

CHAPTER 19

Arthropoda: Chelicerata, Pycnogonida, Palaeoisopus, Myriapoda and Insecta

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Subphylum CHELICERATA Heymons 1901

Class MEROSTOMATA Dana 1852

Subclass XIPHOSURA Latreille 1802

The classification of Novozhilov (*in* Rohdendorf 1962b) is used here without prejudice.

Order AGLASPIDA Walcott 1911

First, Camb L.Camb: *Paleomerus hamiltoni* Størmer, Kinnekulle, Sweden (Størmer 1955).
The first form assigned to the order without doubt is *Beckwithia typa* Resser M.Camb: Marjum
Fm, Weeks Canyon, Utah (Raasch 1939).

Last, Ord Carad: *Neostrabops martini* Caster and Macke, Maysville Fm, Ohio (Caster and
Macke 1952).

Order CHASMATASPIDIDA Caster and Brooks 1956

First and **Last**, Ord Llvirn?: monotypic order known from *Chasmataspis laurencii* Caster and
Brooks, sediments in the Chazyan hiatus of Canada, Tennessee, U.S.A. (Caster and Brooks 1956).

Order SYNZIPHOSURA Packard 1886

First, Sil Wenl: *Neolimulus falcatus* Woodward and *Cyamocephalus loganensis* Currie, Logan
Water, Lanarkshire, Scotland (Woodward 1868, Currie 1927).

Last, Dev Siegen: *Weinbergina opitzi* Richter and Richter, Hunsrückschiefer, Rheinland,
Germany (Richter and Richter 1929).

Order LIMULINA Richter and Richter 1929

First, Dev Gedinn: *Kiaeria limuloides* Størmer, Downtonian, Ringerike, Norway (Størmer
1934). **Extant.**

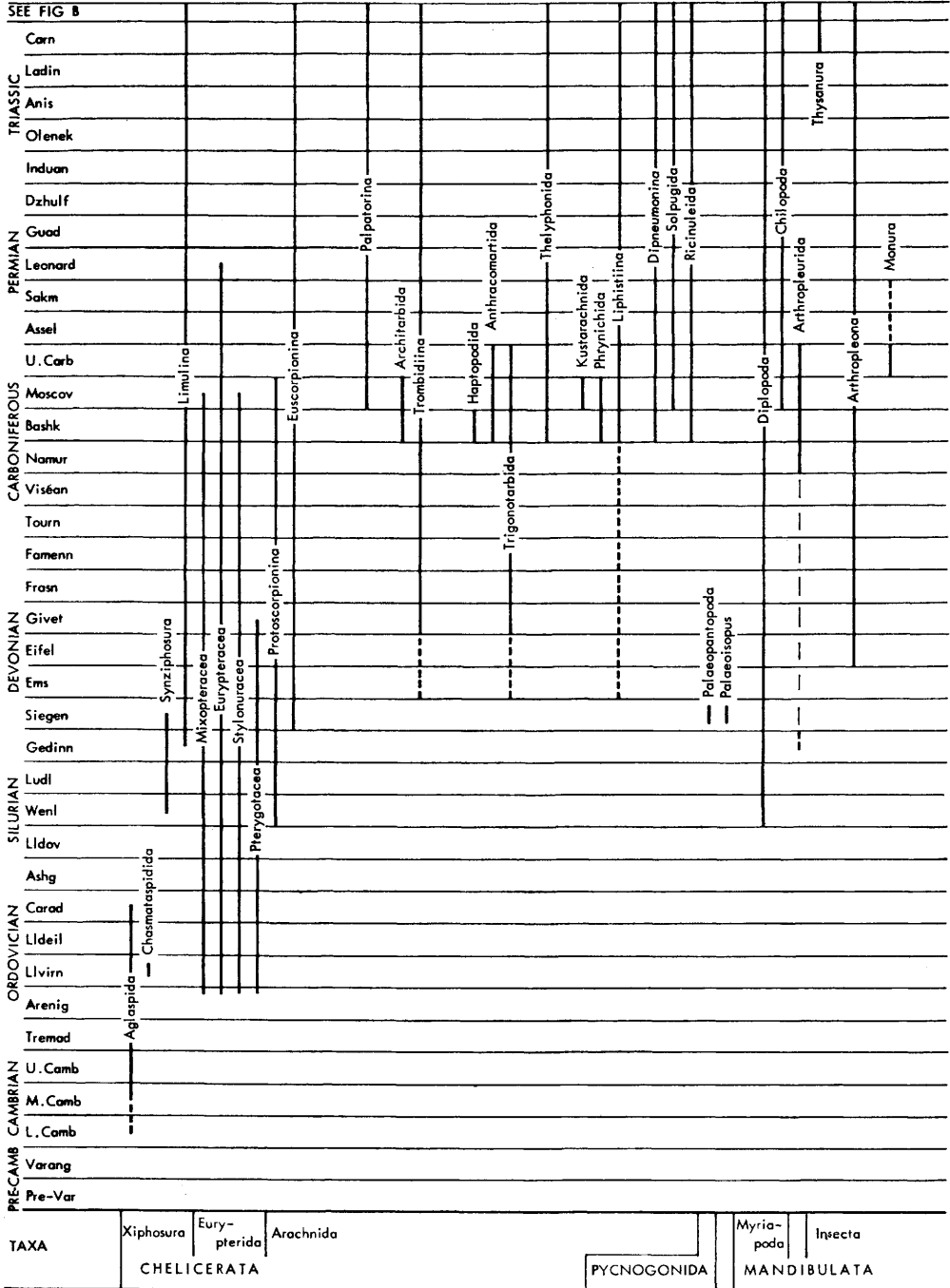
Comment: Represented by extant species belonging to the genera *Limulus*, *Tachypleus* and
Carcinoscorpius.

Order EURYPTERIDA Burmeister 1843

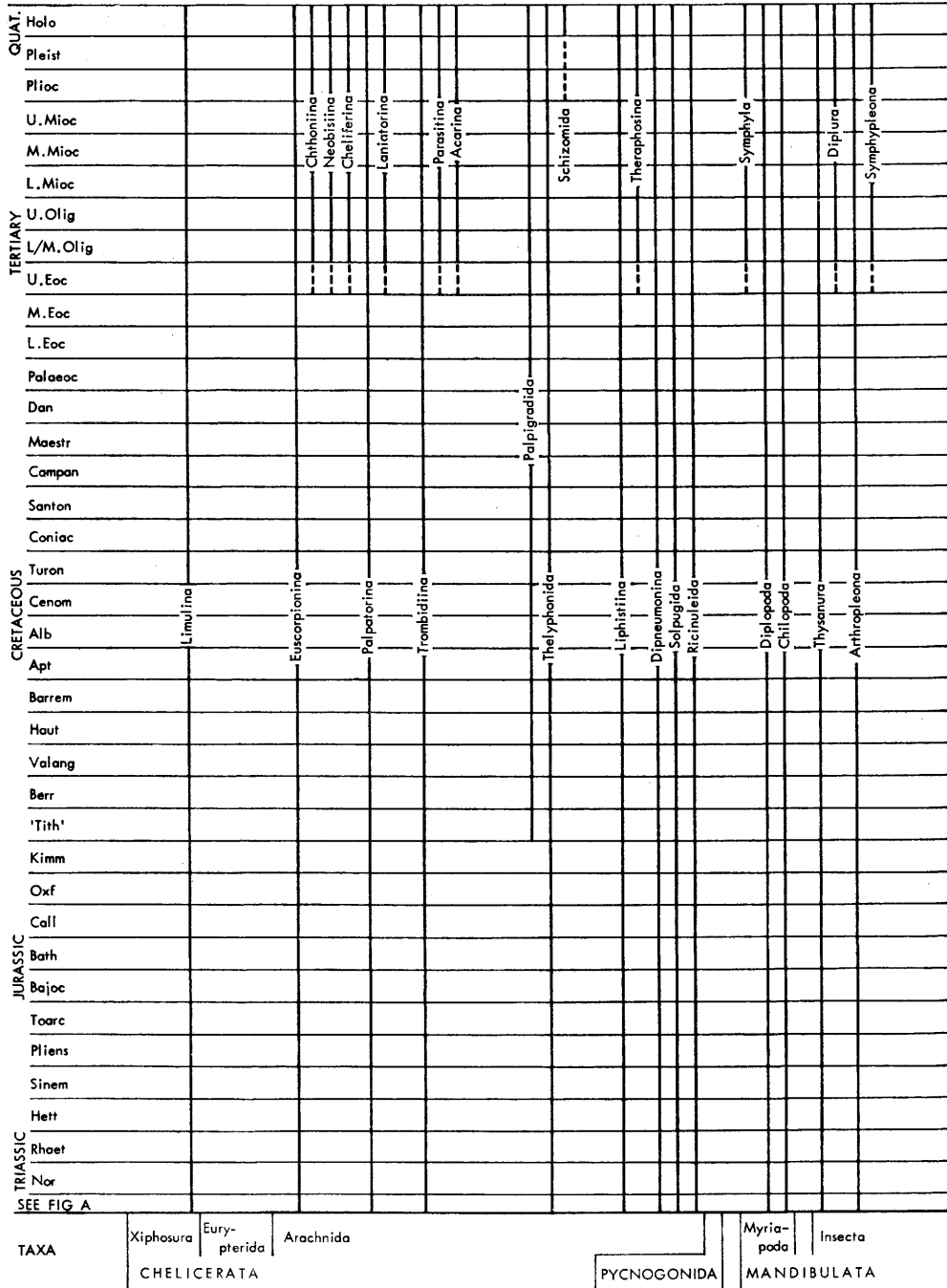
The classification of Caster and Kjellesvig-Waering (1964) is used here without prejudice.

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The Fossil Record, Part II



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FIG. 19.1 B

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Superfamily MIXOPTERACEA Caster and Kjellesvig-Waering 1955

First, Ord Arenig-Llvirn: *Eocarcinosoma ruedemanni* (Flower), Deepkill Fm, Rensselaer Co., New York State (Flower 1945).

Last, Carb Moscov: *Mycterops ordinatus* Cope, Allegheny Fm, Beaver Co., Pennsylvania and *Mycterops mathieui* (Pruvost), Westphalian, Belgium (Kjellesvig-Waering 1959); also fragments of the same genus from Mazon Creek, Illinois (Kjellesvig-Waering 1963).

Constituent families: Megalograptidae Caster and Kjellesvig-Waering, Ord Carad-Ashg; Mixopteridae Caster and Kjellesvig-Waering, Sil Wenl-Dev Gedinn; Carcinomatidae Størmer, Ord Arenig-Llvirn-Dev Gedinn; Mycteropidae Cope, Carb Moscov.

Superfamily EURYPTERACEA Burmeister 1843

First, Ord Arenig-Llvirn: *Waeringopterus? priscus* (Ruedemann) Deepkill Fm, Mt. Merino, Hudson, New York State (Leutze 1961).

Last, Perm Leonard: *Adelophthalmus sellardsi* (Dunbar) Wellington Fm, Dickinson Co., Kansas and Red Rock, Oklahoma (Kjellesvig-Waering 1948).

Constituent families: Hughmilleriidae Kjellesvig-Waering, Ord Carad-Perm Leonard; Slimoniidae Novozhilov, Ord Arenig-Llvirn-U. Carb; Eurypteridae Burmeister, Ord Carad-Dev Siegen.

Superfamily STYLONURACEA Diener 1924

First, Ord Arenig-Llvirn: *Dolichopterus antiquus* Ruedemann, Deepkill Fm, Mt. Merino, Hudson, New York State (Ruedemann 1942).

Last, Carb Moscov: *Mazonipterus cyclophthalmus* Kjellesvig-Waering, Carbondale Fm, Mazon Creek, Illinois and *Hibbertopterus? potens* (Hall) Allegheny Fm, Pennsylvania (Kjellesvig-Waering 1963).

Constituent families: Dolichopteridae Kjellesvig-Waering and Størmer, Ord Arenig-Llvirn-Dev Siegen; Stylonuridae Diener, Ord Carad-Carb Moscov; Rhenopteridae Størmer, Dev Siegen-Givet; Woodwardopteridae Kjellesvig-Waering, L. Dev-Carb Viséan; Hibbertopteridae Kjellesvig-Waering, Dev Famenn?-Perm.

Superfamily PTERYGOTACEA Clarke and Ruedemann 1912

First, Ord Arenig-Llvirn: *Pterygotus (Pterygotus?) deepkillensis* Ruedemann, Deepkill Fm, Deepkill, New York State (Ruedemann 1934).

Last, Dev (M.): *Pterygotus (Pterygotus) bolivianus* Kjellesvig-Waering, Metacryphaeus caffer Z., Sicasica Series, Bolivia (Kjellesvig-Waering 1964); also *Pterygotus (Pterygotus) dicki* Peach, Dev Givet, Thurso Flagstone Group, M. Old Red Sandstone, Caithness, Scotland (Peach 1883).

[C.D.W.]

Class ARACHNIDA Lamarck 1801

Introduction. The classification used is that of Petrunkevitch (Treatise P), which differs slightly from that used by Waterlot (*in* Piveteau 1953), Millot (*in* Grassé 1949) and Dubinin (*in* Rohdendorf 1962b), although the last groups the eurypterids and the scorpions together. According to Wills (1959, 1960) and Kjellesvig-Waering (1966) the classification of the scorpions requires revision.

Many fossil arachnids come from certain horizons in the Carboniferous coal measures of Europe and North America. The amber of localities such as the Baltic coast and Chiapas, Mexico, has produced many excellently preserved specimens. Exceptional conditions, as occurred during

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the formation of the Rhynie Chert of Aberdeenshire and the onyx marble of Arizona, have also resulted in particularly well preserved fossil material. "The fossil record of Arachnida is therefore very incomplete" (Petrunkevitch in Treatise P).

Subclass LATIGASTRA Petrunkevitch 1949

Order SCORPIONIDA Latreille 1817

Suborder PROTOSCORPIONINA Petrunkevitch 1949

First, Sil Wenl: *Dolichophonus loudonensis* (Laurie), U.Sil, Pentland Hills, Scotland (Laurie 1899).

Last, Carb Moscov: *Mazonia woodiana* Meek and Worthen, Francis Creek shales and 1st, Mazon Creek, Illinois (Meek and Worthen 1868, Petrunkevitch 1949).

Comments: *Mazonia woodiana* as well as *Gigantoscopus willsi* Störmer, Carb Tourn-Viséan, Calciferous Sandstone Series, near Langholm, Scotland, which has affinities with *M. woodiana* (see Störmer 1963), may not belong to this suborder (see introduction, and Kjellesvig-Waering 1966); but since the Wenl-L.Dev scorpions are closely related (Kjellesvig-Waering 1966) possible

Last, Dev Ems: gen. et sp. indet. (Störmer 1960), Nellenköpchen Gruppe, Alken a.d. Mosel, Germany, which is considered to have affinities with *Proscorpius* (Kjellesvig-Waering 1966).

Suborder EUSCORPIONINA Petrunkevitch 1949

First, Dev Siegen: *Palaeoscorpius devonicus* Lehmann, Hunsrückschiefer, Germany (Lehmann 1944). **Extant.**

Comment: *P. devonicus* is known from a unique specimen (Petrunkevitch 1953).

Order PSEUDOSCORPIONIDA Latreille 1817

Suborder CHTHONIINA Beier 1932

First, Tert U. Eoc-L/M. Olig): *Chthonius* and *Heterolophus*, Baltic amber (Treatise P). **Extant.**

Suborder NEOBISIINA Beier 1932

First, Tert U. Eoc-L/M. Olig: *Neobisium*, *Garypinus*, *Geogarypus* and *Pseudogarypus*, Baltic amber (Treatise P). **Extant.**

Suborder CHELIFERINA Hagen 1878

First, Tert U. Eoc-L/M. Olig: Six genera belonging to three families, Baltic amber (Treatise P). **Extant.**

Order PHALANGIDA Perty 1833

Suborder PALPITORINA Thorell 1876

First, Carb Moscov: *Nemastomoides longipes* (Petrunkevitch) and *N. depressus* (Petrunkevitch), Francis Creek shales and 1st, Mazon Creek, Illinois (Petrunkevitch 1913, 1953), each known from one specimen. **Extant.**

Suborder LANIATORINA Thorell 1876

First, Tert U. Eoc-L/M. Olig: *Gonyleptes*, Baltic amber (Treatise P). **Extant.**

Suborder CYPHOPHTHALMINA Simon 1879

No fossil record.

Order ARCHITARBIDA Petrunkevitch 1949

(no suborders erected)

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First, Carb Bashk: *Goniotarbus tuberculatus* (Pocock), *G. angulatus* (Pocock), *Mesotarbus intermedius* Petrunkevitch, *M. hindi* (Pocock), *M. angustus* (Pocock) and *Leptotarbus torpedo* (Pocock) all from *Similis-pulchra* Z., Coseley, near Dudley, England (Petrunkevitch 1953).

Last, Carb Moscov: *Orthotarbus nyransensis* Petrunkevitch, Coal Measures (Westphalian D), Nýřany, Czechoslovakia (Petrunkevitch 1953). *Geratarbus bohemicus* Petrunkevitch may also come from this horizon in the coal measures of Nýřany.

Comment: No stratigraphical details are available for *Phalangiotarbus subovalis* (Woodward), Carb Bashk-Moscov, Coal Measures of Burnley, England, and *Ophiliotarbus kliveri* Waterlot, Carb, Westphalian, Sarre, Germany.

Order ACARIDA Nizsch 1818

Suborder NOTOSTIGMATINA With 1903

No fossil record.

Suborder HOLOTHYRINA Reuter 1909

No fossil record.

Suborder TETRAPODILINA Brems 1872

No fossil record.

Suborder TROMBIDIINA Dugès 1839

First, Dev Ems-Givet: *Protacarus crani* Hirst, Rhynie Chert Bed, M. Old Red Sandstone, Aberdeenshire, Scotland (Hirst 1923). **Extant.**

Suborder PARASITINA Reuter 1909

First, Tert U. Eoc-L/M. Olig: *Seius*, Baltic amber (Treatise P). **Extant.**

Suborder ACARINA Leach 1815

First, Tert U. Eoc-L/M. Olig: 19 families represented by 44 genera, Baltic amber (Treatise P) **Extant.**

Subclass STETHOSTOMATA Petrunkevitch 1949

Order HAPTOPODIDA Pocock 1911

(no suborders erected)

First, Carb Bashk: *Pleisiosiro madeleyi* Pocock, Communis Z., Sparth Bottoms, Rochdale, Lancashire, England. The only specimen known from this locality has been erroneously labelled *Architarbus rotundatus* Scudder (Petrunkevitch 1953).

Last, Carb Bashk: *Pleisiosiro madeleyi* Pocock, *Similis-pulchra* Z., Coseley, near Dudley, England (Petrunkevitch 1953).

Comment: This is a monospecific order. Nine specimens of this species are known; details of eight of these have been considered above. No details have been found in the literature for the ninth specimen.

Order ANTHRACOMARTIDA Karsch 1882

(no suborders erected)

First, Carb Bashk: *Cleptomartus denuiti* (Pruvost), Assise de Charleroi (Westphalian A), Morlanwelz, Hainaut, Belgium (Pruvost 1930).

Last, Carb U.Carb: *Pleomartus palatinus* (Ammon), Stephanian, Brücken, Pfalz, Germany (Petrunkevitch 1953).

Comment: Stratigraphical details for *Anthracomartus voelkelianus* Krasch and *A. granulatus* Frič both of Carb, Silesia are not available.

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Subclass SOLUTA Petrunkevitch 1949

Order TRIGONOTARBIDA Petrunkevitch 1949

(no suborders erected)

First, Dev Ems-Givet: *Palaeocharinoides hornei* Hirst, *Palaeocharinus scoursfieldi* Hirst, *P. rhyimensis* Hirst, *P. calmani* Hirst, *P. kidstoni* Hirst and twelve other unnamed species assigned to the genus *Palaeocharinus*, Rhynie Chert Bed, M. Old Red Sandstone, Aberdeenshire, Scotland (Hirst 1923).

Last, Carb U.Carb: *Trigonomartus arnoldi* Petrunkevitch, middle Stephanian, Decazeville, southern France (Petrunkevitch 1955).

Comment: No stratigraphical details are available for *Vratislava silesica* (Romer), Carb, Coal Measures, near Klodzko (Glaz), Poland.

Subclass CAULOGASTRA Pocock 1893

Superorder LATISTERNA Petrunkevitch 1949

Order PALPIGRADIDA Thorell 1888

(no suborders erected)

First, Jur 'Tith': *Sternarthron zitteli* Haase, Lithographischenschiefer, Solenhofen, Germany (Haase 1890). **Extant.**

Superorder CAMAROSTOMATA Petrunkevitch 1949

Order THELYPHONIDA Latreille 1804

(no suborders erected)

First, Carb Bashk: *Prothelyphonus britannicus* (Pocock), *Similis-pulchra* Z., Coseley, near Dudley, England (Petrunkevitch 1953). **Extant.**

Order SCHIZOMIDA Petrunkevitch 1945

(no suborders erected)

First, Tert ?Plioc: *Calcitro fischeri* Petrunkevitch, *Onychothelyphonus bonneri* Pierce and *Calcoscizomus latisternum* Pierce, onyx marble, Bonner, Arizona (Petrunkevitch 1945, Pierce 1950, 1951). **Extant.**

Order KUSTARACHNIDA Petrunkevitch 1913

(no suborders erected)

First and **Last**, Carb Moscov: *Kustarachne tenuipes* Scudder, *K. conica* Petrunkevitch and *K. extincta* (Melander), Francis Creek shales and 1st, Mazon Creek, Illinois (Petrunkevitch 1949, 1953).

Comment: These three species have been described from unique specimens, but no details of their stratigraphical position in the Mazon Creek section are available.

Superorder LABELLATA Petrunkevitch 1949

Order PHRYNICHIDA Petrunkevitch 1945

(no suborders erected)

First, Carb Bashk: *Graeophonus carbonarius* Scudder, Joggins Mines, Nova Scotia, Canada (Petrunkevitch 1949), *G. anglicus* Pocock, *Similis-pulchra* Z., Coseley, near Dudley, England (Petrunkevitch 1953) and *G. anglicus* (= *Protophrynus carbonarius* Pruvost 1930 (Petrunkevitch 1953)), Assise de Charleroi (Westphalian B), Belgium (Pruvost 1930).

Last, Carb Moscov: *Graeophonus carbonarius* Scudder, *Thelyphrynus elongatus* Petrunkevitch and

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Protophrynus carbonarius Petrunkevitch, Francis Creek shales and 1st, Mazon Creek, Illinois (Petrunkevitch 1949) and *Graeophonus anglicus* Pocock, England (Petrunkevitch 1953).

Order ARANEIDA Clerck 1757

Suborder LIPHISTINA Pocock 1892

First, possibly Dev Ems-Givet: *Palaeoeteniza crassipes* Hirst, Rhynie Chert Bed, M. Old Red Sandstone, Aberdeenshire, Scotland (Hirst 1923). If this species does not belong to this suborder, then **First**, Carb Bashk: *Eoeteniza silvicola* Pocock and *Protoeteniza britannica* Petrunkevitch, *Similis-pulchra* Z., Coseley, near Dudley, England (Petrunkevitch 1953). **Extant.**

Comment: No stratigraphical details are available for *Protolycosa anthracophila* Romer, Carb, Upper Silesia, Poland.

Suborder THERAPHOSINA Sundervall 1830

First, Tert U. Eoc-L/M. Olig: *Clostes*, Baltic amber and possibly *Eopluridina*, Tert Olig, Colorado (Treatise P). **Extant.**

Comment: *Eoatypus woodwardii* McCook 1888 is wrongly described as being Tert Eoc, Garnet Bay, Isle of Wight, England (McCook 1888). It is in fact from the Bembridge Limestone (Olig) of Gurnard Bay, Isle of Wight. McCook had doubts about its systematic position.

Suborder HYPOCHILINA Petrunkevitch 1933

No fossil record.

Suborder DIPNEUMONINA Latreille 1817

First, Carb Bashk: *Archaeometea nephilina* Pocock and *Arachnometea tuberculata* Petrunkevitch, *Similis-pulchra* Z., Coseley, near Dudley, England (Petrunkevitch 1953). **Extant.**

Comment: No stratigraphical details are available for *Dinopilio parvus* Petrunkevitch, Coal Measures from tip at Chislet Colliery, Kent, England.

Suborder APNEUMONINA Dahl 1913

No fossil record.

Superorder ROSTRATA Petrunkevitch 1949

Order SOLPUGIDA Leach 1815

(no suborders erected)

First, Carb Moscov: *Protosolpuga carbonaria* Petrunkevitch, Francis Creek shales and limestones, Mazon Creek, Illinois (Petrunkevitch 1949). **Extant.**

Superorder PODOGONA Cook 1899

Order RICINULEIDA Thorell 1892

(no suborders erected)

First, Carb Bashk: *Curculiodes granulatus* Petrunkevitch, *Lenisulcata* Z., Coal Measures, Shipley pit, Bradford, England (Petrunkevitch 1949). **Extant.** [E.C.W.]

Subphylum PYCNOGONIDA Latreille 1810

The classification of J. W. Hedgpeth (*in* Treatise P) is used here.

Order PANTOPODA Gerstaecker 1863

Extant: represented by the families Nymphonidae Wilson 1878; Pallenidae Wilson 1878; Colossendeidae Hoek 1881; Ammotheidae Dohrn 1881; Tanystylidae Shimkevich 1913; Phoxichilidiidae Sars 1891; Endeidae Norman 1908; Pycnogonidae Wilson 1878.

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Order PALAEOPANTOPODA Broili 1930

First and Last Dev Siegen: monotypic order known from *Palaeopantopus maucheri* Broili, Hunsrückschiefer, Germany. (Broili 1929). [C.D.W.]

ARTHROPODA: Incertae sedis

Genus PALAEOISOPUS Broili 1928

First and Last, Dev Siegen: *Palaeoisopus problematicus* Broili, Hunsrückschiefer, Germany (Broili 1928).

Subphylum MANDIBULATA

Class CRUSTACEA

(see Chapter 20)

Class MYRIAPODA Leach 1814

Introduction. The classification of Laurentiaux (*in* Piveteau 1953) and Sharov (*in* Rohdendorf 1962b) has been adopted. In general, the remarks on the fossil record of the Arachnida (see page 502) also apply to this class.

Subclass SYMPHYLA Ryder 1880

First, Tert U. Eoc-L/M. Olig: *Scoloprendrella* sp., Baltic amber (Bachofen von Echt 1942).

Extant.

Subclass PAUROPODA Lubbock 1866

No fossil record.

Comment: Small myriapods (1–1.5 mm). Their absence from Tert amber could be considered significant.

Subclass DIPLOPODA Blainville-Gervais 1844

First, Sil Wenl: *Archidesmus loganensis* Peach, Logan Water, Lesmahagow, Scotland (Peach 1898).

Extant.

Comment: *Archidesmus macnicoli* Peach and four species of *Kampecaris*, all from Dev L. Old Red Sandstone from various localities in Great Britain, and some Carb species (see Peach 1882, 1898, Brade-Birks 1923, Clarke 1952) and *Archidesmus loganensis* are problematic diplopods, and have not been assigned to any order.

Constituent orders: (after Sharov 1962b) Pseudophognatha Latzel 1884, L.Olig-Holo; Palaeocoxopleura Verhoeff 1928, Carb-Perm; Eurysterna Verhoeff 1926, Carb-Trias; Palaeomorpha Verhoeff 1928, Carb; Armadillomorpha Verhoeff 1887 (= Oniscomorpha Pocock 1887), Cret-Holo; Nematophora Verhoeff 1913, L.Olig-Holo; Polydesmoidae Pocock 1887, L.Olig-Holo; Juliformia Saussure & Humbert 1872, L.Olig-Holo; Colobognatha Brandt 1834, L.Olig-Holo.

Subclass CHILOPODA Leach 1814

First, Carb Moscow: *Latzelia primordialis* Scudder, *Eileticus anthracinus* Scudder, *E. aequalis* Scudder, *Palenarthus impressus* Scudder, *Ilyodes divisa* Scudder and *I. elongata* Scudder, Francis Creek shales and limestones, Mazon Creek, Illinois (Scudder 1890).

Extant.

Comment: *Eileticus* may be a crustacean (Pruvost 1919).

[E.C.W.]

Subclass ARTHROPLEURIDA Waterlot 1934

Probably Myriapoda, although critical data lacking (Rolfe & Ingham 1967, Treatise R).

First, Carb Namur: *Arthropleura* aff. *mailleuxi* Pruvost, Ostrauer Schichtengruppe, Czechoslovakia (Příbyl 1960). *Bundenbachellus* Broili, Dev Siegen, and *Camptophyllia* Gill, Carb Bashk, may also be Arthropleurida (Treatise R).

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Last, U.Carb: *Arthropleura fayoli* Boule 1893 and *A.sp.*Remy & Remy 1959, Stephanian C, France and Germany (Van Straelen 1931; Guthörl 1936; Waterlot in Piveteau 1953).

[W.D.I.R.]

Class INSECTA

The classification adopted is based on that of Imms (1957); deviations are inevitable because that classification does not cover the fossil orders.

The earliest fossil insect is believed to be an Apterygote of the Order Collembola. Until quite recently it was believed that the earliest certainly winged insects were members of the Orders Palaeodicyptera, Dicyoptera and Paraplecoptera found in the Upper Carboniferous. Rohdendorf (1961a) has, however, recently reported on an enigmatic Devonian fossil for the reception of which he has erected the Order Archeoptera, which appears to be a winged insect (see p. 515). Most fossil insects consist of wings and in many cases these are fragmentary; the morphology of the insect wing has recently been reviewed in some detail by Seguy (1959).

Smart (1963) has briefly reviewed the phylogeny of both extant and fossil orders of Insects and the field of palaeoentomology has been reviewed by Martynova (1961).

The classification of the fossil orders is discussed at some length by Laurentiaux (*in* Piveteau 1953), and Carpenter (*in* Treatise R) is anticipated with much interest. Other works dealing with Insects that the palaeoentomologist may need to consult are Carpenter (1954b *in* Brues, Melander & Carpenter), Grassé (1949, 1951b), Rohdendorf (1962b) and Rohdendorf, Bekker-Migdisova, Martynova & Sharov (1961).

Subclass I APTERYGOTA

First, Dev Eifel: See Order Collembola below. References: Dennis (1949b) and Imms (1957).

Order THYSANURA Latreille 1796 (= THYSANURA ECTOTROPHI auctt.)

First, Trias ?Carn: *Triassomachilis uralensis* Sharov 1948, Nakyz, Bashkir A.S.S.R., U.S.S.R. **Extant.**

Order DIPLURA Börner 1904 (= THYSANURA ENTOTROPHI auctt.)

First, Tert U. Eoc-L/M Olig: *Campodea darwini* Silvestri 1912, Baltic Amber. **Extant.**

Order PROTURA Silvestri 1907.

No fossil record. **Extant.**

Order COLLEMBOLA Lubbock 1862

First, Dev Eifel; see Suborder Arthropleona below. **Extant.**

Suborder ARTHROPLEONA Börner 1901

First, Dev Eifel: *Rhyniella praecursor* Hirst and Maulik 1926, Rhynie, Aberdeen, Scotland. **Extant.**

Suborder SYMPHYPLEONA Börner 1901

First, Tert U. Eoc-L/M. Olig: *Sminthurus succineus* Stach 1922 and eleven other species (Handschin 1926), Baltic Amber. **Extant.**

Order MONURA Sharov 1951

First, Carb U. Carb: *Dasyleptus lucasi* Brongniart 1885, Commeny, France.

Last, Perm (Lower; Kuznetsk series, correlation uncertain): *Dasyleptus brongniarti* Sharov 1957, Kuznetsk Basin, Kemerov District, U.S.S.R.

Reference: Martynova (1962)

Subclass II PTERYGOTA

The classification adopted in Imms (1957) is followed here with the fossil orders inserted. This classification is based on the condition of the wing pads in the pre-imaginal instars and the

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presence or absence of a pupal stage in the life-history. Neither of these criteria are satisfactory for dealing with fossil insects which can only be placed in such a classification by making use of other characteristics and making presumptions in respect of the development of the wings and the life-history.

An alternative classification, originally developed by Martynov (1925a *et seq.*), based on the structure of the wings themselves and on their mode of articulation is available. This classification has much merit for the palaeoentomologist since many "fossil insects" consist only of wings! The groupings of orders in this classification are indicated in the text below. It is used by Jeannel (1949) where he discusses the classification and phylogeny of the orders of Insects including those known only as fossils.

Division I EXOPTERYGOTA (= HEMIMETABOLA)

(a) Palaeopteran Orders (= PALAEOPTERA, PALAEOPTERYGOTA, *auctt.*)

First, Carb Bashk: see Orders Odonata, Archodonata, Palaeodictyoptera and Protodonata below.

Of the seven orders in this group five are extinct and two are extant.

Order EPHEMEROPTERA Imms 1934 (= EPHEMERIDA Leach 1817)

First, Carb U. Carb: see Suborder Protephemeroptera below. **Extant.**

Suborder PROTEPHEMEROPTERA Handlisch 1906

First and Last, Carb U. Carb: *Triplosoba pulchella* Brongniart 1893, Commentry, France.

Suborder PLECTOPTERA Packard 1886 (emend. Tillyard 1932)

First, Perm Leonard: *Protoreisma permianum* Sellards 1907, Elmo, Kansas, U.S.A. **Extant.**
References: Carpenter (1963a), Rohdendorf (1962a) and Tshernova (1965).

Order ODONATA Fabricius 1792

First, Carb Bashk: see Suborder Eomeganisoptera below. **Extant.**

Comment: On analysis most authors, dealing with the overall systematics of this order, recognize the same segregates within which they place the various genera, families, etc., but they differ in the taxonomic status given to them. Below no particular author is followed; the three suborders of extant Odonata of Imms (1957) are listed with four further suborders which accommodate fossil forms. References: Fraser (1957) and Rohdendorf (1962a).

Suborder EOMEGANISOPTERA Rohdendorf 1962

First and Last, Carb Bashk: *Erasipteron larischi* Pruvost 1934. According to Kukulova (1964a) the fossil came from "the top mudstone of the coal seam 31 (D) in the mine President Gottwald (formerly Frantisek) at Horni Sucha, Upper Silesian Coal Basin, Czechoslovakia. According to K. Patteisky (1928) and S. Dybova (1959) the seam was deposited in Namurian C".

Comment: Kukulova (1964a) has re-examined and reported on the unique holotype of *Erasipteron larischi*.

Suborder ARCHIZYGOPTERA Handlirsch 1906

First, Trias (M. or U; correlation uncertain): *Triassagrion australiense* Tillyard, 1922, Ipswich, Queensland, Australia.

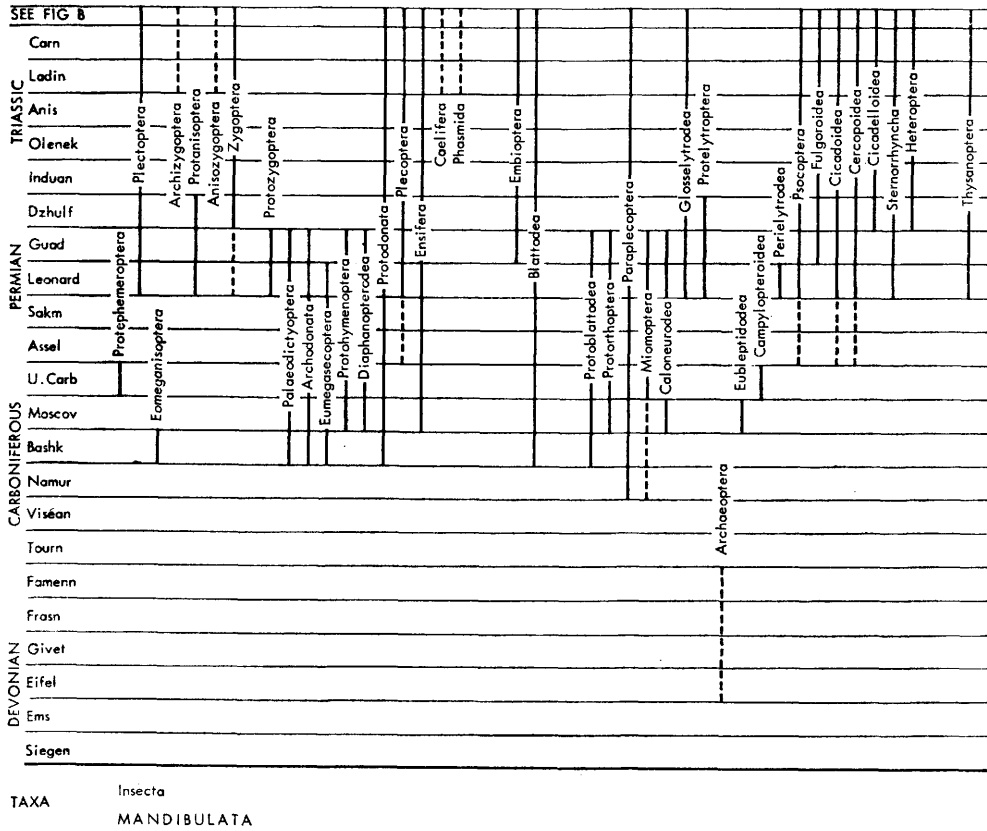
Last, Jur Oxf-Call: *Protomyrmeleon handlirschi* Martynov 1927, Karatau, Kazakhstan, U.S.S.R.

Suborder PROTANISOPTERA Carpenter 1931

First, Perm Leonard: *Ditaxineura anomalostigma* Tillyard 1925, Elmo, Kansas, U.S.A. and one other species from Kansas, one from Tsherkarda and two from Kuznetsk Basin, Kemerov District, U.S.S.R.

Last, Perm Dzhulf: *Polytaxineura stanleyi* Tillyard 1935, Belmont, N.S.W., Australia.

The Fossil Record, Part II



CONTRIBUTORS J. Smart, R. J. Woolton

FIG. 19.2A

Suborder ANISOZYGOPTERA Handlirsch 1906

First, Trias (Middle or Upper; correlation uncertain): *Mesophlebia antinodalis* Tillyard 1916 and *Triassophlebia stigmatica* Tillyard 1922, Ipswich, Queensland, Australia. **Extant.**

Suborder ZYGOPTERA Selys 1840

First, Perm (Upper; correlation uncertain): *Permagrion falklandicum* Tillyard 1928, Bodie Creek Head, Falkland Islands. **Extant.**

Suborder ANISOPTERA Selys 1840

First, Jur Torac: *Liassogomphus propinquus* (Bode 1905), U. Lias, Hatdorf bei Fallersleben, Brunswick, Germany. **Extant.**

Suborder PROTOZYGOPTERA Tillyard 1925

First, Perm Leonard: *Kennedyia mirabilis* Tillyard 1925, Elmo, Kansas, U.S.A. and five other species from Kansas and one from Nizhnee Moshevo, Perm District, U.S.S.R.

Last, Perm Guad: *Sushkinia parvula* Martynov 1930, Tikhie Gory, U.S.S.R. and four other species from the same place and Iva Gora, Archangelsk District, U.S.S.R.

Chapter 19: Arthropoda: Chelicerata, Pycnogonida, Palaeoisopus, Myriapoda, Insecta

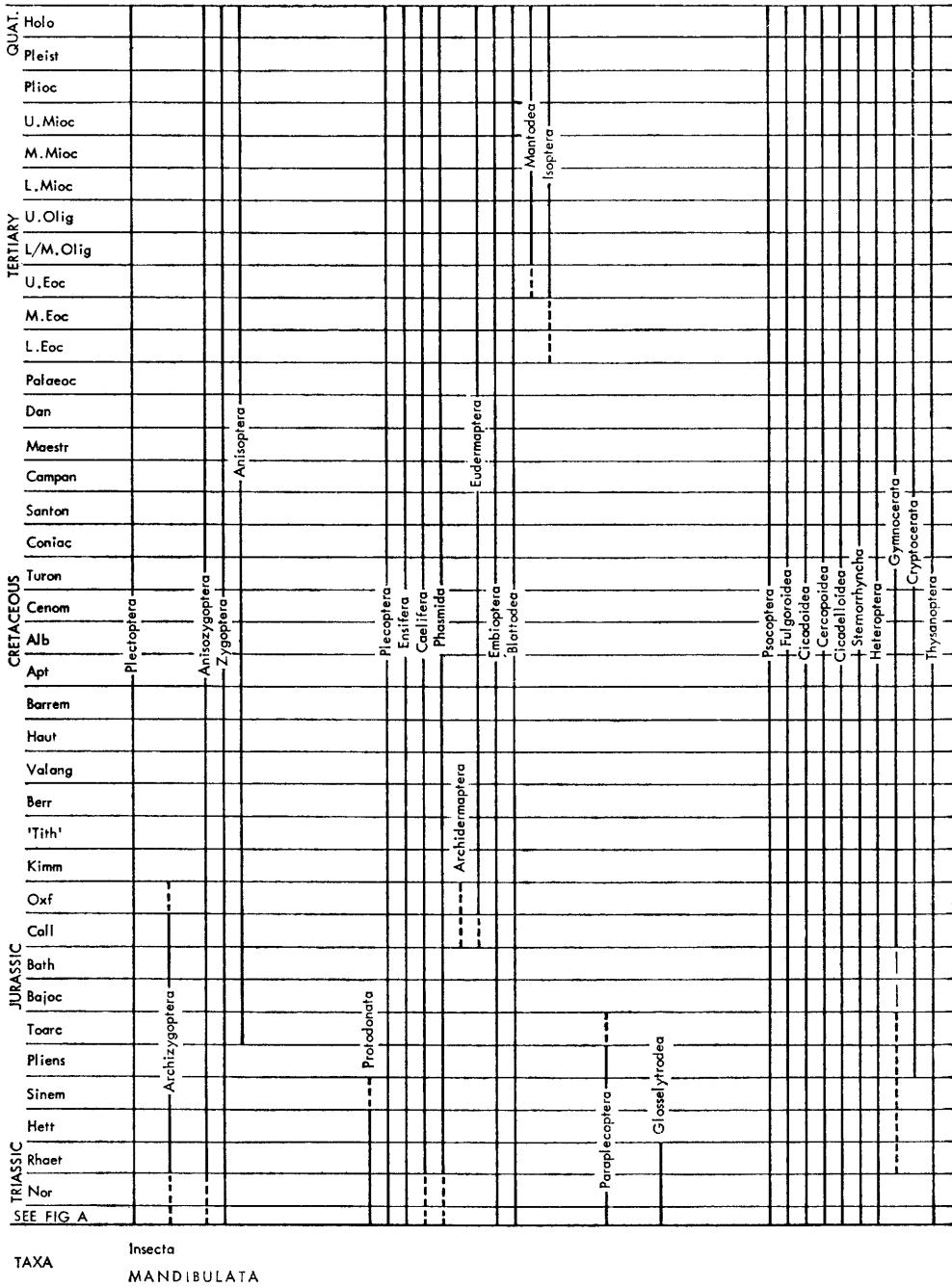


FIG. 19.2B

The Fossil Record, Part II

Order PALAEOICTYOPTERA Goldenberg 1854

First, Carb Bashk: *Severinopsis vetusta* Kukalova 1958 and two other species, Upper Silesian Coal Basin, Czechoslovakia.

Last, Perm Guad: *Eohymen maculipennis* Martynov 1937, Kargala, Orenburgh District, U.S.S.R.

Comments: Following Carpenter (1954b) and Kukalova (1963b) we have not divided the order into suborders. Other authorities have divided the group up and raised some of these divisions to ordinal status (See, for instance, Laurentiaux (*in* Piveteau 1953) and Rohdendorf (1962a)).

Important papers dealing with this Order are: Carpenter (1954b, 1965) Kukalova (1963b), Laurentiaux (*in* Piveteau 1953) and Rohdendorf (1962a).

Order ARCHODONATA Martynov 1932

First, Carb Bashk: *Rectineura lineata* Bolton 1934, Sturry, Kent, England.

Last, Perm Guad: *Permothemis libelluloides* (Martynov 1932), Iva-Gora, Archangelsk district, U.S.S.R. and *Ideliella decora* G. Zaleskii 1937, Tikhie Gory, Tatar A.S.S.R., U.S.S.R.

References: Demoulin (1954) and Rohdendorf (1962a).

Order MEGASECOPTERA Handlirsch 1906

First, Carb Bashk: see Suborder Eumegaseoptera below.

Comment: Rohdendorf's (1962a) classification is followed.

Suborder EUMEGASECOPTERA Carpenter 1947

First, Carb Bashk: *Brodioptera cumberlandensis* Copeland 1957, Plarrsboro, Nova Scotia, Canada.

Last, Perm Leonard: *Vorkutia tshernovi* Rohdendorf 1947, Vorkuta Basin, Komi A.S.S.R., U.S.S.R.

Suborder PROTOHYMENOPTERA Carpenter, 1947

First, Carb U. Carb: *Aspidothorax triangularis* Brongniart 1894, Commeny, France.

Last, Perm Guad: *Ivahymen constrictus* Martynov 1931, Iva-Gora, Archangelsk district, U.S.S.R. References: Carpenter (1947, 1951).

Order DIAPHANOPTEROIDEA Rohdendorf 1962

First, Carb Moscow: *Prochroptera calopteryx* Handlirsch 1911, Mazon Creek, near Morris, Illinois. Possibly *Tchirkovaea guttata* Zaleskii 1932 and *Philiaspitlon masculosum* Zaleskii 1932 L.Carb-L. Perm (correlation uncertain), L. Balakhonka ser., Kuznetsk Basin, Kemerov District, U.S.S.R.

Last, Perm Guad: *Kuloja expansa* Martynov 1928, *Parakuloja pauovenosa* (Martynov 1931) and *Eukuloja cubitalis* (Martynov 1931), Iva-Gora, Archangelsk district, U.S.S.R.

Comment: Rohdendorf (1962a) has suggested a series of three suborders to which the various families recognised by himself and other authors can be allocated. Reference: Carpenter (1963b).

Order PROTODONATA Brongniart 1893 (= MEGANISOPTERA Martynov 1932)

First, Carb Bashk: *Typus durhami* Carpenter 1960, Durham, Georgia, U.S.A.

Last, Jur Hett/Sinem: *Liadotyplus relictus* Martynov 1937, Shurab, Kirgisia, U.S.S.R. Reference: Carpenter (1960).

(b) Polyneopteran or Orthopteroid Orders

First, Carb Namur: See Order Paraplecoptera, below at p. 514.

Extant.

Comment: Of the fifteen orders in this group seven are extinct; the remaining eight are extant. There are some comments on the phylogenetic relationships of the orders in Zeuner (1939). Some authors would place the Order Zoraptera (see p. 516) here rather than with the paraneopteran Orders (see p. 516). See also comments on Protoblattodea below at p. 514.

Order PLECOPTERA Burmeister 1839

First, Perm Leonard: *Uralonympha varica* Zaleskii 1939, and *Perlopsis filicornis* Martynov 1940, Tshckarda, Perm District, U.S.S.R. (both nymphs); and *Palaeoperla exacta* Sharov 1961, Perm

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(Lower; Kuznetsk Ser., correlation uncertain), Kuznetsk Basin, Kemerov District, U.S.S.R. (adult). **Extant.**

References: Illies (1965) and Sharov (1961b, 1962b).

Order GRYLLOBLATTODEA Brues & Melander 1932 (= NOTOPTERA Crampton 1951)

No fossil record. Entomologists, however, regard the few living species as of considerable phylogenetic interest. **Extant.**

Order ORTHOPTERA Latreille 1793 (= SALTATORIA Latreille 1817)

First, Carb Moscov: See Suborder Ensifera below. **Extant.**

Comments: Orthoptera is now used, in a restricted sense, for the insects at one time designated the "Orthoptera-Saltatoria"; the "Orthoptera-Cursoria", such as the Dictyoptera, Phasmida and Grylloblattodea, are excluded and these segregates given ordinal status.

Sharov (1961a, 1962b) includes the extinct families Oedischidae and Tcholmanvissiidea previously assigned to Protorthoptera.

References: Ragge (1955), Sharov (1961a, 1962b) and Smart (1953).

Suborder ENSIFERA Chopard 1920

First, Carb Moscov: *Genentomum validum* Scudder 1885, and *Progenentomum carbonis* Handlirsch 1906, Mazon Creek, near Morris, Illinois. **Extant.**

References: Zeuner (1939) and Sharov (1962b).

Suborder CAELIFERA Ander 1939

First, Trias (Middle; correlation uncertain): *Triassolocusta leptoptera* Tillyard 1922, Ipswich, Queensland, Australia. **Extant.**

Order PHASMIDA Leach 1815 (= PHASMODEA auctt)

First, Trias (M. or U., correlation uncertain): *Aeroplana mirabilis* Tillyard 1918, Ipswich, Queensland, Australia. **Extant.**

Comment: *Aeroplana mirabilis* Tillyard 1918 was originally placed in the Protodonata. Martynov (1928) assigned the genus to Phasmodea; this has been confirmed by Riek (1956).

References: Carpenter (1954b), Martynov (1928) and Martynova (1962).

Order DERMAPTERA Leach 1817

First, Jur Oxf-Call: see suborders below. **Extant.**

Suborder ARCHIDERMAPTERA Martynov 1925

First and **Last**, Jur Oxf-Call: *Protodiplatys fortis* Martynov 1925, Karatau, Kazakhstan, U.S.S.R.

Suborder EUDERMAPTERA

First, Jur Oxf-Call: *Semenoviola obliquotruncata* Martynov 1925b, Karatau, Kazakhstan, U.S.S.R. **Extant.**

Order EMBIOPTERA Hagen 1861

First, Perm Guad: *Sheimia sojanensis* Martynova 1958, Sheimo-Gora, Archangelsk district, U.S.S.R. (Martynova 1962). **Extant.**

Order DICTYOPTERA Leach 1818

First, Carb Bashk: see Suborder Blattodea below. **Extant.**

Suborder BLATTODEA Brunner 1882

First, Carb Bashk: *Aphthoroblattina shottoni* Laurentiaux 1953, Deepfield, Staffordshire, England. **Extant.**

Comment: Laurentiaux (*in* Piveteau 1953) published a figure of the wing of this insect but he has not yet described it in detail.

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Suborder MANTODEA Burmeister 1838

First, Tert U. Eoc-L/M. Olig: *Chaetoessa breviaata* Giebel 1862, Baltic Amber. **Extant.**

Comment: The suborder is poorly represented in the fossil record. A number of fossils have been dubiously attributed to it. References: Bekker-Migdisova (1962), Laurentiaux (in Piveteau 1953), Sharov (1962a,b) and Smart (1956).

Order ISOPTERA Brullé 1832

First, Tert Eoc: *Mastotermes bournemouthisensis* v. Rosen 1913, Bagshot Beds, Bournemouth, Hampshire, England. **Extant.**

Comment: *Termes peccanae* Massalongo 1856, M. Eoc., was regarded by Handlirsch (1906-8) as "Termitidae incertae sedis"; it must so continue.

Reference: Martynov (1937).

Order PROTOBLATTODEA Handlirsch 1906

First, Carb Bashk: *Glaphyrophlebia delicatula* Bolton 1934, Similis-pulchra Z., Cefn Coed Colliery, Glamorgan, Wales.

Last, Perm Guad: *Sindonopsis subcostalis* Martynov 1928 and *S. reducta* Martynov 1928, Iva Gora, Archangelsk District, U.S.S.R., and *Sindon rossicum* Martynov 1930 and *Epimastax parvulus* Martynov 1928, Tikhie Gory, Tatar A.S.S.R., U.S.S.R.

Comments: The polyneopterous insects underwent their principal radiation in the Carboniferous and Permian, and are there represented by a bewildering variety of often fragmentary fossils whose classification is one of the most difficult problems in palaeoentomology. We here follow Sharov (1962b) in considering seven extinct orders; but feel that Protoblattodea, Paraplecoptera and Protorthoptera, at least, may be unnatural taxons. Carpenter (1954b) divided the species between the orders Protorthoptera and Protopterlaria: the latter comprising only the family Lemmatophoridae, whose members are known to have had aquatic larvae. Recently (*in litt.*) he has suggested that it is unrealistic on present information to treat them otherwise than in a single order, the Protorthoptera.

Following Sharov (1962b) the Protoblattodea are here considered almost in the original sense of Handlirsch (1906).

Laurentiaux (in Piveteau 1953) published a figure of the wing of *Protoblattinopsis stubblefieldi* Laurentiaux (Carb Bashk, Deepfield, Staffordshire, England), which belongs to this order but he does not seem to have yet described it in detail. The fossil is of Westphalian A age, and would antedate the above-cited first record.

Reference: Kukalova (1959).

Order PROTORTHOPTERA Handlirsch 1906

First, Carb Moscow: *Nacekomia rossae* Richardson 1956, Mazon Creek, nr. Morris, Illinois.

Last, Perm Guad: *Kamia angustovenosa* Martynov 1928, Tikhie Gory, Tatar A.S.S.R., U.S.S.R.

Comment: The order is here restricted, following Sharov (1961a), to comprise only the family Sthenaropodidae. Carpenter (1943a, *et seq.*) has conceived the order in very wide terms (see comment under Protoblattodea above).

Order PARAPLECOPTERA Martynov 1938

First, Carb Namur: *Stygne roemeri* Handlirsch 1906, Laurahütte, Upper Silesia, Czechoslovakia.

Last, Jur Pliens-Toarc: *Geinitzia schlieffeni* (Geinitz 1884) and 2 other spp., Dobbertin, Mecklenburg, Germany.

Comment: We follow Sharov (1961a, 1961b, 1962b) in our concept of this order. The order thus comprises the Protopterlaria of Tillyard (1928a, 1928b, and 1937) and many genera that Carpenter (1935) places in his broadly conceived Protorthoptera. The Paraplecoptera are one of the largest and most important of all the extinct orders of Insects. See also comments on Protoblattodea on p. 514. References: Carpenter (1936, 1950) and Kukalova (1964b,c).

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Order MIOMOPTERA Martynov 1927

First, Carb U. Carb: *Archimioptera carbonaria* Guthörl 1939, Saarland, Germany; or Carb Namur: *Metroptator pusillus* Handlirsch 1906, Altamont, Pennsylvania.

Last, Perm Guad: *Palaeomantis schmidti* Handlirsch 1904, Tikhie Gory, Tatar A.S.S.R., four spp. from Iva Gora, Archangelsk District; and one from Ilyinski Ser (correlation uncertain), Kuznetsk Basin, Kemerov District, Siberia.

Comment: The genera comprised in this order were distributed by Carpenter (1954b) amongst Protorthoptera, Protoperlaria and Psocoptera but the order has been maintained by Martynova (1962) and Kukalova (1963a). Carpenter (1965) has placed *Metroptator* (Carb Namur) in Miomoptera (see p. 518).

Order CALONEURODEA Martynov 1938

First, Carb Moscov: *Euthyneura lecomtei* Pruvost 1919 and *Emphyloptera lecrivaini* Pruvost 1919, Lens, Pas-de-Calais, France.

Last, Perm Guad: *Euthygramma parallelum* (Martynov 1928), Iva-Gora and Sheimo-Gora, Archangelsk District, U.S.S.R. and three other species from the same localities and from Tikhie Gory, Tatar A.S.S.R., U.S.S.R.

References: Carpenter (1943a, 1961), Laurentiaux (*in* Piveteau 1953), Martynov (1938b) and Martynova (1962).

Order GLOSSELYTRODEA Martynov 1938

First, Perm Leonard: *Permoberothes villosa* Tillyard 1932 and several other species, Elmo, Kansas.

Last, Trias Rhaet: *Mesojurina sogjutensis* Martynov 1943, Issyk-Kul, Kirgisia, U.S.S.R.

References: Martynov (1938a) and Martynova (1952, 1962).

Order PROTELYTROPTERA Tillyard 1931

First, Perm Leonard: *Protelytron permianium* Tillyard 1931 and 13 other spp. from Elmo, Kansas, U.S.A.; 8 spp. from Obora, Moravia, Czechoslovakia; and 1 from Tshkarda, Perm District, U.S.S.R.

Last, Perm Dzhulf: *Protocoleus mitchelli* Tillyard 1934, Belmont, New South Wales, Australia.

Comment: We follow Carpenter and Kukalova (1964) and place *Protocoleus* here; we do not recognise the Order Protocoleoptera Tillyard 1934, erected for the reception of this genus.

Reference: Kukalova (1964c).

Orders Incertae Sedis

Placed here are four orders erected by various authors about which we feel that too little is known to allow of their placement in a formal classification. All are Palaeozoic. We regard the Orders Protocoleoptera Tillyard 1924 and Paracoleoptera Laurentiaux 1953 as being merged in Protelytroptera and Coleoptera respectively (see above and 525).

Order ARCHAEOPTERA Rohendorf 1961

First and Last, Dev (Upper): *Eopterum devonicum* Rohendorf 1961, Upper Devonian, Komi A.S.S.R., U.S.S.R.

Comment: The fossil is a little enigmatic and it is difficult fully to elucidate its nature. It is to be hoped that more specimens can be obtained because the occurrence of a winged insect in the Devonian is a matter of major significance when considering the phylogeny of the class. It is figured in Rohendorf (1961a, 1962b).

Order EUBLEPTIDODEA Laurentiaux 1953

First and Last, Carb Moscov: *Eubleptus danielsi* Handlirsch 1906, Mazon Creek, nr. Morris, Illinois, U.S.A.

Comment: Carpenter (1965) assigns *Eubleptus* to the Order Palaeodictyoptera (see page 512).

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Suborder CAMPYLOPTEROIDEA Carpenter 1943

First and Last, Carb U.Carb: *Campyloptera eatoni* Brongniart 1894, Commentry, France.

Comment: The monotypic family Campylopteridae and the Suborder Campylopteroidea (Order Megasecoptera) were "tentatively" erected by Carpenter (1943b) who said that a "distinct order will probably be needed eventually" for the species. However, he omitted the family from his (1954) key to the families of Megasecoptera. Laurentiaux (*in* Piveteau 1953) recognised the suborder.

Order PERIELYTRODEA Zalesky 1948

First and Last, Perm Leonard: *Perielyton mirabile* Zalesky 1948, Tshekarda, Perm District, U.S.S.R.

Reference: Sharov (1962b).

(c) Paraneopteran or Hemipteroid Orders

First, Perm Leonard: see Order Hemiptera, Suborder Homoptera below at p. 516.

The six orders grouped here are rather loosely associated. Some authors would place the Zoraptera with the Polyneopteran or Orthopteroid orders (See p. 512). The six orders are all extant.

Order ZORAPTERA Silvestri 1913

No fossil record.

Extant.

Comment: Small insects with a body length of about 3 mm. and a wing-span of 7 mm. which eluded the neoentomologist until 1913! Reference: Dennis (1949a).

Order PSOCOPTERA Shipley 1904

First, Perm Leonard: *Dichentomum tinctum* Tillyard 1926, Elmo, Kansas, U.S.A., and several other spp. from Kansas and Perm District, U.S.S.R., also three spp. from Kuznetsk Basin, Kemerov District, U.S.S.R. (L. Perm; correlation uncertain).

Extant.

References: Bekker-Migdisova & Vishnyakova (1962) and Carpenter (1932, 1933).

Order SIPHUNCULATA Latreille 1825 (= ANOPLURA Leach 1815)

No fossil record.

Extant.

Comment: The sucking lice, usually associated with mammals.

Order MALLOPHAGA Nitzsch 1918

No fossil record.

Extant.

Comment: The Chewing or Bird Lice which are not, however, exclusively associated with birds. [J.S. & R.J.W.]

Order HEMIPTERA Linnaeus 1758

First, Perm Leonard: see Suborder Homoptera below.

Extant.

Comment: The two Suborders, Homoptera and Heteroptera, are often given separate ordinal status. References: Bekker-Migdisova (1962) and Evans (1956).

Suborder HOMOPTERA Leach 1815

First, Perm Leonard: *Archescytina permiana* Tillyard 1926, Elmo, Kansas, U.S.A., and many other Archescytinidae from Elmo, and from Tshekarda, Perm District, and Kuznetsk Basin, Kemerov District, (Kuznetsk Series, correlation uncertain), U.S.S.R., and *Tshekardaella tshekardensis* Bekker-Migdisova 1960, Tshekarda, Perm District, U.S.S.R.

Extant.

Comment: *Protoprosbole straeleni* Laurentiaux 1952, Carb Namur, Monceau-Fontaine, Belgium; *Blattoprosbole tomiensis* Bekker-Migdisova 1958, and *Archeglyphis crassinervis* Martynov

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1935, M. Carb, L. Balakhonka Series (correlation uncertain), Kuznetsk Basin, Kemerov District, U.S.S.R., and *Dictyocicada antiqua* Brongniart 1885, U. Carb, Commentry, France, have all been claimed to be Homoptera. The position of each is uncertain; *B. tomiensis* and *A. crassinervis* are the most probable Homoptera.

References: Bekker-Migdisova (1960a,b, 1961) and Evans (1963).

Series COLEORRHYNCHA Myers & China 1929

No fossil record.

Extant.

Comment: Members of the Family Actinoscytinidae (U. Perm-U. Jur) have been claimed to be Coleorrhyncha (Bekker-Migdisova, 1958), as have the Mesozoic Ipsviciidae (China, 1962). Both suggestions are probably wrong. China's proposal to include the only known coleorrhynchous family, the Peloriidiidae, in the Auchenorrhyncha is not here followed.

Series AUCHENORRHYNCHA Dumeril 1806

First, Perm (Lower: Kuznetsk Series, correlation uncertain): see Superfamilies Cicadoidea and Cercopoidea below. **Extant.**

Comment: Evans (1964) has discussed the diversity and possible origins of this group.

Superfamily CICADOIDEA

First, Perm (Lower; Kuznetsk Series, correlation uncertain): *Evanscicada speciosa* (Bekker-Migdisova, 1961) and several other species, Kuznetsk Basin, Kemerov District, U.S.S.R. **Extant.**

Comment: *Arheglyphis crassinervis* Martynov 1930, U. Carb, L. Balakhonka Series, Kuznetsk Basin, Kemerov District, U.S.S.R., has been claimed to belong to a cicadoid family (Martynov 1930, Bekker-Migdisova 1961). It is, however, poorly preserved and is here regarded as *incertae sedis*.

Superfamily FULGOROIDEA

First, Perm Guad; *Scytophara extensa* Martynov 1937, and *Scytocixius mendax* Martynov 1937, Kargala, Orenburg District, U.S.S.R. **Extant.**

Comment: *Neuropibrocha* and *Kaltanopibrocha* Bekker-Migdisova 1961 (L. Perm; Kuznetsk Series correlation uncertain), Kuznetsk Basin, Kemerov District, U.S.S.R., are here regarded as *incertae sedis*.

Superfamily CERCOPOIDEA

First, Perm (Lower; Kuznetsk Series correlation uncertain): *Scytinoptera picturata* Bekker-Migdisova 1961 and 5 other spp. Kuznetsk Basin, Kemerov District, U.S.S.R. **Extant.**

Comment: *Scytinoptera* and related genera, previously thought cicadelloid, probably cercopoid (Evans 1964).

Superfamily CICADELLOIDEA

First, Perm Dzhulf: *Homaloscytina plana* Tillyard 1926, Belmont, N.S.W., Australia. **Extant.**

Comment: Permian supposed cicadelloids have usually been placed in the Scytinopteridae (e.g. Evans 1956, Bekker-Migdisova 1962). *Scytinoptera*, though, is probably cercopoid (Evans 1964), and definite Permian cicadelloids are hard to determine.

Series STERNORRHYNCHA Amyot and Serville 1843

First, Perm Leonard: *Tshekardaella tshekardensis* Bekker-Migdisova 1948, Tshekarda, Perm District, U.S.S.R. **Extant.**

Comment: Series usually divided into 4 superfamilies; but assignment of fossils too controversial to be worthwhile here. Archescytinidae, many spp. Leonard-Dzhulf, may be sternorrhynchous (Martynov 1933, Bekker-Migdisova 1960b, etc.) but thought auchenorrhynchous by Evans (1956, etc.)

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Suborder HETEROPTERA Latreille 1810

First, Perm Dzhulf: *Actinoscytina belmontensis* Tillyard 1926, and *Paraknightia magnifica* Evans 1943, Belmont, N.S.W., Australia. **Extant.**

Comments: Most fossil Heteroptera have been insufficiently described and need re-examination. Many described fossils cannot, therefore, safely be assigned to either of the two series into which the suborder is divided. The two species cited above are both Heteroptera but otherwise *incerae sedis*.

Series GYMNO CERATA Fieber 1851

First, Jur Call-Oxf: *Lygaenocoris prynadai* Popov 1961, and three other spp., Karatau, Kazakhstan, U.S.S.R. **Extant.**

Comment: *Darnioptis tragopea* Bekker-Migdisova 1958, and three spp. of *Ceresopsis* Bekker-Migdisova 1958, Trias Rhaet, Issyk-Kul, Kirgisia, U.S.S.R., and many species from the Lias, Mecklenburg and Lower Saxony, Germany (Handlirsch 1906, 1938; Bode 1953) may well be earlier records. The family Dunstaniidae Tillyard 1916 (L.-U. Trias) are Homoptera.

Series CRYPTO CERATA Fieber 1851

First, Jur Pliens: *Shurabella lepyroniopsis* Bekker-Migdisova 1949, locality II, nr. Shurab, Tadzhikistan, U.S.S.R. **Extant.**

Comment: *Triassocoris myersi* Tillyard 1922 may belong here (Southwood & Leston 1959, Bekker-Migdisova 1962). [R.J.W.]

Order THYSANOPTERA Haliday 1836

First, Perm Leonard: *Permothrips longipennis* Martynov 1935, Tshekarda, Perm District, U.S.S.R. **Extant.**

Reference: Martynova (1962).

Division II ENDOPTERYGOTA (= HOLOMETABOLA)

(d) Oligoneopteran Orders

First, Carb U. Carb: see Order Neuroptera, Superfamily Raphidioidea below at p. 519.

Comments: Mecoptera, with Lepidoptera, Trichoptera, Diptera and Siphonaptera are frequently designated the "Panorpoid Complex". *Metropator pusillus* Handlirsch 1906 from the Upper Carboniferous of North America, "Near Altamont Colliery, Pennsylvania, Nordamerika. Lower-Pottsville, Lower Lykens Group. Unteres Obercarbon" in U.S. National Museum (Handlirsch 1906: 112-113) has been considered by some authors to be a member of the Order Mecoptera and, therefore, by inference, an endopterygote insect with a holometabolous life-history. If this assignment be correct then *Metropator* and not *Fatjanoptera* may be the earliest endopterygote Insect. The assignment to Mecoptera on the basis of the features of the fossil (an incomplete wing) can be questioned and, of course, nothing is known of its life-history. Carpenter (1965) has, in fact, placed *Metropator* in the polyneopteran exopterygote Order Miomoptera! (see also under Eumecoptera on p. 522)

All orders of the Endopterygota are extant.

Order NEUROPTERA Linnaeus 1758.

First, Carb. U. Carb: See Suborder Megaloptera, Superfamily Raphidioidea, below at p. 519.

Comments: The Neuroptera along with the Mecoptera are orders of considerable interest not only as insects but in respect of their zoo-geography and palaeontological record. Authors are by no means in agreement on the classification of the Neuroptera. We propose to follow Imms (1957), mainly as a matter of convenience, (1) in the initial division of the order into two sub-orders, and (2) in the classification of the Suborder Megaloptera. However, we propose to follow Berland & Grassé (1951) in recognising five rather than four superfamilies of the Suborder Planipennia.

Authors also differ in the status to be accorded to the various taxonomic segregates even when agreeing on their delimitation. *Permoberotha* Tillyard 1932 and *Permoberothella* Riek 1953 have

Chapter 19: Arthropoda: Chelicerata, Pycnogonida, Palaeoisopus, Myriapoda, Insecta

both been removed from Neuroptera and placed in Glosselytrodea by Martynova (1961).

We outline below the classification adopted and append a few notes indicating how it compares with other classifications.

Order NEUROPTERA

Suborder Megaloptera with Superfamilies Sialoidea and Raphidioidea.

Suborder Planipennia with Superfamilies Ithonoidea, Coniopterygoidea, Osmyloidea, Hemerobioidea and Myrmeleontoidea.

Notes.

1. Berland & Grassé (1951) and Martynova (1962) designate the superfamilies Sialoidea and Raphidioidea as Orders Megaloptera and Raphidioptera. They also treat the Suborder Planipennia as an order. They accord subordinal rank to the taxonomic segregates of Planipennia here designated superfamilies.

2. Martynova (1962) places the families comprised in Ithonoidea and Osmyloidea in a segregate designated the Suborder Polystoechotidea.

3. Imms (1957) has the families here comprised in Osmyloidea within the Superfamily Hemerobioidea.

4. Handlirsch (1925) and Tillyard (1926) are two other important authors on the Neuroptera.

Suborder MEGALOPTERA Latreille 1802

First, Carb U. Carb/Perm; See Superfamily Raphidioidea below.

Extant.

Superfamily SIALOIDEA.

First, Perm (Lower; Kuznetsk series, correlation uncertain): *Permosialis sibirica* Martynova 1961, with *P. asiatica* Martynova 1961 and *P. matutina* Martynova 1961, Kuznetsk Basin, Kemerov District, U.S.S.R.

Extant.

Comment: The larva of a sialid, *Mormolucoidea articulatus* Hitchcock 1858 has been described from the Trias of Turner's Falls, Massachusetts, U.S.A.

Constituent families: Corydalidae and Sialidae.

Superfamily RAPHDIOIDEA

First, Carb U. Carb or Perm (Lower; Burgukli Series, correlation uncertain see comment below): *Fatjanoptera mnemonica* Martynova 1961, Tunguska Basin, Krasnoyarsk region, U.S.S.R.

Extant.

Comment: Martynova (1961) gives the age of the L. Burgukli Series as Carb. N. Shvedov, *Lexique Stratigraphique International* II, U.S.S.R., part I pp. 259-260 considers it L. Perm, with a flora comparable with that of Leon beds in the Pechora river basin, Komi A.S.S.R., U.S.S.R.

Suborder PLANIPENNIA Heymons 1915

First, Perm (Lower): see Superfamily Ithonoidea below.

Extant.

Superfamily CONIOPTERYGOIDEA Enderlein 1905

First, Tert U. Eoc-L/M. Olig: *Coniopteryx timidus* (Hagen 1854), Baltic Amber.

Extant.

Constituent family: Coniopterygidae Burmeister 1839.

Superfamily ITHONOIDEA

First, Perm (Lower; Kuznetsk Series, correlation uncertain): *Permithonopsis kaltanensis* Martynova 1961 (with *P. perantiqua* Martynova 1961 and *P. sharovi* Martynova 1961), Kuznetsk Basin, Kemerov District, U.S.S.R.

Extant.

Comment: The discontinuity of the distribution of the extant genera is remarkable: *Ithone* and *Heterithone*—Australia; *Oliarce*—California; *Rapisma*—Himalayas.

Constituent families: Ithonidae Tillyard 1919 and Permithonidae Tillyard 1922 (= Permegalomidae Martynova 1952 and Permopsychopsidae Riek 1953).

The Fossil Record, Part II

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|---------------|-------------------------|--|--|--|--|--|--|--|--|------------|
| SEE FIG B | | | | | | | | | | |
| TRIASSIC | Carn | | | | | | | | | |
| | Ladin | | | | | | | | | |
| | Anis | | | | | | | | | |
| | Olenek | | | | | | | | | |
| | Induan | | | | | | | | | |
| | Dzhulf | | | | | | | | | |
| | Guad | | | | | | | | | |
| PERMIAN | Leonard | | | | | | | | | |
| | Sakm | | | | | | | | | |
| | Assel | | | | | | | | | |
| | U. Carb | | | | | | | | | |
| CARBONIFEROUS | Moscov | | | | | | | | | |
| | Bashk | | | | | | | | | |
| | Namur | | | | | | | | | |
| | Viséan | | | | | | | | | |
| | | | | | | | | | | |
| TAXA | Insecta | | | | | | | | | Coleoptera |
| | MANDIBULATA | | | | | | | | | |
| CONTRIBUTORS | J. Smart, R. J. Woolton | | | | | | | | | R. Crowson |

FIG. 19.3A

Superfamily OSMYLOIDEA Brauer 1868

First, Trias Rhaet: *Petrushevskia borisi* Martynova 1958, Issyk-Kul, Kirgisia, U.S.S.R.

Extant.

Constituent families: Osmylidae Brauer 1868, Osmylitidae Martynova 1949, Mesopolystoechotidae Martynova 1949, Dilaridae Handlirsch 1906, Berothidae Handlirsch 1908, Sisyridae Handlirsch 1906, Mantispidae Westwood 1840, and Polystoechotidae Handlirsch 1906.

Superfamily HEMEROBIOIDEA Westwood 1840

First, Perm (Lower; Kuznetsk Series, correlation uncertain) *Palaemerobius latibasis* Martynova 1961, Kuznetsk Basin, Kemerov District, U.S.S.R.

Extant.

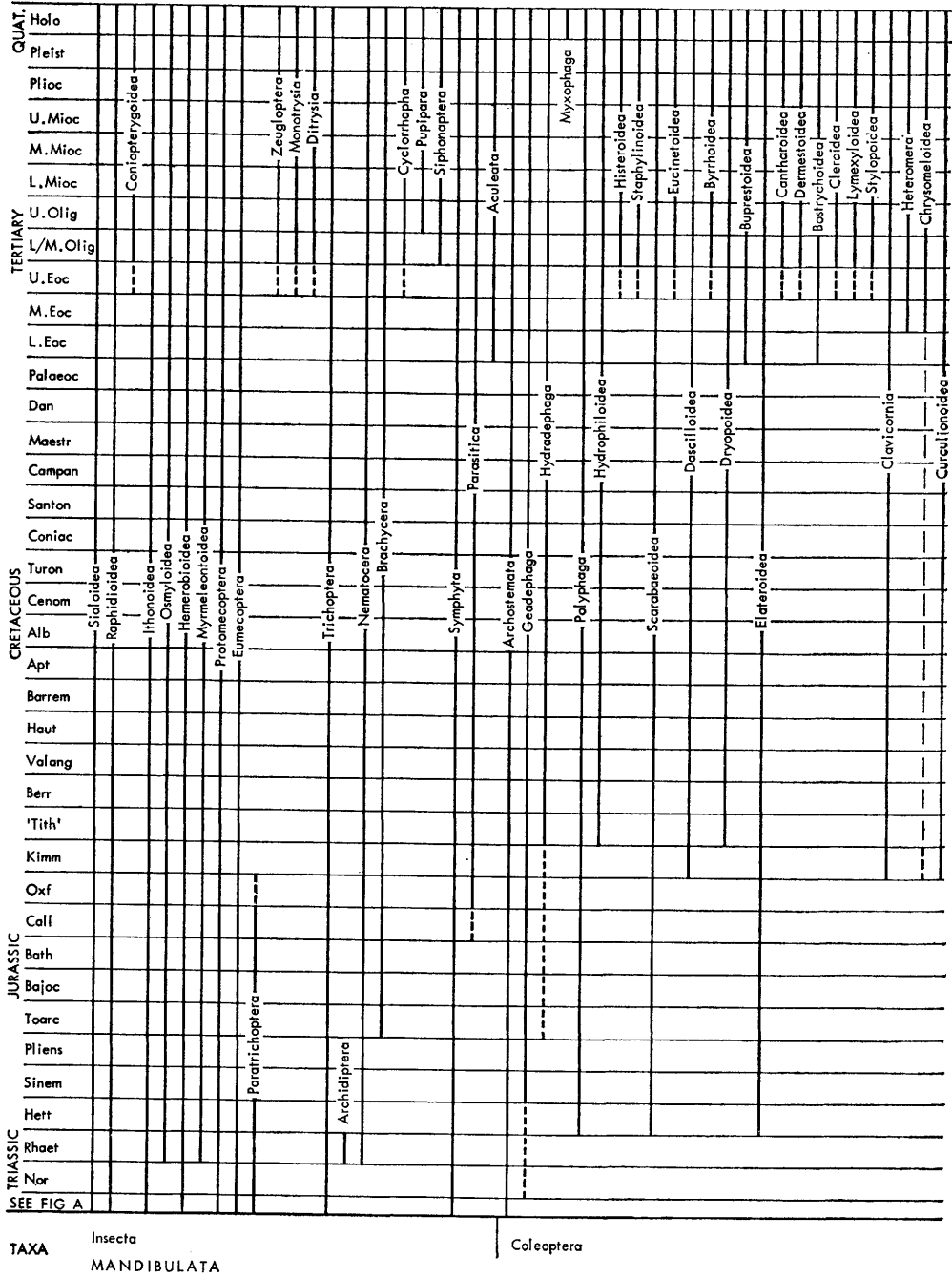
Constituent families: Psychopsidae Handlirsch 1908, Chrysopidae Hagen 1866, Hemerobiidae Westwood 1840, Kalligrammatidae Handlirsch 1906, Brongniartiellidae Martynova 1949, Palaemerobiidae Martynov 1928, Sialidopseidae Zalessky 1926 (= Permosisyridae Martynov 1933), Mesochrysopidae Handlirsch 1908, Sympherobiidae Brues & Melander 1932, Apochrysidae Brues & Melander 1910.

Superfamily MYRMELEONTOIDEA Burmeister 1829

First, Trias Rhaet: *Sogjuta speciosa* Martynova 1958, Issyk-Kul, Kirgisia, U.S.S.R. **Extant.**

Constituent families: Myrmeleontidae Burmeister 1829 (= Myrmeleonidae *auctt.*), Nymphidae Brauer 1868, Nemopteridae Hagen 1861, Ascalaphidae Schneider 1845, Solenoptilidae Handlirsch 1906, Nymphitidae Handlirsch 1906, Stilbopterygidae Tillyard 1926 and Myoidactylidae Handlirsch 1925.

Chapter 19: Arthropoda: Chelicerata, Pycnogonida, Palaeoisopus, Myriapoda, Insecta



TAXA Insecta Coleoptera
 MANDIBULATA

CONTRIBUTORS J. Smart, R. J. Woolton R. Crowson

FIG. 19.3B

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Order MECOPTERA Packard 1886

First, Perm Leonard: see under suborders Protomecoptera and Eumecoptera below. **Extant.**

Comments: In the arrangement which follows, where we recognise four sub-orders, Protomecoptera, Eumecoptera, Paratrachoptera, and Neomecoptera, we have relied much on Martynova (1962) and on the important survey of the group by Grassé (1951a) in which he took cognisance of both extant and fossil forms. We include the suborder Protodiptera Tillyard 1937 in Paratrachoptera, following Martynova (1962). Suborder Paramecoptera Tillyard 1919, known only from two incomplete wings cannot be safely assigned to any of the suborders.

The taxonomy of the order has been complicated by the enigmatic nature of many of the fossils—some merely fragments of wings—assigned, probably quite correctly, to it. This has resulted in the erection of a great many families for their reception and the authorities are not in agreement as to which might be synonyms of which (See further in notes under Suborder Eumecoptera).

Some authors treat the order simply as comprising a series of families and make no attempt to group them in any way.

The literature on the Mecoptera is extensive, some of the more important references, relating especially to phylogeny, are: Carpenter (1930, 1954a, 1965), Crampton (1930), Hinton (1958), Grassé (1951a), Imms (1944), Martynova (1948, 1959, 1962) and Riek (1953).

Suborder PROTOMECOPTERA Tillyard 1917

First, Perm Leonard: *Platychorista venosa* Tillyard 1926, Elmo Kansas, U.S.A., *Marimerobius splendens* Zaleskii 1946, Tshekarda, Perm District, U.S.S.R., and many spp. from Perm (Lower; Kuznetsk Series., correlation uncertain), Kuznetsk Basin, Kemerov District, U.S.S.R. **Extant.**

Comment: Represented at the present time by the rare species: *Merope tuber* Newman 1838, Eastern U.S.A. *Austromerope poulteni* Killington 1933, Australia; and *Notiothauma reedi* McLachlan 1877, Chile.

Constituent families: Protomeropidae Tillyard 1926 (=Platychoristidae Carpenter 1930), Archipanorpidae Tillyard 1917, Kaltanidae Martynova 1958, Tomiochoristidae Martynova 1958, Permomeropidae Reik 1953 and the two families Meropidae Handlirsch 1906 and Notiothaumidae Esben-Petersen 1921 to which the extant species are assigned.

Suborder EUMECOPTERA Tillyard 1917

First, Perm Leonard: *Permopanorpa formosa* Tillyard 1926, Elmo, Kansas, U.S.A. and many other spp. from Elmo, Kansas; and from the Urals, and the Kuznetsk Basin (Kuznetsk Series), U.S.S.R. **Extant.**

Comment: *Metropator pusillus* Handlirsch 1906, Carb Namur, Pennsylvania, was placed in Mecoptera by Tillyard (1926). This assignment was questioned by Carpenter (1930) but was accepted by Martynova (1962) who placed it in Order Eumecoptera. Crampton (1930) assigned *Metropator* to the Order Protorthoptera. Carpenter (1965) has now assigned *Metropator* to the Order Miomoptera. (See also p. 518). We consider it here as *incert. sed.*

Constituent families: Agetopanorpidae Carpenter 1930⁰, Anormochoristidae Tillyard 1926, Belmontiidae Tillyard 1919⁰, Cladochoristidae Reik 1953⁺, Idelopanorpidae Zalesky 1929⁰, Lithopanorpidae Carpenter 1930⁺, Mesochoristidae Tillyard 1926⁰, (= Eosetidae Tindale 1944), Mesopanorpidae Tillyard 1918⁰, Metropatridae Handlirsch 1906, Neorthophlebiidae Handlirsch 1920⁺, Orthophlebiidae Handlirsch 1906, Parachoristidae Tillyard 1926⁺, Permo-centropidae Martynov 1933, Permochoristidae Tillyard 1918⁺, Permopanorpidae Tillyard 1926⁺, Petromantidae Handlirsch 1904⁺, Protochoristidae Tillyard 1926⁺, Protopanorpidae Handlirsch 1937, Stereochoristidae Tillyard 1919⁺, Tyctopsychidae Martynova 1958 and Xenochoristidae Riek 1953⁺, the extant families: Bittacidae Enderlein 1910 (= Bittacusidae

⁰ . . . These families are comprised in the family Permochoristidae Tillyard by Martynova (1962); she assigns Cladochoristidae to Order Trichoptera.

⁺ . . . These families are comprised in the family Orthophlebiidae Handlirsch by Carpenter (1954b).

Chapter 19: Arthropoda: Chelicerata, Pycnogonida, Palaeoisopus, Myriapoda, Insecta

Handlirsch, 1906), Choristidae Tillyard 1919, Nannochoristidae Tillyard 1917 and Panorpidae Stephens 1835.

Suborder PARATRICHOPTERA Tillyard 1919

First, Perm (Upper; Ilyinsk Series, correlation uncertain); *Permotipula borealis* Martynova 1961, Kuznetsk Basin, Kemerov District, U.S.S.R. or Perm Dzhulf: *Permotipula patricia* Tillyard 1929, *Robinjohnia tillyardi* Martynova 1948, *Permotanyderus ableptus* Riek 1953 and *Choristotanyderus nanus* Riek 1953, Belmont and Warner's Bay, N.S.W., Australia.

Last, Jur Call-Oxf: *Pseudopolycentropus latipennis* Martynov 1927, Karatau, Kazakhstan, U.S.S.R.

Comments: Constitution and validity of suborder queried by Riek (1956), but accepted by Martynova (1959, 1961, 1963).

Widely believed that the Order Diptera must have arisen from Paratrichoptera but see Imms (1944) on comparison of Diptera with *Nannochorista*, etc., Suborder Eumecoptera.

Constituent families: Permotipulidae Tillyard 1937 (= Robinjohniidae Martynova 1948), Pseudopolycentropididae Handlirsch 1921 (= "Pseudocentropidae Handlirsch 1921" of Laurentiaux 1953), Pseudodipteridae Martynova 1961, Choristopsychidae Martynov 1937, Mesopsychidae Tillyard 1917, Liassophilidae Tillyard 1933, Triassopsychidae Tillyard 1919, Permotanyderidae Riek 1953 and Dobbertiniidae Handlirsch 1921.

Suborder NEOMECOPTERA Crampton 1930

No fossil record. The suborder comprises but one species *Boreus hymenalis* Latreille 1816, an obscure, apterous insect of holarctic distribution. Hinton (1958) would remove the Neomecoptera from the Mecoptera and set them apart with full ordinal status. **Extant.**

Order LEPIDOPTERA Linnaeus 1758

First, Tert U. Eoc-L/M. Olig: many spp. from Baltic amber. **Extant.**

Comments: It is now generally accepted that the families Palaeontinidae Handlirsch 1906 and Dunstaniidae Tillyard 1916 are Homoptera and not Lepidoptera.

Eoses triassica Tindale 1944 was thought to be a Lepidopteran and was treated as representing a Suborder Eoneura Tindale 1944 by Laurentiaux (in Piveteau 1953) but Riek (1955) presents convincing evidence that the species is a synonym of *Mesochorista proavita* Tillyard 1916 (Family Mesochoristidae, Suborder Eumecoptera; see p. 522).

The classification below is that of Imms (1957). Other references: Kuznetsov (1941), Laurentiaux (1953), Rebel (1936) and Riek (1955).

Suborder ZEUGLOPTERA Chapman 1916

First, Tert U. Eoc-L/M. Olig: *Micropteryx proavitalla* Rebel 1936, Baltic Amber. **Extant.**

Suborder MONOTRYSLA Borner 1938

First, Tert U. Eoc-L/M. Olig: *Electrocrania immensipalpia* Kuznetsov 1941 and many others from Baltic Amber. **Extant.**

Suborder DITRYSLA Borner 1938

First, Tert U. Eoc-L/M. Olig: *Palaeoscardiites mordvilkoii* Kuznetsov 1941 and many others from Baltic Amber. **Extant.**

Order TRICHOPTERA Kirby 1913

First, Perm (Lower; Kuznetsk Series, correlation uncertain): *Microptysma sibiricum* Martynova 1958, Kuznetsk Basin, Kemerov District, U.S.S.R. **Extant.**

Reference: Martynova (1962).

[J.S. & R.J.W.]

Order DIPTERA Linnaeus 1758

First, Trias Rhaet: see Suborders Archidiptera, and Nematocera. **Extant.**

Comments: Laurentiaux (in Piveteau 1953) says "Le Trias inférieur de l'est de la France,

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dont la faune reste inédite, a livré les plus anciennes traces de diptères, associées précurseurs encore contemporains, paratrichoptères (Pseudodiptera) et aux permochoristides. Cette découverte ramène a l'ordre du jour, le problème du berceau géographique".

We follow the classification of Imms (1957) with the addition of a suborder set up by Rohdendorf for the accommodation of certain fossils described by him.

Rohdendorf in a series of papers (see refs. below) has elaborated a very interesting phylogenetic classification of Diptera (adopted in Rohdendorf 1962a): unfortunately this classification has not yet received the critical attention of English-language writers.

The Permian fossil, *Permotipula patricia* Tillyard 1929, is now regarded as definitely not in any way belonging to the Diptera but is assigned to the Suborder Paratrichoptera.

References: Imms (1944, 1957), and Rohdendorf (1946, 1951, 1959, 1961b, 1964).

Suborder ARCHIDIPTERA Rohdendorf 1961

First and Last, Trias Rhaet: Several species described by Rohdendorf (1962a), including: *Dictyodiptera multinervis*, *Paradictyodiptera triachalis*, *Dipterodictya tipuloidea*, *Hyperophlyneura phryganeoides*, *Dyspolyneura longipennis* and *Diplopolyneura mirabilis*, Issyk-kul, Kirgisia, U.S.S.R.

Suborder NEMATOCERA Latreille 1825

First, Trias Rhaet: Many species described by Rohdendorf (1962a), including: *Eopolyneura tenuinervis*, *Pareopolyneura costalis*, *Musidoromima crassinervis*, *Tipulodictya minima*, *Architipula radiata*, *Architendipes tshernovskiji*, *Rhaetomyiacosta*, *Rhaetofungivora reticulate*, *Palaeoplecia rhaetica*, *Phragmili-goneura incerta*, *Oligophryne fungivoroides* and *Protorhyphus turanicus*, Issyk-Kul, Kirgisia, U.S.S.R. **Extant.**

Suborder BRACHYCERA Macquart 1834

First, Jur Torac: *Protobrachyceron liasinum* Handlirsch 1938, Upper Lias, Dobbertin, Mecklenberg, Germany. **Extant.**

Suborder CYCLORRHAPHA

First, Tert U. Eoc-L/M. Olig: many species referable to extant genera in Baltic Amber. **Extant.**

Suborder PUPIPARA

First, Tert U. Olig: *Ornithoponus rottensis* Statz 1940, Graugruner Schiefer, Rott, Germany. **Extant.**

Order SIPHONAPTERA Latreille 1825 (= APHANIPTERA Kirby 1826)

First, Tert U. Eoc-L/M. Olig: *Palaeopsylla klebsiana* Dampf 1910, Baltic Amber. **Extant.**
Comment: Holland (1964) has reviewed the scant knowledge of fossil fleas. [J.S.]

Order HYMENOPTERA Linnaeus 1758

First, Trias (Lower; Madigen Series, correlation uncertain): see under Suborder Symphyta below. **Extant.**

Comment: Reviews of our information about fossil Hymenoptera will be found in Laurentiaux (in Piveteau 1953) and Martynova (1962).

Suborder SYMPHYTA Gerstaecker 1867

First, Trias (Lower; Madigen Series, correlation uncertain). *Triassoxyela foveolata* Rasnitsyn 1964 and nine other species, Madigen, Kirgisia, U.S.S.R. **Extant.**

Constituent superfamilies: Xyeloidea Benson 1951, L. Trias (correlation uncertain) see *Triassoxyela* above; Megalodontoidea Ross 1937, Jur Call-Oxf; Siricoidea Ross 1937, Jur Call-Oxf; Orussoidea Bischoff 1926; Cephoidea Ross 1937, Tert L/M Olig. All extant.

References: Rasnitsyn (1963, 1964).

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Suborder APOCRITA Gerstaecker 1867

First, Jur Call-Oxf: see under Section Parasitica below. **Extant.**

Comment: For convenience we here employ the traditional but obsolete division of the suborder into Parasitica and Aculeata.

Section PARASITICA Kirby 1837

First, Jur Call-Oxf: *Mesaulacinus oviformis* Martynov 1925 and *Mesohelorus muchini* Martynov 1925, Karatau, Kazakhstan, U.S.S.R. **Extant.**

Constituent superfamilies: Cynipoidea Ashmead, Cret (correlation uncertain): Ichneumonoidea Konow, Jur Call-Oxf, (See *Mesaulacinus* above): Chalcidoidea Ashmead, Cret (correlation uncertain): Serphoidea Kieffer, Jur Call-Oxf, (see *Mesohelorus* above); Bethyloidea Handlirsch, Tert L/M Olig. All Extant.

Section ACULEATA Latreille 1807

First, Tert L. Eoc: *Eoponera berryi* Carpenter 1930, Wilcox, Tennessee. **Extant.**

Comment: The aculeates probably underwent their principal radiation in the Cretaceous, but no certain fossils of this age are known. *Cretavus sibiricus* Sharov 1957, Cret Coniac-Santon-Campan, Kas river, Krasnoyarsk Region, U.S.S.R., has been claimed to be aculeate, but is here regarded as *incert. sed.*

Constituent superfamilies: Scolioidea Ashmead, Tert L/M Olig; Formicoidea Ashmead, Tert L. Eoc (see *Eoponera* above); Pompiloidea Berland, Tert L/M Olig; Vespoidea Ashmead, Tert L/M Olig; Sphecoidea Ashmead, Tert L/M Olig; Apoidea Ashmead, Tert L/M Olig. All Extant. [J.S. & R.J.W.]

Order COLEOPTERA Linnaeus 1758

First, Perm Leonard: *Tshekardocoleus magnus* Rohd. & *T. minor* Ponomarenko, Kungursk series, Urals, Russia (Rohdendorf & Ponomarenko 1962). **Extant.**

Comment: Fossils of this order usually readily recognisable and common from Upper Permian onwards.

Suborder ARCHOSTEMATA Kolbe 1911

First: As for Coleoptera. 2 extant families, Cupedidae & Micromalthidae. **Extant.**

Comment: The Lower Permian fossils all more or less aberrant in elytral structure. All Permian specimens in which ventral structures are seen agree in this with family Cupedidae, though some have elytra unlike extant Cupedidae and resembling various Polyphaga.

Suborder ADEPHAGA Clairville 1806

Section GEADEPHAGA

First, Jur ?Sinem: *Notokistus brodiei* Handlirsch (1908) (?Carabidae), Lower Lias, Gloucestershire, England. **Extant.**

Comment: Ponomarenko informs me (*in litt.*) that he has seen fossils apparently intermediate between Cupedidae and Geadephaga from Triassic deposits in Russia.

Section HYDRADEPHAGA

First, Jur ?Toarc: *Angaragabus jurassicus* Ponomarenko (1963) (?Noteridae; *Liadytes avus* Ponom. from same deposits may be adult of same species), Angara River, Siberia, USSR. **Extant.**

Comment: Large Dytiscid-like forms occur in Solnhofen Lithographic Stone, 'Tith' (Handlirsch 1908); *Coptoclava longipoda* Ping (Ponomarenko 1961) from Lower Cretaceous of China apparently the larva of an Amphizoid-like form.

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Suborder MYXOPHAGA Crowson 1955

No fossil record.

Comment: Existing species very small, probably overlooked as fossils.

Suborder POLYPHAGA Emery 1886

First, Jur Hett: *Aphodiites protogaea* Heer (1865), Lower Lias, Schambelen, Aargau, Switzerland. **Extant.**

Comment: Suborder reliably separable from Archostemata and Myxophaga only by lack of noto-pleural suture in prothorax, a character rarely visible in fossils.

Superfamily HYDROPHILOIDEA (PALPICORNIA auctt.)

First, Jur 'Tith': *Pseudohydrophilus avitus* Heyden (?Hydrophilidae), Lithographic stone, Solnhofen, Germany (Handlirsch 1908). **Extant.**

Comment: Most distinctive feature of the superfamily is in antennae, very rarely visible in fossils.

Superfamily HISTEROIDEA Crowson 1955

First, Tert U. Eoc-L/M. Olig: several spp., Baltic Amber, Kaliningrad region, U.S.S.R. (Klebs 1910). **Extant.**

Comment: The group should be recognisable in fossils from truncate elytra and general form.

Superfamily STAPHYLINOIDEA Ganglbauer 1895

First, Tert U. Eoc-L/M. Olig: several spp. and several families, Baltic Amber, Kaliningrad region, U.S.S.R. (Klebs 1910). **Extant.**

Comment: Family Staphylinidae readily recognisable in fossils, but other families not so.

Superfamily SCARABAEOIDEA (LAMELLICORNIA auctt.)

First, as for Polyphaga (q.v.). **Extant.**

Comment: Probably the first Polyphagan group to develop a distinctive facies, recognisable in fossils.

Superfamily EUCINETOIDEA Crowson 1960

First, Tert U. Eoc-L/M. Olig: *Brachelodes motschulskyi* and other spp., (Helodidae), Baltic Amber, Kaliningrad region, U.S.S.R. (Yablokoff-Khnzorian 1961). **Extant.**

Comment: Klebs (1910) also lists spp. of Clambidae from Baltic Amber. *Praemordella martynovi* Scegoleva-Barovskaya (U. Jur, Kara-Tau, U.S.S.R.; see Rohdendorf & Ponomarenko 1962), attributed to Mordellidae, might well be a Eucinetid.

Superfamily DASCILLOIDEA Boving & Craighead 1931

First, Jur Kimm: *Mesodascilla jacobsoni* Martynov (see Rohdendorf & Ponomarenko 1962) (Dascillidae), Kara-Tau, U.S.S.R. **Extant.**

Superfamily BYRRHOIDEA Boving & Craighead 1931

First, Tert U. Eoc-L/M. Olig: several spp. (Byrrhidae), Baltic Amber, Kaliningrad region, U.S.S.R. (Klebs 1910). **Extant.**

Comment: Fossils will be difficult to distinguish from Chelonariidae, Limnichidae, Nosodendridae, etc..

Superfamily DRYOPOIDEA Boving & Craighead 1931

First, Jur 'Tith': *Parasilphites angusticollis* Oppenheimer probably family Dryopidae, Lithographic stone, Solnhofen, Germany (Handlirsch 1908). **Extant.**

Comment: *Tersus crassicornis* Martynov (Jur Kimm: Kara-Tau, U.S.S.R.; Rohdendorf & Ponomarenko 1962), described as Elateridae, could as well belong in this superfamily.

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Superfamily BUPRESTOIDEA Crowson 1955

First, L. Eoc: *Chlorodema primordialis* (Pongracz), family Buprestidae, Brown Coal, Geiseltal, Germany (Haupt 1950). **Extant.**

Comment: Many Mesozoic fossils attributed to Buprestidae, but unreliably in absence of ventral structures.

Superfamily ELATEROIDEA Leng 1920

First, Jur Hett: *Megacentrus tristis* Heer (1865) (?Elateridae), Lower Lias, Schambelen, Switzerland. **Extant.**

Comment: *Tersus crassicornis* Martynov may belong here or in Dryopoidea (*q.v.*).

Superfamily CANTHAROIDEA Reitter 1906

First, Tert U. Eoc-L/M. Olig: several families and many spp., Baltic Amber, Kaliningrad region, U.S.S.R. (Klebs 1910). **Extant.**

Comment; In fossils, probably liable to confusion with Cleroidea, Lymexyloidea, Heteromera and perhaps some Dascilloidea or Staphylinoidea.

Superfamily DERMESTOIDEA Crowson 1955

First, Tert U. Eoc-L/M. Olig: several spp. of Dermestidae, Baltic Amber, Kaliningrad region, U.S.S.R. (Klebs 1910). **Extant.**

Comment: The group will not be readily recognisable in Mesozoic fossils.

Superfamily BOSTRYCHOIDEA Kolbe 1908

First, L. Eoc: *Venablesia colluvium* Britton (1960) (Anobiidae), London Clay, Bognor, England. **Extant.**

Comment: The special form of the prothorax should aid the recognition of this group among older fossils, though this is approached in Curculionoidea-Scolytidae.

Superfamily CLEROIDEA Böving & Craighead 1931

First, Tert U. Eoc-L/M. Olig: *Prospinoza baltica* Crowson (1964) (Cleridae). Klebs (1910) lists several spp. each of families Trogossitidae, Cleridae, Melyridae; Baltic Amber, Kaliningrad region, U.S.S.R. **Extant.**

Comment: Group not likely to be readily recognized in Mesozoic fossils.

Superfamily LYMEXYLOIDEA Böving & Craighead 1931

First, Tert U. Eoc-L/M. Olig: 3 genera of Lymexylidae, Baltic Amber, Kaliningrad region, U.S.S.R. (Klebs 1910). **Extant.**

Superfamily STYLOPOIDEA (STREPSIPTERA auctt.).

First, Tert U. Eoc-L/M. Olig: *Mengea tertiaria* Menge, Baltic Amber, Kaliningrad region, U.S.S.R. (Ulrich 1943). **Extant.**

Comment: *Mengea* notably more primitive than extant Stylopoids, suggests that ancestry of the group not much older than Tertiary.

Superfamily CUCUJOIDEA Böving & Craighead 1931

Section CLAVICORNIA

First, Jur Kimm: *Nitidulina eclavata* Martynov, Kara-Tau, U.S.S.R. (Rohdendorf & Ponomarenko 1962). **Extant.**

Comment: *Parandrexia* Martynov, from the same locality, probably belongs in Clavicornia rather than Cerambycidae.

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Section HETEROMERA

First, Tert M. Eoc: *Eodromus agilis* (Meunier) (Tenebrionidae), Brown Coal, Geiseltal, Germany (Haupt 1950). **Extant.**

Comment: Mesozoic fossils attr. to Heteromera all doubtful, e.g. the Jurassic (Kara-Tau) spp. *Necromera baeckmanni* (see Chrysomeloidea) and *Praemordella martynovi* Sceg.-Bar. (see Eucineoidea).

Superfamily CHRYSOMELOIDEA (PHYTOPHAGA auctt.)

First, Tert M. Eoc: *Eosagra subparallela* Haupt (1950), Brown coal, Geiseltal, Germany. (Chrysomelidae). **Extant.**

Comment: *Necromera baeckmanni* Martynov (Jur Kimm, Kara-Tau, U.S.S.R.) seems to me likely to be an ancestral Cerambycid type rather than a Heteromeran.

Superfamily GURCULIONOIDEA (RHYNCHOPHORA auctt.)

First, Jur Kimm: *Archaeorrhynchus tenuicornis* Martynov (?Nemonychidae), Kara-Tau, U.S.S.R. (Rohdendorf & Ponomarenko 1962). **Extant.**

Comment: Group readily recognisable by rostrate head. [R.A.C.]

Order STREPSIPTERA Kirby 1913

Imms (1957) gives this group full ordinal status. This procedure is questioned by many authors who regard the insects comprised in the order as constituting a Superfamily, Stylopoidea, of the Order Coleoptera. It is so treated on page 527. [J.S. & R.J.W.]

REFERENCES

- BACHOFEN VON ECHT, A. F. 1942. Über die Myriapoden des Bernstein. *Palaeobiologica*, **7**, 394-403.
- BEKKER-MIGDISOVA, E. E. 1958. [New Homopterous insects, Part 1]. *Mater. Osnov. paleont.* **2**, 57-67 (Russian).
- 1960a. [Palaeozoic Homoptera of the U.S.S.R. and the question of the phylogeny of the Order]. *Paleont. Zh.*, **3**, 28-42 (Russian).
- 1960b. [New Permian Homoptera of the European part of the U.S.S.R.]. *Trudy paleont. Inst.*, **76**, 1-112 (Russian).
- 1961. Homoptera, in ROHDENDORF, BEKKER-MIGDISOVA, MARTYNOVA & SHAROV 1961. (*q.v.*).
- 1962. Various groups, in ROHDENDORF, B. B. (Editor) 1962b. (*q.v.*).
- & VISHNYAKOVA, V. N. 1962. Psocoptera, in ROHDENDORF, B. B. (Editor) 1962b. (*q.v.*).
- BERLAND, L. & GRASSÉ, P.-P. 1951. Super-Ordre des Néuroptéroïdes, in GRASSÉ, P.-P. (Editor) 1951, (*q.v.*).
- BODE, A. 1953. Die Insektenfauna des Ostniedersächsischen Oberen Lias. *Palaeontographica.*, **103A**, 1-375.
- BRADÉ-BIRKS, G. 1923. Notes on Myriapoda XXVIII. *Kampecaris tuberculata* nov. sp. from the Old Red Sandstone of Ayrshire. *Proc. R. phys. Soc. Edinb.*, **20**, 277-280.
- BRITTON, E. B. 1960. Beetles from the London Clay at Bognor Regis, Sussex. *Bull. Br. Mus. nat. Hist., Geol.*, **4**, 29-50.
- BROILI, F. 1928. Crustaceenfunde aus dem rheinischen Unterdevon, I. Über extremitätenresten. *Sber. bayer. Akad. Wiss. (Math.-Naturh. Abt.)*, 1928, 197-201.
- 1929. Beobachtungen an neuen Arthropodenfunden aus den Hunsrückschiefern; ein Pantopode aus dem rheinischen Unterdevon; *Sber. bayer. Akad. Wiss. (Math.-Naturh. Abt.)*, 1929, 272-280, pl. 5.
- CARPENTER, F. M. 1930. The Lower Permian insects of Kansas. Part I. *Bull. Mus. comp. Zool. Harv.*, **70**, 69-101.
- 1932. The Lower Permian insects of Kansas, Part 5. *Am. J. Sci.*, **24**, 1-22.

Chapter 19: Arthropoda: Chelicerata, Pycnogonida, Palaeoisopus, Myriapoda, Insecta

- 1933. The Lower Permian insects of Kansas. Part 6 *Proc. Am. Acad. Arts. Sci.*, **68**, 411–503 pl. 1.
- 1936. The Lower Permian insects of Kansas. Part 7. *Proc. Am. Acad. Arts. Sci.*, **70**, 103–146.
- 1943a. The Lower Permian insects of Kansas, Part 9. *Proc. Am. Acad. Arts. Sci.*, **75**, 55–84.
- 1943b. Studies on Carboniferous Insects from Commentry; Part I. Introduction and Families Protagriidae, Meganeuridae and Campylopteridae. *Bull. geol. Soc. Am.*, **54**, 527–554.
- 1947. Lower Permian insects from Oklahoma, Part 1. *Proc. Am. Acad. Arts. Sci.*, **76**, 25–54.
- 1950. The Lower Permian insects of Kansas. Part 10. *Proc. Am. Acad. Arts. Sci.*, **78**, 185–210.
- 1951. Studies on Carboniferous insects from Commentry, France: Part II. The Megaseoptera. *J. Paleont.*, **25**, 336–355.
- 1954a. The Baltic Amber Mecoptera. *Psyche, Camb.*, **61**, 31–40.
- 1954b. In BRUES, C. T., MELANDER, A. L. and CARPENTER, F. M. Classification of Insects. *Bull. Mus. comp. Zool. Harv.*, **108**, 777–827.
- 1960. Studies on North American Carboniferous Insects. 1. The Protodonata. *Psyche, Camb.*, **67**, 98–110.
- 1961. Studies on Carboniferous Insects of Commentry, France; Part III. The Caloneurodea. *Psyche, Camb.*, **68**, 145–153.
- 1963a. Studies on Carboniferous insects from Commentry, France: Part IV. The Genus *Triplosoba*. *Psyche, Camb.*, **70**, 120–128.
- 1963b. Studies on Carboniferous Insects of Commentry, France: Part V. The genus *Diaphanoptera* and the order Diaphanopteroidea. *Psyche, Camb.*, **70**, 240–256.
- 1965. Studies on North American Carboniferous insects. 4. The genera *Metroptator*, *Eubleptus*, *Hapaloptera* and *Hadentomum*. *Psyche, Camb.*, **72**, 175–190.
- & KUKALOVA, J. 1964. The structure of the Protelytroptera, with description of a new genus from Permian strata of Moravia. *Psyche, Camb.*, **71**, 193–197.
- CASTER, K. E. & BROOKS, H. K. 1956. New Fossils from the Canadian-Chazyan (Ordovician) Hiatus in Tennessee. *Bull. Am. Paleont.*, **36**, 157–99, pls. 12–23.
- & KJELLESVIG-WAERING, E. N. 1964. Upper Ordovician Eurypterids of Ohio. *Palaeontogr. am.*, **4**, no. 32, 301–54, pls. 43–53.
- & MACKE, W. B. 1952. An aglaspid Merostome from the Upper Ordovician of Ohio. *J. Paleont.*, **26**, 753–7, pl. 109, fig. 1.
- CHINA, W. E. 1962. South American Peloridiidae (Hemiptera-Homoptera: Coleorrhyncha). *Trans. R. ent. Soc., Lond.*, **114**, 131–161.
- CLARKE, B. B. 1952. The geology of Dinmore Hill, Herefordshire, with a description of a new Myriapod from the Dittonian rocks there. *Trans. Woolhope nat. Fld Club.*, **33**, 222–236.
- CRAMPTON, G. C. 1930. The wings of the remarkable archaic Mecopteron *Notiothauma reedi* McLachlan, with remarks on their Protoblattoid affinities. *Psyche, Camb.*, **38**, 1–21.
- CROWSON, R. A. 1955. *The Natural Classification of the Families of Coleoptera*, 187 pp. London, Lloyd.
- 1960. The Phylogeny of Coleoptera. *A. Rev. Ent.*, **5**, 111–134.
- 1964. A Review of the Classification of Cleroidea. *Trans. R. ent. Soc. Lond.*, **116**, 275–327.
- CURRIE, L. D. 1927. On Cyamocephalus, a new Synxiphosuran from the Upper Silurian of Lesmahago, Lanarkshire. *Geol. Mag.*, **64**, 153–7, text fig.
- DEMOULIN, G. 1954. Quelques remarques sur les Archodonates. *Bull. Anns. Soc. ent. Belg.*, **90**, 327–337.
- DENNIS, R. 1949a. Ordre des Zoraptères, in GRASSÉ, P.-P. (Editor), 1949. (*q.v.*).
- 1949b. Sous-Classe des Aptérygotes, in GRASSÉ, P.-P., (Editor), 1949. (*q.v.*).
- EVANS, J. W. 1956. Palaeozoic and Mesozoic Hemiptera (Insecta). *Aust. J. Zool.*, **4**, 165–258.
- 1963. The Phylogeny of the Homoptera. *A. Rev. Ent.*, **8**, 77–94.
- 1964. The periods of origin and diversification of the Superfamilies of the Homoptera-Auchenorrhyncha (Insecta) as determined by a study of the wings of Palaeozoic and Mesozoic fossils. *Proc. Linn. Soc. Lond.*, **175**, 171–181.

The Fossil Record, Part II

- FLOWER, R. H. 1945. A new Deepkill Eurypterid; *Am. Midl. Nat.*, **34**, 717–9, fig.
- FRASER, F. C. 1957. *A reclassification of the Order Odonata, Handbook No. 12*, 133 pp.. Royal Zoological Soc. N.S.W. (A revised edition of Tillyard & Fraser, (1938–1940). (*q.v.*)).
- GRASSÉ, P.-P. (Editor). 1949. *Traité de Zoologie*, **9**, 1117 pp. (Insectes: Paléontologie, Géonémie, Aptérygotes, Ephéméroptères, Odonatoptères, Blattoptéroïdes, Orthoptéroïdes, Dermaptéroïdes, Coléoptères). Masson, Paris.
- 1951a. Ordre des Mécoptères, in GRASSÉ, P.-P. (Editor). 1951b (*q.v.*).
- (Editor). 1951b. *Traité de Zoologie*, **10** (2 fascicules), 1948 pp. (Insectes Supérieurs et Hémiptéroïdes). Masson, Paris.
- GUTHÖRL, P. 1936. *Arthropleura*, der Riesengliederfüßler des Oberkarbons und seine Verbreitung in dem europäischen Steinkohlenbecken. *Glückauf*, **72**, 965–975.
- HAASE, E. 1890. Beiträge zur Kenntnis der fossilen Arachniden. *Z. dt. geol. Ges.*, **42**, 629–657.
- HANDLIRSCH, A. 1906–1908. *Die fossilen Insekten und die Phylogenie der Rezenten Formen*. Engelmann, Leipzig.
- 1925. Überordnung: Neuropteroidea Handl. oder Plannipennia (Banks) (Netzflugler). in SCHRODER, C. *Handbuch der Entomologie*, **3**, 825–840.
- 1938. Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nächstträgen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme, Teil II. *Annl. naturh. Mus. Wien.*, **49**, 1–240.
- HANDSCHIN, E. 1926. Revision der Collembollen des baltischen Bernsteins. *Ent. Mitt.*, **15**, 161–185, 211–223, 330–342.
- HAUPT, H. 1950. Die Käfer aus der Eozänen Braunkohle Geiseltales. *Geologica Berl.*, no. 6, vii + 168 pp.
- HEER, O. 1865. *Urwelt der Schweiz*. Zürich.
- HINTON, H. E. 1958. The phylogeny of the Panorpid Orders. *A. Rev. Ent.*, **3**, 181–206.
- HIRST, S. 1923. On some arachnid remains from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire). *Ann. Mag. nat. Hist.* (9), **12**, 455–474.
- HOLLAND, G. P. 1964. Evolution, Classification and Host Relationships of Siphonaptera. *A. Rev. Ent.* **9**, 123–146.
- ILLIES, J. 1965. Phylogeny and zoogeography of the Plecoptera. *A. Rev. Ent.*, **10**, 117–140.
- IMMS, A. D. 1944. On the constitution of the maxillae and labium in Mecoptera and Diptera. *Q. Jl microsc. Sci.*, **85**, 73–96.
- 1957. *A General Textbook of Entomology*, (RICHARDS, O. W., and DAVIES, R. G. Editors), 886 pp., Methuen, London.
- JEANNEL, R. 1949. Classification et Phylogénie des Insectes, in GRASSÉ, P.-P. (Editor) 1949 (*q.v.*).
- KJELLESVIG-WAERING, E. N. 1948. The Mazon Creek Eurypterid; A Revision of the Genus *Lepidoderma*. *Ill. St. Mus., Sci. Pap.*, 2 no. 4, 46 pp, 1 text fig, 8 pls.
- 1959. A taxonomic Review of some late Palaeozoic Eurypterida. *J. Paleont.*, **33**, 251–6, pl. 38.
- 1963. Pennsylvanian Invertebrates of the Mazon Creek Area, Illinois: Eurypterida. *Fieldiana: Geol.*, 12, no. 6, 85–106.
- 1964. A Synopsis of the Family Pterygotidae Clarke and Ruedemann, 1912 (Eurypterida) *J. Paleont.*, **38**, 331–61, pls. 53–6.
- 1966. Silurian scorpions from New York. *J. Paleont.*, **40**, 359–375.
- KLEBS, R. 1910. Über Bernsteineinschlüsse in allgemeinen und die Coleopteren meiner Bernsteinsammlung. *Schr. phys.-ökon. Ges. Königsb.*, **51**, 217–242.
- KUKALOVA, J. 1959. On the Family Blattinopsidae Bolton, 1925. (Insecta, Protorthoptera). *Rozpr. ěsl. Akad. Věd, Rada M.P.V.*, **69**, 1–30, pl. 1–2.
- 1963a. Permian insects of Moravia. 1. Miomoptera. *Sb. geol. Věd series P*, **1**, 7–52, pls. 1–16.
- 1963b. To the taxonomy of Palaeodictyoptera (Insecta). *Vest. ústřed Úst. geol.*, **38**, 197–200.
- 1964a. To the Morphology of the oldest known dragon fly *Erasipteron larischi* Pruvost, 1933. *Vest. ústřed Úst. geol.*, **39**, 463–464, 1 plate.

Chapter 19: Arthropoda: Chelicerata, Pycnogonida, Palaeoisopus, Myriapoda, Insecta

- 1964b. Permian insects of Moravia, Part 2. *Sb. geol. Véd series P*, **3**, 39–118, 24 plates.
- 1964c. Permian Protelytroptera, Coleoptera and Protorthoptera (Insecta) of Moravia. *Sb. geol Véd series P*, **6**, 61–98, 8 plates.
- KUZNETZOV, N. Y. 1941. [A revision of the Amber *Lepidoptera*], 136 pp. Akademii Nauk SSSR, Moscow and Leningrad (Russian with English summary).
- LAURIE, M. 1899. On a Silurian scorpion and some additional eurypterid remains from the Pentland Hills. *Trans. R. Soc. Edinb.*, **39**, 575–590.
- LEHMANN, W. M. 1944. *Paleoscorpilus devonicus* n.g., n.sp., ein Skorpion aus dem rheinischen Unterdevon. *Neues Jb. Miner. Geol. Paläont., Mh.*, 1944, 177–185.
- LEUTZE, W. P. 1961. Arthropods from the Syracuse Formation, Silurian of New York. *J. Paleont.*, **35**, 49–64, pls. 15–16.
- MCCOOK, H. C. 1888. A new fossil spider, *Eoatypus woodwardii*. *Proc. Acad. nat. Sci. Philad.*, 1888, 200–202.
- MARTYNOV, A. V. 1925a. Über zwei Grundtypen der Flügel bei den Insekten und ihre Evolution. *Z. Morph. Ökol. Tiere*, **4**, 465–501.
- 1925b. [To the knowledge of fossil insects from Jurassic beds in Turkestan, Part 2]. *Izd. Akad. nauk. SSSR*, **19**, 569–598 (Russian).
- 1928. A new fossil form of Phasmatodea from Galkino (Turkestan) and on Mesozoic Phasmids in general. *Ann. Mag. nat. Hist.* (10), **1**, 319–328.
- 1930. [Palaeozoic Insects from the Kuznetz Basin]. *Izv. glav. geol.-razved. Uprav.*, **49** (10), 73–100 (Russian).
- 1933. [On the Permian family Archescytinidae (Homoptera) and its relationship]. *Izv. Akad. nauk SSSR*, for 1933, 833–894. (Russian).
- 1937. [Wings of termites and phylogeny of Isoptera and of allied groups of Insects] in *N. V. Nasonov Commemorative volume*, 93–150. *Inst. Evol. Morph.*, Akademii Nauk SSSR, Moscow and Leningrad (Russian with English summary).
- 1938a. [On a new Permian order of orthopterous insects, Glosselytrodea]. *Izv. Akad. nauk SSSR Ser. Biol.*, for 1938, 187–206 (Russian).
- 1938b. [Permian fossil insects from the Archangelsk District. Part V]. *Trudy Paleont. Inst.*, **7**(3), 69–80 (Russian).
- MARTYNOVA, O. M. 1948. [Material on the evolution of the Mecoptera]. *Trudy Paleont. Inst.*, **14**, 1–77 (Russian).
- 1952. [The Order Glosselytrodea in Permian deposits of the Kemerov District]. *Trudy Paleont. Inst.*, **40**, 187–196 (Russian).
- 1959. [Phylogenetic inter-relationships of insects of the mecopteroid complex]. *Trudy Inst. Morf. Zhivot.*, **27**, 221–229 (Russian).
- 1961. Palaeoentomology. *Ann. Rev. Ent.*, **6**, 285–293.
- 1962. Various groups in ROHDENDORF, B. B. (Editor). 1962. (*q.v.*).
- MEEK, F. B. & WORTHEN, A. H. 1868. Arachnida, pp. 560–563 in *Geological Survey of Illinois*, Volume 3, Springfield, Illinois.
- PEACH, B. N. 1882. On some fossil myriapods from the Old Red Sandstone of Forfarshire. *Proc. R. phys. Soc. Edinb.*, **7**, 177–188.
- 1883. On the occurrence of Pterygotus and a limuloid in the Caithness Flagstones and on the nature and mode of formation of “Adam’s Plates”. *Proc. R. phys. Soc. Edinb.*, **7**, 343–50, pl. 7.
- 1898. On some new myriapods from the Palaeozoic rocks of Scotland. *Proc. R. phys. Soc. Edinb.*, **14**, 113–126.
- PETRUNKEVITCH, A. 1913. A monograph of the terrestrial Paleozoic arachnids of North America. *Trans. Conn. Acad. Arts. Sci.*, **18**, 1–137.
- 1949. A study of Paleozoic Arachnida. *Trans. Conn. Acad. Arts. Sci.*, **37**, 60–315.
- 1953. Paleozoic and Mesozoic Arachnida of Europe. *Mem. geol. Soc. Am.*, **53**, 128 pp., 58 plates.
- 1955. *Trigonotarbus arnoldi*, a new species of fossil arachnid from southern France. *J. Paleont.*, **29**, 475–477.

The Fossil Record, Part II

- PIERCE, W. D. 1950–1951. Fossil arthropods from the onyx marble. *Bull. Sth. Calif. Acad. Sci.*, **49**, 101–104 and **50**, 34–49.
- PIVETEAU, J. (Editor) 1953. *Traité de Paléontologie*, Volume 3. Paris, Masson.
- PONOMARENKO, A. G. 1961. [On the systematic position of *Coptoclava* Ping]. *Paleont. Zh.*, **3**, 67–72 (Russian).
- 1963. [Early Jurassic Water-beetles from Angara]. *Paleont. Zh.*, **4**, 128–131 (Russian).
- PŘIBYL, A., 1960. Nove poznatky o Svrchnokarbonske sladkovodni a kontinentalni faune z Ostravskokarvinske oblasti. *Rozpr. čsl. Akad. Věd.*, **70**, 1–71.
- PRUVOST, P. 1919. La faune du terrain Houiller du Nord de la France. *Mem. Serr. carte géol. det. Fr.*
- 1930. La faune continentale du terrain houiller de la Belgique. *Mém. Mus. r. Hist. nat. Belg.*, **44**, 206–217.
- RAASCH, G. O. 1939. Cambrian Merostomata. *Spec. Pap. geol. Soc. Am.*, **19**, 146 pp, pl. 1–21, fig. 1–14.
- RAGGE, D. R. 1955. *The wing-venation of the Orthoptera Saltatoria, with notes on dictyopteran wing-venation*. British Museum (Natural History), London.
- RASNITZYN, A. P. 1963. [Late Jurassic Hymenoptera of Karatau]. *Paleont. Zh.*, 1963, (1), 86–99 (Russian).
- 1964. [New Triassic Hymenoptera of Central Asia]. *Paleont. Zh.*, 1964, (1), 88–96 (Russian).
- REBEL, H. 1936. Mikrolepidopteren aus dem baltischen Bernstein. *Naturwissenschaften*, **24** (33), 519–520.
- RICHTER, R. & RICHTER, E. 1929. Weinbergina opitzi, n.g., n.sp., ein Schwertträger (Merost., Xiphos.) aus dem Devon (Rheinland). *Senckenbergiana*, **11**, 193–209, figs. 1–4.
- RIEK, E. F. 1953. Fossil Mecopteroïd insects from the Upper Permian of New South Wales. *Rec. Aust. Mus.*, **23**, 55–87.
- 1955. Fossil Insects from the Triassic beds at Mt. Crosby, Queensland. *Aust. Jl Zool.*, **3**(4): 654–691.
- 1956. A re-examination of the Mecopteroïd and Orthopteroïd fossils (Insecta) from the Triassic beds of Denmark Hill, Queensland, with descriptions of further specimens. *Aust. J. Zool.*, **4**, 98–110.
- ROHDENDORF, B. B. 1946. [The evolution of the wing and the Phylogeny of Oligoneura (Diptera, Nematocera)]. *Trudy paleont. Inst.*, **13** (2), 1–108, 16 pls. (Russian with an English summary).
- 1951. [Organs of locomotion of two-winged insects and their origin]. *Trudy paleont. Inst.*, **35**, 1–179 (Russian).
- 1959. Die Bewegungsorgane der Zweiflügerinsekten und ihre Entwicklung, parts I–III. *Wiss. Z. Humbolt-Univ. Berl.*, **8**, 73–119, 269–308 and 435–454 (ROHDENDORF 1951 translated into German).
- 1961a. [The description of the first winged insect from the Devonian Beds of the Timan (Insecta, Pterygota)]. *Ent. Obozr.*, **40**, 485–489, 2 figs. (Russian with English summary).
- 1961b. Neue Angaben über das System der Dipteren. *Proc. 11th Int. Congr. Ent., Wien*, 1960, **I**, 153–158.
- 1962a. Various groups in ROHDENDORF, B. B. (Editor) 1962b (*q.v.*).
- (Editor). 1962b. *Osnovy Paleontologii: Chlenistonogie Trakheinye i Kheliterovye*. Akademii Nauk SSSR, Moscow.
- 1964. [Historical development of two-winged insects]. *Trudy paleont. Inst.*, **100**, 1–311. (Russian).
- , BEKKER-MIGDISOVA, E. E., MARTYNOVA, O. M. & SHAROV, A. G. 1961. [Palaeozoic insects of the Kuznetsk Basin]. *Trudy paleont. Inst.*, **85**, 1–705 (Russian).
- & PONOMARENKO, A. G. 1962. In ROHDENDORF, B. B. (Editor) 1962b (*q.v.*).
- ROLFE, W. D. I. & INGHAM, J. K. 1967. Limb structure, affinity and diet of the Carboniferous “centipede” *Arthropleura*. *Scott. J. Geol.*, **3** (1): in press.
- RUEDEMANN, R. 1934. Eurypterids in Graptolite Shales. *Am. J. Sci.*, **157**, 374–85.

Chapter 19: *Arthropoda: Chelicerata, Pycnogonida, Palaeoisopus, Myriapoda, Insecta*

- 1942. Some new Eurypterids from New York, in *Paleontology and Geology, Cambrian and Ordovician Fossils*, pt. 2. *Bull. N.Y. St. Mus.*, **327**, 24–9.
- SCUDDER, S. H. 1890. New Carboniferous myriapoda from Illinois. *Mem. Boston. Soc. nat. Hist.*, **4**, 417–442.
- 1893. Tertiary Rynchophorous Coleoptera. *Monographs U.S. geol. Surv.*, **21**.
- SEGUY, E. 1959. Introduction a l'etude morphologique de l'aile des Insectes. *Mem. Mus. natn. Hist. nat., Paris*, Ser. A, **21**, 1–238.
- SMART, J. 1953. On the wing-venation of *Physemacris variolosa* (Linn.) (Insecta; Pneumoridae). *Proc. zool. Soc. Lond.*, **123**, 199–202.
- 1956. On the wing-venation of Chaetessa and other Mantids (Insecta; Mantodea). *Proc. zool. Soc. Lond.*, **127**, 545–553.
- 1963. Explosive Evolution and the Phylogeny of Insects. *Proc. Linn. Soc., Lond.*, **172**, 125–126.
- SHAROV, A. G. 1961a. On the system of the orthopterous insects. *Proc. 11th. Int. Congr. Ent., Wien*, **1**, 295–296.
- 1961b. The origin of the Order Plecoptera. *Proc. 11th. Int. Congr. Ent., Wien*, **1**, 296–298.
- 1962a. Redescription of *Lithophotona floccosa* Cock. (Manteodea) with some notes of the manted wing venation. *Psyche, Camb.*, **69**, 102–106.
- 1962b. Various groups in ROHDENDORF, B. B. (Editor) 1962b (*q.v.*).
- SOUTHWOOD, T. R. E. & LESTON, D. 1959. *Land and water bugs of the British Isles*. Warne, London and New York.
- STØRMER, L. 1934. Merostomata from the Downtonian Sandstone of Ringerike, Norway. *Skr. norske Vidensk-Akad.* 1933, no. 10, 1–125, pl. 1–12, figs. 1–39.
- 1955. A new Merostome from the Lower Cambrian of Kinnekulle, Sweden. *Ark. Zool.* (2) **9**, nr 25, 507–19.
- 1960. A scorpion-like eurypterid from the Lower Devonian of Germany. *21st Int. geol. Congr.*, part XXII, 87–91.
- 1963. *Gigantoscorpis willsi*, a new scorpion from the Lower Carboniferous of Scotland and its associated preying organisms. *Skr. norske Vidensk-Akad.*, new series, No. 8, 171 pp., 22 plates.
- TILLYARD, R. J. 1926. Order Neuroptera, in *The insects of Australia and New Zealand*, chap. 23, pp. 308–325. Angus & Robertson, Sydney.
- & FRASER, F. C. 1938–1940. A reclassification of the Order Odonata. Based on some new interpretations of the venation of the Dragonfly Wings. *Aust. Zool.*, **9**, 125–169, 195–221, 349–396 (see FRASER 1957).
- TREATISE, P. 1955. MOORE, R. C. (Editor). *Treatise on Invertebrate Paleontology, Part P: STØRMER, L., PETRUNKEVITCH, A. AND HEDGPETH, J. W., Chelicerata with sections on Pycnogonida and Palaeoisopus*. University of Kansas Press.
- TREATISE, R. (in press). MOORE, R. C. (Editor). *Treatise on Invertebrate Paleontology, Part R: Arthropoda 4*, University of Kansas Press.
- TREATISE, W. 1962 MOORE, R. C. (Editor). *Treatise on Invertebrate Paleontology, Part W: HAAS, W. H. et al. Miscellaneous*. University of Kansas Press.
- TSHERNOVA, O. A. 1965. [Some Fossil Mayflies (Ephemeroptera, Mesthodidae) from Permian-beds of the Ural]. *Ent. Obozr.*, **44**, 353–361 (Russian).
- ULRICH, W. 1943. Die Mengeiden und die Phylogenie der Strepsipteren. *Z. Parasit Kde*, **13**, 62–101.
- VAN STRAELEN, V., 1931. *Crustacea Eumalacostrac (Crustaceis decapodis exclusis)*. Foss. Cat. 1, pars 48, 98 pp.
- WILLS, L. J. 1959–1960. The external anatomy of some Carboniferous “Scorpions”. *Palaeontology*, **1**, 261–282 and **3**, 276–332.
- WOODWARD, H. 1868. On a new limuloid crustacean (*Neolimulus falcatus*) from the Upper Silurian of Lesmahagow, Lanarkshire. *Geol. Mag.*, **5**, 1–5.
- YABLOKOFF-KENZORIAN, S. M. 1961. [Representatives of the family Helodidae (Coleoptera) from the Baltic Amber]. *Paleont. Zh.*, **1**, 108–116 (Russian).

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- ZEUNER, F. E. 1939. *Fossil Orthoptera Ensifera*. British Museum (Natural History), London.
— 1960. A Triassic insect fauna from the Molteno beds of S. Africa. *Proc. 11th. Int. Congr. Ent., Wien*, 1, 304–306.

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