphs as well as adults, are known from the Permian. The peak of diversity appears to have been reached in the Jurassic, from which nine families have been obtained, including the existing families Siphonuridae, Leptophlebiidae, Palingeniidae, Behningiidae, and possibly the Ephemerellidae. So far as known, the imagoes of all the Permian species had fully developed mouthparts with functional, dentate mandibles, normally developed legs, and similar fore and hind wings. These imagoes appear to be the most primitive of the known pterygote insects. The nymphs, however, were apparently as well adapted to an aquatic life as those now existing.

The classification of the Ephemeroptera has been discussed by several specialists in the order in recent years (TSHERNOVA, 1970; LANDA, 1979; McCAFFERTY & EDMUNDS, 1979; RIEK, 1979), mainly with reference to the existing families. There seems to be general agreement that division of the order into the suborders Permoplectoptera and Euplec- toptera, separating the Permian families from the later ones, as proposed by TILLYARD (1932b), is unsatisfactory. In the following account the sequence of families follows that of McCAFFERTY and EDMUNDS (1979) and TSHERNOVA (1970).

Family TRIPLOSOBIDAE Handlirsch, 1906

[Triplosobidae HANDLIRSCH, 1906b, p. 312]

Fore and hind wings apparently similar in form and venation; crossveins numerous; costal brace apparently absent; vein SC extending to wing apex; RS arising directly from

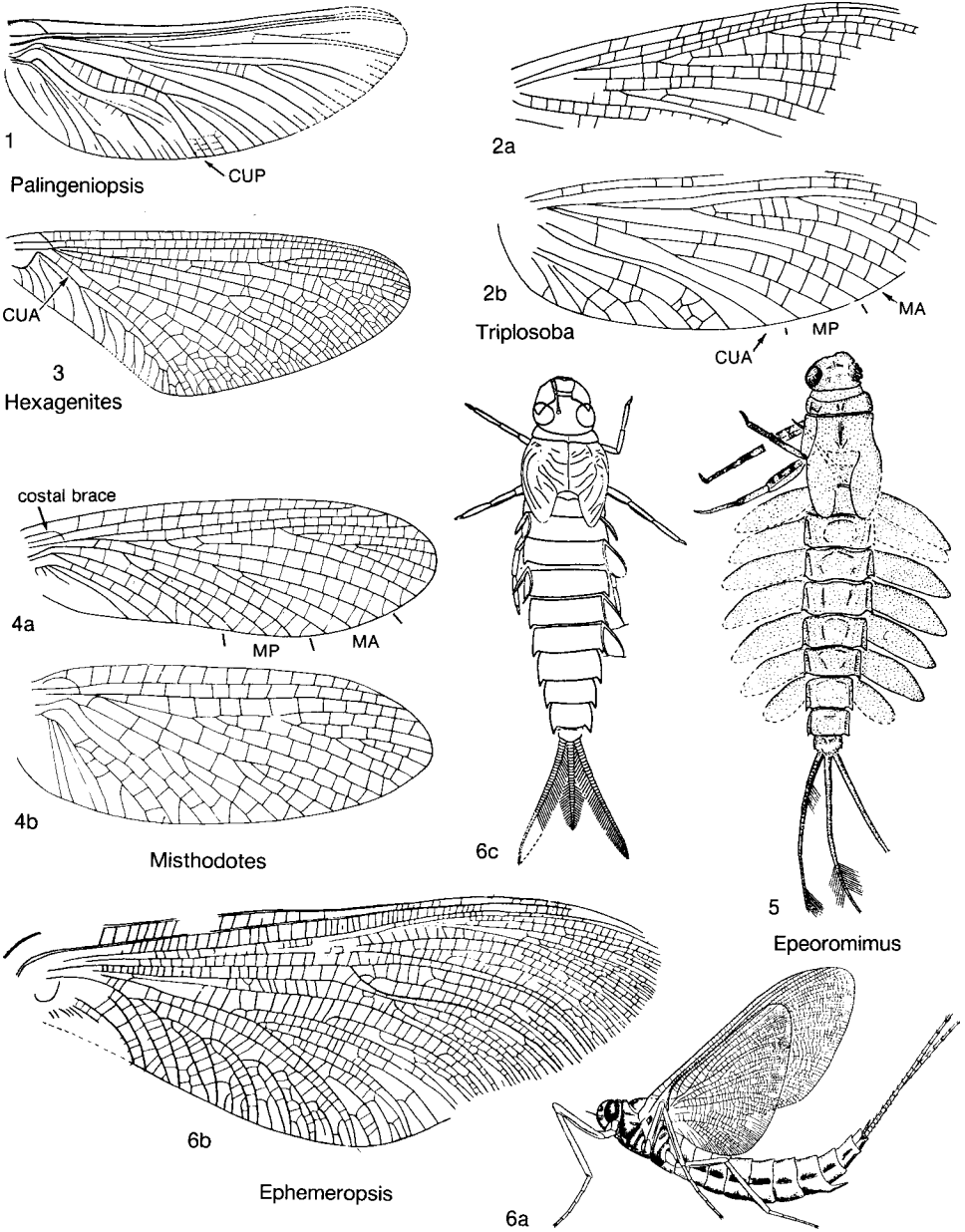


FIG. 14. Triplosobidae, Misthodoridae, Palingeniopsidae, Hexagenitidae, and Epeoromimidae (p. 20-24).

R, free from MA and including 2 intercalary veins; abdomen slender, with prominent cerci and a median caudal process. *U. Carb.*

Triplosoba HANDLIRSCH, 1906b, p. 312, *nom. subst. pro Blanchardia* BRONGNIART, 1893, p. 325, *non*

CASTELNAU, 1875 [**Blanchardia pulchella* BRONGNIART, 1893, p. 325; OD]. MA and CUA unbranched in both wings; MP branched. CARPENTER, 1963c. *U. Carb.*, Europe (France).— FIG. 14.2. **T. pulchella* (BRONGNIART); a, fore and b, hind wings, $\times 2.5$ (Carpenter, new).

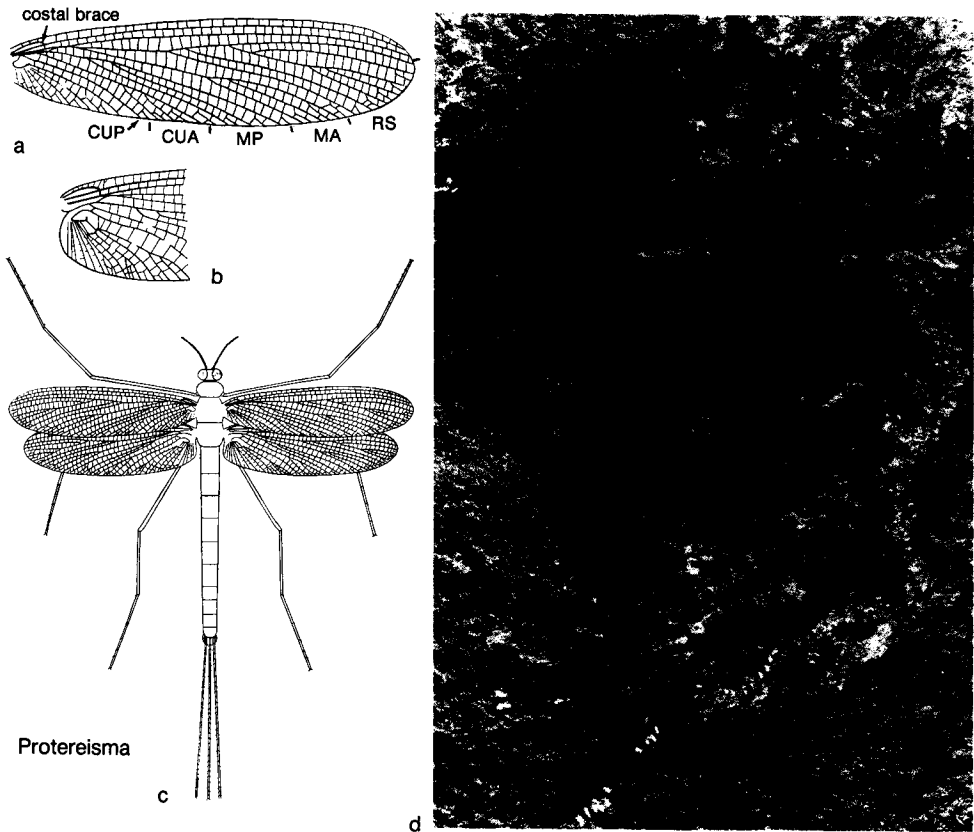


FIG. 15. Prottereismatidae (p. 21–22).

Family PROTTEREISMATIDAE Lameere, 1917

[*nom. correct.* TILLYARD, 1932b, ex Prottereismidae LAMEERE, 1917a, p. 45] [=Kukalovidae DEMOULIN, 1970b, p. 6]

Adults moderate to large in size. Wings elongate-oval; fore and hind wings similar in form and venation, hind pair only slightly shorter; crossveins numerous; costal brace strongly developed in both wings (Fig. 15, a); vein SC extending almost to wing apex; RS coalesced with MA immediately after its origin, and including 3 intercalary veins; MP and CUA each with a single triad; antennae short but longer than in existing mayflies; mandibles sclerotized and dentate; compound eyes large; legs very long and slender, with 5 tarsal segments; cerci and median caudal process elongate; males with prominent claspers. Nymphs with well-developed man-

dibles; legs subequal, with 5 tarsal segments; cerci and median caudal process well developed; abdomen with 9 pairs of tracheal gills; wing pads independent of each other, attached to thorax only along equivalent of the articular area of adult wings, projecting obliquely. *Perm.*

Prottereisma SELLARDS, 1907, p. 347 [**P. permianum*; OD] [=*Protechma* SELLARDS, 1907, p. 349 (type, *P. acuminatum*); *Prodromus* SELLARDS, 1907, p. 349 (type, *P. rectus*); *Bantiska* SELLARDS, 1907, p. 349 (type, *B. elongata*); *Pinctodia* SELLARDS, 1907, p. 352 (type, *P. curta*); *Recter* SELLARDS, 1909, p. 151, *pro Recter* SELLARDS, 1907, p. 349 (type, *R. arcuatus*); *Esca* SELLARDS, 1909, p. 151 (type, *Therates planus* SELLARDS, 1907, p. 354); *Mecur* SELLARDS, 1909, p. 151 (type, *Scopus gracilis* SELLARDS, 1907, p. 352); *Loxophlebia* MARTYNOV, 1928b, p. 8, *non* BUTLER, 1876 (type, *L. apicalis*)]. MP forked more deeply than RS. TILLYARD, 1932b; CAR-

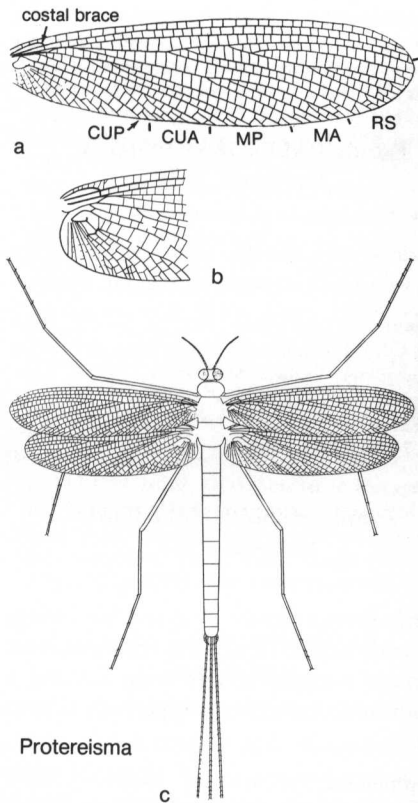


FIG. 15. Protoreismatidae (p. 21-22).

PENTER, 1933a, 1979; ROHDENDORF, 1962a; GUTHÖRL, 1965; DEMOULIN, 1970b. *Perm.*, USA (Kansas, Oklahoma), ?Europe (Germany).—FIG. 15, *a-c*. **P. permianum*, Kansas; *a*, fore wing, *b*, base of hind wing, both $\times 3.5$; *c*, reconstruction, dorsal view, $\times 1.5$ (all Carpenter, 1933a).—FIG. 15, *d*. *P. americanum* DEMOULIN, Oklahoma; photograph of nymph, dorsal view, $\times 5$ (Carpenter, new).

Family MISTHODOTIDAE Tillyard, 1932

[Misthodotidae TILLYARD, 1932b, p. 260] [=Eudoteridae DEMOULIN, 1954c, p. 561]

Adults small to moderate in size. Wings broadly oval; fore and hind wings similar in venation but hind wings distinctly broader; vein CUA unbranched, lacking a triad; cross-veins less numerous than in Protereismatidae; legs of moderate length; tarsi with 4 segments; cerci and median caudal process very long. Nymphs with 9 pairs of tracheal gills. *Perm.*

Misthodotes SELLARDS, 1909, p. 151, *nom. subst. pro Dromeus* SELLARDS, 1907, p. 351, *non* REICHE, 1854 [**Dromeus obtusus* SELLARDS, 1907, p. 351; OD] [=*Eudoter* TILLYARD, 1936, p. 443 (type, *E. delicatulus*)]. Posterior margin of hind wing strongly convex. LAMEERE, 1917a; TILLYARD, 1932b; CARPENTER, 1933a, 1979; DEMOULIN, 1954c; TSHERNOVA, 1965. *Perm.*, USA (Kansas, Oklahoma), USSR (Asian RSFSR).—FIG. 14, *4a*. **M. obtusus* (SELLARDS), Kansas; fore wing, $\times 5.5$ (Carpenter, 1933a).—FIG. 14, *4b*. *M. edmundsi* CARPENTER, Oklahoma; hind wing, $\times 5.5$ (Carpenter, 1979).

Family JARMILIDAE Demoulin, 1970

[Jarmilidae DEMOULIN, 1970b, p. 7]

Little-known family (nymph only); mesothorax and metathorax nearly twice as broad as long; mesonotum larger than metanotum; tracheal gills narrow and elongate. *Perm.*

Jarmila DEMOULIN, 1970b, p. 7 [**J. elongata*; OD]. Diagnostic characters same as for family. *Perm.*, Europe (Czechoslovakia).

Family OBORIPHLEBIIDAE Hubbard & Kukalová-Peck, 1980

[Oboriphlebiidae HUBBARD & KUKALOVÁ-PECK, 1980, p. 29]

Little-known family (nymph only); mesothorax slightly larger than metathorax; wing pads divergent. *Perm.*

Oboriphlebia HUBBARD & KUKALOVÁ-PECK, 1980, p. 30 [**O. tertia*; OD]. Diagnostic characters same as for family. *Perm.*, Europe (Czechoslovakia).

Family PALINGENIOPSIDAE Martynov, 1938

[Palingeniopsidae MARTYNOV, 1938b, p. 35]

Little-known family, based on hind wing only; vein CUP strongly sigmoidal. *Perm.*

Palingeniopsis MARTYNOV, 1932, p. 10 [**P. praecox*; OD]. Little-known genus; intercalary veins incompletely known. MARTYNOV, 1938b; ROHDENDORF, 1962a. *Perm.*, USSR (European RSFSR).—FIG. 14, *1*. **P. praecox*; hind wing, $\times 1.7$ (Martynov, 1932).

Family MESEPHEMERIDAE Lameere, 1917

[Mesephemeridae LAMEERE, 1917a, p. 47]

Little-known family. Fore and hind wings apparently similar in size and venation; inner and outer margins of fore wing forming a smooth curve; costal brace apparently absent.

Jur.

Mesephemera HANDLIRSCH, 1906b, p. 600 [**Tineites lithophilus* GERMAR, 1842, p. 88; SD CARPENTER, herein]. Little-known genus; hind wings apparently at least as broad as fore wings. CARPENTER, 1932a; DEMOULIN, 1955b; TSHERNOVA, 1970. *Jur.*, Europe (Germany).

Family HEXAGENITIDAE Lameere, 1917

[*nom. transl.* DEMOULIN, 1954c, p. 566, *ex* Hexagenitinae LAMEERE, 1917a, p. 74] [=Paedephemeridae LAMEERE, 1917a, p. 49; Ephemeropsidae COCKERELL, 1927a, p. 1; Stenodicranidae DEMOULIN, 1954c, p. 567]

Mayflies of moderate to very large size. Fore wing triangular owing to well-developed tornus of hind margin; vein CUA of fore wing forked, one of its branches with a series of loop-shaped veinlets leading to wing margin. Nymphs with 7 pairs of gills along sides of abdomen. *Jur.*—*Cret.*

Hexagenites SCUDDER, 1880, p. 6 [**H. weyenberghi*; OD; =*Ephemera cellulosa* HAGEN, 1862, p. 115] [=*Paedephemera* HANDLIRSCH, 1906b, p. 601 (type, *Ephemera multivenosa* OPPENHEIM, 1888, p. 225)]. Adults of moderate size. Fore wing about twice as long as wide; MA1 and MA2

- forming a symmetrical fork; few crossveins. CARPENTER, 1932a; TSHERNOVA, 1961; DEMOULIN, 1970c; TSHERNOVA & SINITSHENKOVA, 1974. *Jur.*, Europe (Germany).—FIG. 14,3. **H. weyenberghi*; fore wing, $\times 3.5$ (Carpenter, 1932a).
- Ephemeroopsis** EICHWALD, 1864, p. 21 [**E. tristalis*; OD] [= *Phacelobranchus* HANDLIRSCH, 1906b, p. 604 (type, *P. braueri*)]. Adults very large. Fore wing more than 2.5 times as long as its width; hind wing more than half as long as fore wing. PING, 1928; UENO, 1935; DEMOULIN, 1954a, 1956d; MESHKOVA, 1961; TSHERNOVA, 1961; SINITSHENKOVA, 1975. *Cret.*, USSR (Asian RSFSR).—FIG. 14,6. **E. tristalis*; *a*, restoration, $\times 0.8$ (Tshernova, 1961); *b*, fore wing, $\times 2.0$ (Tshernova & Sinitschenkova, 1974); *c*, nymph, restoration, dorsal view, $\times 2.0$ (Meshkova, 1961).
- Hexameropsis** TSHERNOVA & SINITSHENKOVA, 1974, p. 131 [**H. selini*; OD]. Similar to *Hexagenites*, but MA1 and MA2 forming asymmetrical fork; hind wing less than half length of fore wing. SINITSHENKOVA, 1975. *Cret.*, USSR (Ukraine), Africa (Algeria).
- Family SIPHLONURIDAE**
Banks, 1900
- [Siphonuridae BANKS, 1900, p. 246]
- Fore wings narrow and triangular; hind wings relatively large; crossveins numerous in both wings; vein CUA of fore wing connected to hind margin by several veinlets; forks of MP and CUA almost symmetrical. *Jur.*—*Holo.*
- Siphonurus** EATON, 1868, p. 89. DEMOULIN, 1968c. *Oligo.*, Europe (Baltic)—*Holo.*
- Baltameletus** DEMOULIN, 1968c, p. 238 [**B. oligocaenicus*; OD]. Little-known genus, based on subimago; apparently related to *Ameletus* (recent). *Oligo.*, Europe (Baltic).
- Balticophlebia** DEMOULIN, 1968c, p. 237 [**B. benigni*; OD]. Based on female imago; similar to *Chaquihua* (recent) but with hind wings more elongate. *Oligo.*, Europe (Baltic).
- Cronicus** EATON, 1871, p. 133 [**Baetis anomala* PICTET in PICTET & HAGEN, 1856, p. 75; OD]. Gonostyle of male subimago with 5 segments, the third about twice as long as the second and as long as segments 4 and 5 combined. DEMOULIN, 1955a, 1968c, 1974. *Oligo.*, Europe (Baltic).—FIG. 16,2. **C. anomalus* (PICTET); fore and hind wings and part of body, dorsal view, $\times 3.5$ (Demoulin, 1968c).
- Isonychia** EATON, 1871, p. 33. LEWIS, 1977b. *Oligo.*, USA (Montana)—*Holo.*
- Oligisca** DEMOULIN, 1970c, p. 6 [**Paedephemera schwertschlageri* HANDLIRSCH, 1906b, p. 602; OD]. Little-known genus, based on poorly preserved wing; similar to *Stackelbergisca*, but branches of CUA simple; MP with long branches. *Jur.*, Europe (Germany).
- Proameletus** SINITSHENKOVA, 1976, p. 86 [**P. caudata*; OD]. Imago: fore wing similar to that of *Oligisca* but with an intercalary vein between RS1 and RS2; median caudal process long, with 10 segments. Nymph: legs long and slender; 7 pairs of oval gills along abdomen. *Cret.*, USSR (Asian RSFSR).
- Siphurites** COCKERELL, 1923d, p. 170 [**S. explanatus*; OD]. Little-known genus, apparently related to *Murphyella* (recent). DEMOULIN, 1970d, 1974. *Oligo.*, USA (Colorado).
- Stackelbergisca** TSHERNOVA, 1967, p. 323 [**S. sibirica*; OD]. Imago: fore wing triangular; anal margin long; CUA straight and connected to wing margin by a series of veinlets; CUP slightly curved. Nymph: with 7 pairs of foliate gills along sides of abdomen. DEMOULIN, 1968a. *Jur.*, USSR (Asian RSFSR).—FIG. 16,3. **S. sibirica*; *a*, fore wing, *b*, nymph, dorsal view, both $\times 3.5$ (Tshernova, 1967).
- Family AMETROPODIDAE**
Bengtsson, 1913
- [Ametropodidae BENGTSSON, 1913, p. 305]
- Fore tarsi of male very long; hind tarsi with 4 segments; basal tarsal segment fused to tibia; fore wing with only 1 or 2 unattached cubital intercalaries; vein 1A of fore wing connected to hind margin by several veinlets. *Oligo.*—*Holo.*
- Ametropus** ALBARDA, 1878, p. 129. *Holo.*
- Brevitibia** DEMOULIN, 1968c, p. 245 [**B. intricans*; OD]. Similar to *Ametropus* (recent), with shorter median caudal process. *Oligo.*, Europe (Baltic).
- Metretopus** EATON, 1901, p. 253. DEMOULIN, 1968c. *Oligo.*, Europe (Baltic)—*Holo.*
- Siphloplecton** CLEMENS, 1915, p. 245. DEMOULIN, 1968c, 1970a. *Oligo.*, Europe (Baltic)—*Holo.*
- Family BAETIDAE** Leach, 1815
- [Baetidae LEACH, 1815, p. 137]
- Eyes of males divided; fore wing with veins IMA, MA2, IMP, and MP2 detached basally; hind wing reduced or absent; median caudal process absent. *Plio.*—*Holo.*
- Baetis** LEACH, 1815, p. 137. *Holo.*
- Cleon** LEACH, 1815, p. 137. [Generic assignment of fossil (nymph) doubtful.] RIEK, 1954b. *Plio.*, Australia (New South Wales)—*Holo.*

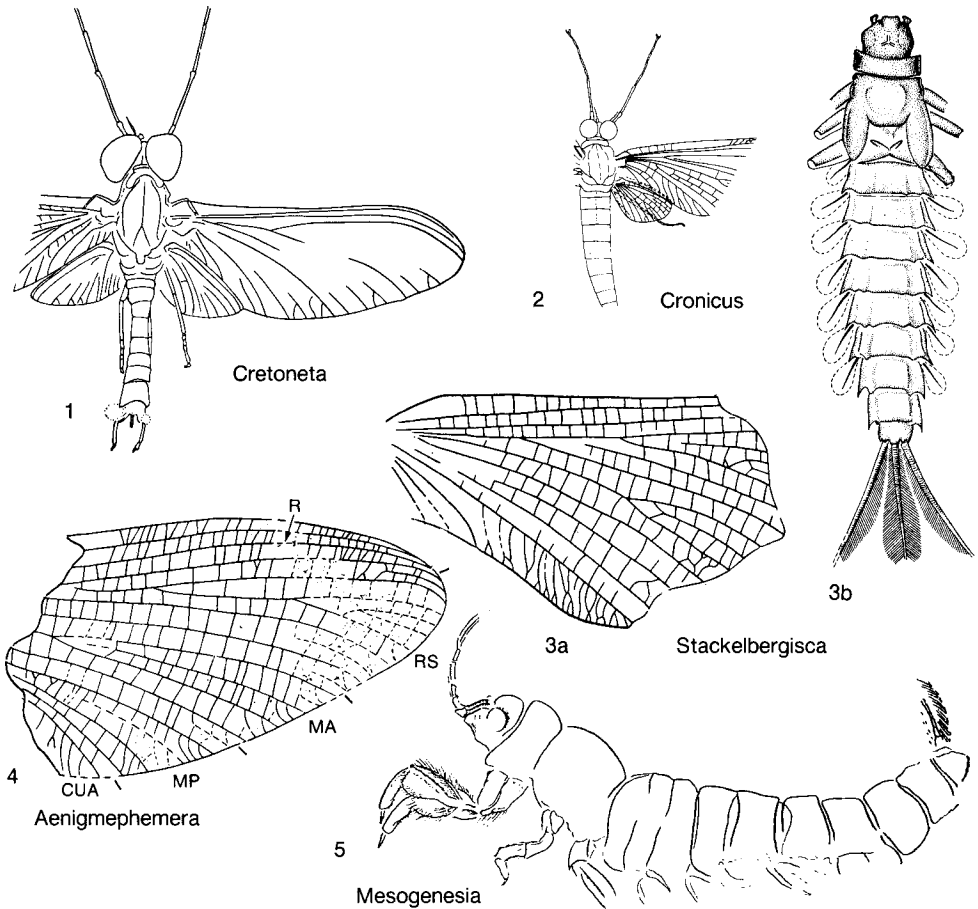


FIG. 16. Siphonuridae, Aenigmephemeridae, Leptophlebiidae, and Palingeniidae (p. 23–26).

Family EPEOROMIMIDAE

Tshernova, 1969

[Epeoromimidae TSHERNOVA, 1969, p. 154]

Known only from nymphs, apparently related to the Heptageniidae. Head and thorax short; abdomen elongate; legs thin and short; abdomen 3 times as long as thorax; fifth abdominal segment 2 or 3 times as wide as long; 7 pairs of gill plates along sides of abdomen. *Jur.*—*Cret.*

Epeoromimus TSHERNOVA, 1969, p. 155 [**E. kuzlauskasi*; OD]. Anterior margin of pronotum strongly concave; gill plates long and foliaceous. SINITSHENKOVA, 1976. *Jur.*—*Cret.*, USSR (Asian RSFSR).—FIG. 14,5. **E. kuzlauskasi*; dorsal view of nymph, $\times 5.5$ (Tshernova, 1969).

Family HEPTAGENIIDAE

Needham, 1901

[Heptageniidae NEEDHAM in NEEDHAM & BETTEN, 1901, p. 419]

Cubitus of fore wing with 2 pairs of intercalary veins; MP1 and MP2 forming symmetrical fork; hind tarsi with 5 segments; median caudal process absent. *Oligo.*—*Holo.*

Heptagenia WALSH, 1863, p. 197. DEMOULIN, 1968c, 1970a. *Oligo.*, Europe (Baltic)—*Holo.*

Cinygma EATON, 1885, p. 236. [Generic assignment of fossil doubtful.] DEMOULIN, 1968c. *Oligo.*, Europe (Baltic)—*Holo.*

Electrogenia DEMOULIN, 1956a, p. 95 [**E. dewalshbei*; OD]. MA of hind wing unbranched; crossveins dense over fore wing; third tarsi with first segment longer than second; gonostyle with 4 segments. *Oligo.*, Europe (Baltic).

- Miocoenogenia** TSHERNOVA, 1962, p. 943 [**M. gorbunovi*; OD]. Little-known genus, nymph only; similar to *Heptagenia* but with relatively small head; pronotum broad, with anterior angles projecting forward. *Mio.*, USSR (Asian RSFSR).
- Rhithrogena** EATON, 1881, p. 23. DEMOULIN, 1968c. *Oligo.*, Europe (Baltic)—*Holo.*
- Succinogenia** DEMOULIN, 1965, p. 151 [**S. larssoni*; OD]. Little-known genus, based on young nymph. *Oligo.*, Europe (Baltic).

Family AENIGMEPHEMERIDAE

Tshernova, 1968

[Aenigmephemeridae TSHERNOVA, 1968, p. 23]

Apparently related to the Heptageniidae. Fore wing narrow, inner and outer margins forming a smooth curve; longitudinal veins straight, almost equidistant from each other; fork of MA very deep. *Jur.*

- Aenigmephemera** TSHERNOVA, 1968, p. 23 [**A. demoulini*; OD]. Fore wing with forking of MA at level of origin of RS; 5 longitudinal veins between MA2 and CUA; crossveins numerous. DEMOULIN, 1969a. *Jur.*, USSR (Kazakh).—FIG. 16, 4. **A. demoulini*; fore wing, $\times 3$ (Tshernova, 1968).

Family LEPTOPHLEBIIDAE

Banks, 1900

[Leptophlebiidae BANKS, 1900, p. 246]

Eyes of male divided; 2 to 4 long intercalary veins between veins CUA and CUP; CUP usually strongly curved; median caudal process present. *Jur.—Holo.*

- Leptophlebia** WESTWOOD, 1840, p. 31. *Holo.*
- Atalophlebia** EATON, 1881, p. 193. ETHERIDGE & OLLIFF, 1890; RIEK, 1954b. *Plio.*, Australia (New South Wales)—*Holo.*
- Blasturophlebia** DEMOULIN, 1968c, p. 268 [**B. hirsuta*; OD]. Little-known genus, based on a subimaginal exuvium of a male. [Family assignment doubtful.] HUBBARD & SAVAGE, 1981. *Oligo.*, Europe (Baltic).
- Cretoneta** TSHERNOVA, 1971, p. 614 [**C. zherichini*; OD]. Fore wing with MA about half length of stem M; base of MP2 connected to MP1; cubital area very narrow; eyes of male not divided. HUBBARD & SAVAGE, 1981. *Cret.*, USSR (Asian RSFSR).—FIG. 16, 1. **C. zherichini*; dorsal view, male, $\times 10$ (Tshernova, 1971).
- Lepismophlebia** DEMOULIN, 1968b, p. 7 [**Lepisma platymera* SCUDDER, 1890, p. 102; OD]. Little-

- known nymph. [Family assignment doubtful.] DEMOULIN, 1956b. *Oligo.*, USA (Colorado).
- Mesoneta** BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 4 [**M. antiqua*; OD]. Little-known genus, nymph only. Head small, thorax very short; femur longer than tibia; 7 pairs of tracheal gills along sides of abdomen. TSHERNOVA, 1971; SINITSHENKOVA, 1976. *Jur.—Cret.*, USSR (Asian RSFSR).
- Paraleptophlebia** LESTAGE, 1917, p. 340 [= *Oligophlebia* DEMOULIN, 1965, p. 146 (type, *O. calliarcys*)]. DEMOULIN, 1968c, 1970a; HUBBARD & SAVAGE, 1981. *Oligo.*, Europe (Baltic)—*Holo.*
- Xenophlebia** DEMOULIN, 1968c, p. 267 [**X. aenigmatica*; OD]. Only male adult known. Forking of MA and MP in fore wing symmetrical; median caudal process absent. DEMOULIN, 1970a; HUBBARD & SAVAGE, 1981. *Oligo.*, Europe (Baltic).

Family EPHEMERELLIDAE

Klapálek, 1909

[Ephemerellidae KLAPÁLEK, 1909, p. 13]

Fore wing with 1 or 2 long intercalary veins between veins MP and CUA and usually with detached marginal intercalary veins; crossveins usually absent or very weak. *Jur.—Holo.*

- Ephemerella** WALSH, 1862, p. 377. *Holo.*
- Philolimnias** HONG, 1979, p. 336 [**P. sinica*; OD]. Similar to *Ephemerella* (recent), but costal area narrower and CUA1 with 5 branches. *Eoc.*, China (Liaoning).
- Turfanerella** DEMOULIN, 1954a, p. 324 [**Ephemeropsis tingi* PING, 1935, p. 107; OD]. Little-known genus, based on nymph. *Jur.*, China (Sichiang).

Family BEHNINGIIDAE

Motas & Bocasco, 1938

[Behningiidae MOTAS & BOCASCO, 1938, p. 25]

Legs of adults much reduced; forelegs of nymphs resembling palpi; middle and hind legs modified to protect the tracheal gills; gills ventral. *Jur.—Holo.*

- Behningia** LESTAGE, 1930, p. 436. *Holo.*
- Archaeobehningia** TSHERNOVA, 1977, p. 94 [**A. edmundsi*; OD]. Little-known genus, based on nymph. Similar to *Protobehningia* (recent) but with claws present on all tarsi, and forelegs not functionally part of trophi. *Jur.*, USSR (Asian RSFSR).

Family NEOEPHEMERIDAE Needham, 1935

[Neophemeridae NEEDHAM in NEEDHAM, TRAYER, & HSU, 1935, p. 288]

Adults resembling those of ephemerids, but crossveins in basal half of fore wing weak or atrophied; costal angle of hind wing acute. Nymphs as in caenids but gills operculate, fused medially. *Oligo.-Holo.*

Neophemera McDUNNOUGH, 1925, p. 168. *Holo.*
Potamanthellus LESTAGE, 1930, p. 120. LEWIS, 1977b. *Oligo.*, USA (Montana)—*Holo.*

Family EPHEMERIDAE Leach, 1815

[Ephemeridae LEACH, 1815, p. 137]

Legs well developed; veins MP2 and CUA abruptly diverging from MP1 basally; 1A unbranched but connected to hind margin of wing by at least 3 veinlets. *Oligo.-Holo.*

Ephemera LINNÉ, 1758, p. 546. COCKERELL, 1908e. *Oligo.*, USA (Colorado)—*Holo.*

Family POLYMITARCIDAE Banks, 1900

[Polymitarcidae BANKS, 1900, p. 246]

Adults as in Euthyplociidae (recent) but with veins MP2 and CUA strongly divergent from MP1 basally; middle and hind legs weakly developed. Nymphs with fossorial legs; gills dorsal. *Mio.-Holo.*

Ephoron WILLIAMSON, 1802, p. 71. *Holo.*
Asthenopodichnum THENIUS, 1979, p. 185 [**A. xylobiontum*; OD]. Trace fossils; burrows in fossil wood, resembling those now made by polymitarcid nymphs. *Mio.*, Europe (Austria).

Family PALINGENIIDAE Selys-Longchamps, 1888

[Palingeniidae SELYS-LONGCHAMPS, 1888, p. 147]

Main veins of fore wings arranged in pairs, converging at wing margin; crossveins numerous; forelegs of nymphs flattened and fossorial in nature; tibiae toothed. *Jur.-Holo.*

Palingenia BURMEISTER, 1839, p. 802. *Holo.*
Mesogenesia TSHERNOVA, 1977, p. 92 [**M. petersae*; OD]. Little-known genus, nymph only; similar to *Heterogenesia* (recent), with very short mandibles and lacking a distinct frontal process. *Jur.*, USSR (Asian RSFSR).—FIG. 16,5. **M.*

petersae; lateral view of nymph, $\times 7.5$ (Tshernova, 1977).

Family UNCERTAIN

The following genera, apparently belonging to the order Ephemeroptera, are too poorly known to permit assignment to families.

Aphelophlebodes PIERCE, 1945, p. 3 [**A. stocki*; OD]. Little-known genus, based on small fragment of wing. [Type of family Aphelophlebotidae and order Aphelophlebia PIERCE, 1945.] CARPENTER, 1960b; DEMOULIN, 1962. *Mio.*, USA (California).

Mesobaetis BRAUER, REDTENBACHER, & GANGLBAUER, 1889, p. 5 [**M. sibirica*; OD]. Little-known nymph. DEMOULIN, 1954a, 1968b; ROHDENDORF, 1962a; TSHERNOVA, 1970; HUBBARD & SAVAGE, 1981. *Jur.*, USSR (Asian RSFSR).

Mesoptectropteron HANDLIRSCH, 1918, p. 112 [**M. longipes*; OD]. Little-known genus, based on nymph. *Trias.*, Europe (Germany).

Parabaetis HAUPT, 1956, p. 32 [**P. eocaenicus*; OD]. Little-known genus, based on small fragment of wing. DEMOULIN, 1957. *Eoc.*, Europe (Germany).

Phthartus HANDLIRSCH, 1904b, p. 6 [**P. rossicus* HANDLIRSCH, 1904b, p. 6; SD CARPENTER, herein]. Little-known genus, based on nymph. HANDLIRSCH, 1906b. *Perm.*, USSR (Asian RSFSR).

Protoligoneuria DEMOULIN, 1955d, p. 270 [**P. limai*; OD]. Little-known genus, based on nymph only, possibly related to Oligoneuridae. COSTA LIMA, 1950. *Paleoc.-Plio.*, Brazil.

Order PALAEODICTYOPTERA Goldenberg, 1877

[Palaeodictyoptera GOLDENBERG, 1877, p. 8] [=Protohemiptera HANDLIRSCH, 1906b, p. 387; Synarmogoidea HANDLIRSCH, 1919b, p. 28; Protocicadida HAUPT (in part), 1941, p. 75; Archaeymenoptera HAUPT, 1941, p. 102; Archodonata MARTYNOV, 1932, p. 12; Anisaxia FORBES, 1943, p. 403; Hemiodonata ZALESKY, 1946a, p. 63; Breyerida HAUPT, 1949, p. 23; Eopalaeodictyoptera LAURENTIAUX, 1952a, p. 234; Eubleptidodea LAURENTIAUX, 1953, p. 423; Synronopterodea LAURENTIAUX, 1953, p. 425; Dictyoneurida ROHDENDORF, 1977, p. 20; Permochemistida SINITSHENKOVA, 1980a, p. 49]

Palaeoptera of moderate to very large size. Wings containing all main veins, including MA, MP, CUA, and CUP, with alternation of convexities and concavities; main veins usually without coalescence and always arising independently; area between veins with a delicate, irregular network (archedictyon) or with true crossveins, or with a combination of both; intercalary veins present in a very few families (e.g., Syntonopteridae); fore and