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 BROSIEUS, 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
**Palaeoptera—Order Uncertain**

*Fig. 54.* Stenophilebiidae and Uncertain (p. 88–89).

1. **Sieblosia**

2a. 

2b. **Stenophilebia**

---

tenevii; OD). Wing fragment, with few crossveins and weak pterostigma. Probably protosipopterygous. (Type of family Kaltanoneuriidae ROHENDORF.) Perm., USSR (European RSFSR).


*Orthaeschnites Haupt, 1956, p. 31 [*O. primus*; OD]. Little-known genus, based on small wing fragment. Eoc., Europe (Germany).


*Sieblosia Handlirsch, 1907, p. 896 [*Heterophilebia jucunda Hagen, 1858a, p. 121; OD]. Little-known genus, based on poorly preserved wing, with closed discoidal cell and weakly developed nodus much nearer to arculus than to pterostigma. (Type of family Sieblosiidae Handlirsch, 1907; placed by Handlirsch in the Anisozygoptera.) Oligo., Europe (Germany).—Fig. 54, I. *(S. jucunda* (Hagen); fore(? wing, ×1.8 (Hagen, 1858a).

*Syrphoe* Bode, 1953, p. 69 [*S. commissa*; OD]. Wing fragment. Jur., Europe (Germany).

---

**Infraclasse PALAEOPERA**

**Order UNCERTAIN**

The following genera, apparently belonging to the infraclasse Palaeoptera, are too poorly known to permit assignment to orders.

*Aedoeophasma* Scudder, 1885g, p. 265 [*A. anglica*; OD]. Little-known genus, based on distal fragment of wing. (Placed by Scudder (1885g), Handlirsch (1906b, 1919b), and Bolton (1916, 1917b) in the Palaeodictyoptera, incertae sedis, but transferred to the Protodonta, incertae sedis, by Handlirsch (1922).) U. Carb., England.

*Archaeoptilites* Handlirsch, 1919b, p. 534 [*Archaeoptilus lucasi* Bronnijart, 1885a, p. 60; OD]. Little-known genus, based on very small fragment of wing. (Originally placed in the Palaeodictyoptera.) Bronnijart, 1893; Handlirsch, 1922. U. Carb., Europe (France).

*Archaeoptilus Scudder, 1881b, p. 295 [*A. ingens*; OD]. Little-known genus, based on small fragment of large wing. (Type of the family Archaeoptilidae Handlirsch, 1906b. Originally considered by Scudder to be "neuropterus," this genus was subsequently (1883b) placed by him in the orthopteroid complex. However, Handlirsch (1906b) and Bolton (1925) were of the opinion that it was more likely a member of the Palaeodictyoptera.) U. Carb., England.

*Bardapteron* Zalessky, 1944a, p. 342 [*B. ovale;
OD). Little-known genus, based on fragment of wing. [Type of the family Bardaperidae Zalesky, 1944a. Originally placed in a new order, Permodictyoptera, but transferred by Rohden-dorf (1962a) to the Palaeodictyoptera.] Perm., USSR (European RSFSR).


Campyloptera BRONGNIART, 1893, p. 406 [*C. eatoni; OD]. Little-known genus, based on incomplete wing. [The generic name Campyloptera was first used in 1885 (BRONGNIART, 1885a), but no species was mentioned until 1893. Placed in the Megasectoptera by BRONGNIART (1885a), HANDLIRSCH (1906b), CARPENTER (1943b), and LAURENTIAX (1953); in the Protodictoptera by BRONGNIART (1893) and Tillyard (1928d); and in a new order, Campylopterodea, by ROHDENDORF (1962a).] U. Carb., Europe (France).


Dicyoneuellida LAURENTIAX, 1949b, p. 207 [*D. perfecta; OD]. Little-known genus, based on incomplete wing. [Type of the family Dicyoneuellidae KUKALOVÁ-PECK, 1975. Placed in the Palaeodictyoptera by LAURENTIAX (1949b); transferred to the Megasectoptera by KUKALOVÁ-PECK (1975).] U. Carb., Europe (France).

Dyadentomum HANDLIRSCH, 1904b, p. 7 [*D. permens; OD]. Little-known genus, based on a body fragment thought by HANDLIRSCH to be that of an ephemeral nymph. Perm., USSR (European RSFSR).

Eohymen MARTYNOV, 1937b, p. 9 [*E. maculipennis; OD]. Little-known genus, based on poorly preserved wing. [Type of the family Eohymenidae MARTYNOV, 1937b. Placed in the Megasectoptera (Protodictyoptera) by MARTYNOV (1937b), in the Palaeodictyoptera by ROHDENDORF (1962a), and in the Caloneurodea by RASNITSYN (1980b).] Perm., USSR (European RSFSR).

Eois Eyskyn RIK, 1976, p. 169 [*E. plectrogenia; OD]. Little-known genus, based on fragments of fore and hind wings. [Almost certainly a member of the odonate complex, but order doubtful.] U. Carb., Europe (Germany).

Eois Eyskyn RIK, 1976, p. 151 [*E. larischi; OD]. Little-known genus, based on incomplete wings. [Type of the family Erasipteridae Carpenter, 1939. Placed in the Odonata by Pruvost (1933a) and KUKALOVÁ (1964b); transferred to the Protodictoptera by Carpenter (1939), LAURENTIAX (1953), WHALLEY (1979), and PRYTGINA (1980b).] U. Carb., Europe (Czechoslovakia), England.


Frakenholzia GUTHÖRL, 1962c, p. 227 [*F. culmanni; OD]. Little-known genus, based on wing fragment. [Originally placed in the Palaeodictyoptera, but transferred to the Megasectoptera by KUKALOVÁ-PECK (1975).] U. Carb., Europe (Germany).

Gerephemera SCUDDER, 1880, p. 12 [*G. simplex; OD]. Little-known genus, based on small fragment of wing. [Originally placed in the order Ephemeroptera by SCUDDER, but later (1890) transferred to the Orthoptera; assigned to the Odonata by HAGEN (1881a, 1881b, 1885) and to the Palaeodictyoptera by HANDLIRSCH (1906a, 1906b).] U. Carb., Canada (Nova Scotia).

Hypermegethes HANDLIRSCH, 1906a, p. 672 [*H. schuebertii; OD]. Little-known genus, based on a small, proximal fragment of very large wing. [Type of the family Hypermegethidae HANDLIRSCH, 1906a. Placed in the Palaeodictyoptera by HANDLIRSCH (1906a, 1906b, 1922), but transferred to the Protohemiptera by LAMEERE (1917c).] U. Carb., USA (Illinois).


Leipsanusa HANDLIRSCH, 1906b, p. 120 [*L. reticulatum; OD]. Little-known genus, based on minute wing fragment. [Originally placed in the Palaeodictyoptera, incertae sedis.] HANDLIRSCH, 1919b. U. Carb., Europe (Belgium).


Litorina MARTYNOV, 1928a, p. 169 [*Litorina antirrhopbila GOLDENBERG, 1854, p. 35; SD HANDLIRSCH, 1906b, p. 77]. Little-known genus, based on fragment of small wing. [Originally placed in the Palaeodictyoptera.] U. Carb., Europe (Germany).

Litophlebia HUBBARD & RIK, 1978, p. 260, nom. subst. pro Xenophlebia RIK, 1976c, p. 130, non


Melanoblatula Cockerell, 1927b, p. 415 [*M. nigrissens*; OD]. Little-known genus, based on fragment of small wing. [Originally placed in the Protorrophoptera.] *U. Carb.*, USA (Maryland).

Microbratella Scudder, 1895b, p. 57 [*M. perdita;* OD]. Little-known genus, based on wing fragment. [Originally placed in the Blattaria, but transferred by Handlirsch (1906a, 1906b) to the Protoblastoidea.] *U. Carb.*, USA (Rhode Island).


Palaecopala Handlirsch, 1904a, p. 10 [*P. gracilis;* OD]. Little-known genus, based on small fragment of wing. [Placed in the Megasecoptera by Handlirsch (1906b) and KuKovalová-Peck (1975).] *U. Carb.*, Europe (Belgium).


Perissophlebia Tillyard, 1918c, p. 422 [*P. multisepia;* OD]. Little-known genus, based on small wing fragment. [Placed in the Odonata by Tillyard (1918c) and Pritykina (1981).] Trias., Australia (Queensland).

Permaneura Carpenter, 1931b, p. 124 [*P. laevis;* OD]. Little-known genus, based on complete hind wing. [Type of the family Permaneuridae Carpenter, 1931b. Placed in the order Palaedoctyoptera by Carpenter (1931b) and Tillyard (1937); transferred to a new order, Permaneuroidea (allied to the Palaedoctyoptera), by Laurentiaux (1953); and included in a new order, Archodonata (along with several other genera formerly in the Palaedoctyoptera), by Rowdendorf (1962a). The ordinal name Archodonata was changed by Sinitshenko (1980a, 1980b) to Palaemethesida. Carpenter (1976) proposed that the genus *Permaneura* be assigned to the Palaedoptytera, *incertae sedis.*] Per., USA (Kansas).

Piroutetia Meunier, 1907, p. 522 [*P. liassina; OD]. Little-known genus, based on wing fragment and placed in the Odonata. Meunier, 1908b. *Jur.,* Europe (France).


Proctagion Brongniart, 1893, p. 403 [*P. audouini; OD]. Little-known genus, based on incomplete wing. [Type of the family Protagriionidae Handlirsch, 1906b. The generic name Proctagion was first used in 1885 (Brongniart, 1885a), but no species was mentioned until 1893. Placed in the Protodonata by Brongniart (1893), Handlirsch (1906b), and Martynov (1932); transferred to the Palaedoctyoptera by Carpenter (1943b) and Rowdendorf (1962a).] *U. Carb.*, Europe (France).


Reisia Handlirsch, 1909c, p. 81, nom. subs. pro Handlirschia Reis, 1909, p. 693, nom. Kohl, 1896 [*Handlirschia gelastis* Reis, 1909; OD]. Little-known genus, based on small fragment of wing. [Placed by Handlirsch (1909c, 1920) and Reis (1909) in the Protodonata.] Trias., Europe (Germany).


Sherborniella Handlirsch, 1919b, p. 535
Hexapoda


**Sypharopera** Handlirsch, 1911, p. 372 [*S. pneuma*; OD]. Little-known genus, based on incomplete wings. [Originally placed in the new order Sypharoperoidea by Handlirsch (1911); transferred to order Diaphanapteroidea by Rohdendorf (1962a).] Handlirsch, 1919b, 1922. *U. Carb.*, USA (Illinois).


**Triadologus** Riek, 1976b, p. 793 [*T. biseriatus*; OD]. Little-known genus, based on small fragment of wing. [Placed in the Protodonata by Riek (1976b) and in the Odonata by Pritykina (1981).] Trias., South Africa.

**Wulasua** T' an, 1980, p. 159 [*W. maculata*; OD]. Little-known genus, based on a poorly preserved, small fragment of a wing. [Originally placed in the Diaphanapteroidea.] Perm., China (Inner Mongolia).

**Xenoneura** Scudder, 1868c, p. 206 [*X. antiquorum*; OD]. Little-known genus, based on wing fragment. [Type of the family Xenoneuridae Scudder, 1885b. Originally placed in the Palaeodictyoptera.] Scudder, 1880; Handlirsch, 1906b, 1922. *U. Carb.*, Canada (New Brunswick).

### Infraclass NEOPTERA

**Martynov, 1923**  
(*Neoptera Martynov, 1923, p. 89*)

Wings articulated to thorax by sclerotized plates (axillaries), not fused or rigidly connected; third axillary Y-shaped and attached to second axillary and posterior natal process, and connected by flexor muscle to thorax; venation basically as in Palaeoptera, but vein MA flat or nearly so or absent; cerci commonly present but vestigial or absent in higher orders. Immature stages very diverse in structure and development. *U. Carb.*—Holo.

This infraclass has been the predominant one since the Permian. It includes 25 existing orders and about 98 percent of the existing species of insects.

### Division EXOPTERYGOTA

**Sharp, 1899**  
(*Exopterygota Sharp, 1899, p. 247*)

Immature stages typically resembling the adults in general form, living in the same kind of environments, and having similar feeding habits; metamorphosis to adults gradual, wings developing within an externally visible cuticular sheath; pupal stage absent. *U. Carb.*—Holo.

Fifteen existing orders are generally recognized in this division, including about 11 percent of the existing species of insects. The orders are usually grouped into two categories, the orthopteroids and the hemipteroids, which have basic structural differences and which appear to represent two distinct lines of exopterygote evolution, although there is some doubt that either one is monophyletic (Richards & Davies, 1977; J. M. Mackerras, 1970). The orthopteroids have mandibulate mouthparts; the fore wings are commonly tegminous or rarely elytroid; the hind wings commonly have a large fan-shaped anal area; cerci are present and are commonly well developed. These insects are known from the Upper Carboniferous to the present. Four very small, existing orders (Grylloblattodea, Zoraptera, Mallophaga, and Anoplura) belonging here are the only existing orders of insects absent from the geological record. They are discussed briefly below, within the Exopterygota.

The hemipteroids have haustellate mouthparts and feed on liquid food; the fore wings are diverse in structure, membranous or modified to hemelytra or elytra. The hind wings are broad, commonly with an anal fan in the more primitive families, but are small or very small in the more specialized families. Cerci are absent. These orders are known from the Permian to the present.