ARACHNIDA

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INTRODUCTION

Many arachnids were known and described before LINNÉ's time, but the history of arachnology begins with LAMARCK, who was the first to propose for them in 1801 a separate class which he named Arachnidae. Before him they were always treated as insects. In the 10th edition of LINNÉ's *Systema Naturae* the genera *Acarus, Aranea, Phalangium* and *Scorpio* are placed with the wingless insects, crustaceans, centipedes and millipedes in the 7th order, Aptera, a name which was still used by WALCKENAER in 1837-41. LINNÉ did not recognize families. In his classification genera were placed directly under orders. DEGEER seems to be one of the first zoologists who used the "family" in his classification, but he divided the genera into families and in 1778 listed 7 families under the genus *Aranea*. His classification also persisted for a number of years and was adopted by WALCKENAER in his celebrated *Histoire Naturelle des Insectes Aptères*. However, at the same time with DEGEER, BATSCH (1778) introduced the concept of the family as a group below the order and above the genus. This concept also found followers and we find LATREILLE using the term "family" in this sense in 1806 and LEACH in 1815. Thus two different concepts of the term "family" existed side by side for more than half a century until BATSCH's concept prevailed and was incorporated in the report of the Committee of the British Association for the Advancement of Science in 1842. Since the 14th International Congress of Zoology gave a precise definition of the Family-Group and Ordinal-Group categories, family names proposed by DEGEER and WALCKENAER cannot be used even when they have been latinized by the authors themselves, because according to WALCKENAER's own statement his families have been placed "under more general divisions called *Genera*." This complicates the problem of family priority in the case of all families proposed before 1842. I intend to discuss this subject in a separate paper which will be published elsewhere. Here I mention it only because certain changes in the names of higher categories introduced in the present paper may give the impression that I have changed the principles of my classification as laid down in my various studies of fossil Arachnida. The principles of classification remain the same. The changes involve only some names in conformity with the rules which I tried to follow to my best ability by tracing the priority of familial and ordinal names by careful examination of the original publications all the way back to LINNÉ's 10th edition. In doing so I had, of course, to depend upon the author's own statement as to which category he applied a certain name and to accept it as a family name when he called it "Family" and placed it under an order and above the genus, or as an order or class if he called it so. Such classes, orders and families rarely, if ever, correspond to the classes, orders and families which we now recognize. Thus, for example, Class Arachnida LAMARCK, 1801, does not mean at all that this class is used here in LAMARCK's sense, who included in it crustaceans, wingless insects, pycnogonids and myriapods, as well as spiders, scorpions, etc., which constitute only a small portion of it. It means only that LAMARCK was the first to propose the name Arachnida. In reality, his class was whittled down and added to and again trimmed many times in the course of the 150 years since its inception, until it assumed the content given it independently by STØRMER in Norway and myself in America.

Although the orders recognized by LAMARCK and his contemporaries differed greatly by their content from the orders which are recognized now, representatives of all but 3 of the latter were already known. The first representative of the order Ricinuleida was described by GUÉRIN in 1838 under the name of *Cryptostemma* (now *Ricinoides*) *westermanni* and placed in the order Phalangiida (harvestmen), in which it remained until the order Ricinulei was proposed by THORELL in 1892. The first representative of the order Schizomida was described by CAMBRIDGE in 1872 under the name of *Nyctalops* (now *Schizomus*) *crassicaudatus* and placed into a new family Tartarides in the order Pedipalpi. This family was raised to the rank of an order by me in 1945. Finally, the first representative of the order Palpigradida was described by GRASSI & CALANDRUCCIO in 1885 and named *Koenenia* (now *Eukoenenia*) *mirabilis*.

Fossil Arachnida found in Baltic amber must have been seen in ancient times, for TACITUS mentions insects enclosed in transparent amber. Since the middle of the past century many spiders were described, first in the Baltic amber (Fig. 31) and later in such Tertiary deposits as those of Aix-en-Provence and Florissant. However, the first scientific mention of fossil Arachnida was published in 1819 when SCHWEIGGER described and figured a spider, later named *Entomocephalus formicoides* by HOLL (1829), and a scorpion which HOLL named *Scorpio schweiggeri*.

The first Paleozoic arachnid, a scorpion, was described by CORDA in 1835 from the Carboniferous of Czechoslovakia. He named it *Cyclophthalmus senior*. No other fossil scorpions were found until 1868 when MEEK & WORTHEN described *Mazonia woodiana* and *Eoscorpius carbonarius*, both specimens from the Pennsylvanian of Mazon Creek, Illinois.

In the year 1836, following upon the description of *Cyclophthalmus,* Buckland figured in the first edition of his Bridgewater Treatise 2 fossils from the ironstone of Coalbrook Dale, naming them *Curculioides ansticii* and *C. prestvicii.* The former was recognized as an arachnid related to *Poliochera* by Scudder in 1884, who placed his family Poliocheridae in the order Anthracomarti (here Anthracomartida), from which it was removed by Pocock in 1902 into the order Ricinulei (here Ricinuleida), established by Thorell in 1892 for Recent arachnids of the family Cryptostemmidae (now Ricinoididae), formerly placed in the same order with harvestmen. *C. prestvicii* Buckland was removed to the genus *Eophrynus* by Woodward in 1877 and became the first representative of that order, which in 1949 I proposed to call Trigonotarbi (here Trigonotarbida) (Fig. 32). The first spider, i.e., the first representative of the order Araneida, was described by Römer in 1866 under the name *Protolycosa anthracophila,* from the Carboniferous of Upper Silesia. Eight years later, in 1874, the first American fossil spider *Arthrolycosa antiqua* was described by Harger from the Pennsylvanian of Mazon Creek (Fig. 32).

The first anthracomartid, *Brachypyge carbonis,* was discovered by Woodward in 1878, but he thought it to be a crab, and its true nature was recognized only in 1885 by Scudder, after *Anthracomartus völkelianus* had been described and figured by Karsch in 1882.

The first fossil whip scorpion was described by Kušta in 1884, who named it *Prothelyphonus bohemicus.* It was found in Rakonitz, Czechoslovakia. In the same year an American whip scorpion, *Geralinura carbonaria,* was described by Scudder.

The first representative of the fossil order Architarbida, *Architarbus rotundatus,* was discovered in America and described by Scudder in 1868. Four years later, in 1872, the first European species was discovered and named by Woodward *Architarbus* (now *Phalangiotarbus*) *subovalis.* In 1878 Scudder described and figured a fossil which he thought to be an insect and named *Libellula carbonaria.* In 1890 he realized his mistake, proposed for the fossil the new generic name *Graeophonus* and placed it in the arachnid order Pedipalpi. At his time, as indeed even much later, Latreille's order Pedipalpi was still generally accepted, although already reduced to include only whip scorpions, schizonotids (schizomids) and phrynichids. Pocock was the first to elevate the phrynichids to the rank of an order in 1900, for which he retained Thorell's suborder name Amblypygi. Thus, *Graeophonus carbonarius* became the first fossil representative of the order called here Phrynichida. A fossil representative of the former small suborder of Pedipalpi Tartarides, later elevated by me to the rank of an order which I named Schizomida (a *nom. transl.* from the family name of the type genus) was discovered by me in 1945 in the onyx marble of Arizona and named *Calcitro fisheri.*

A fossil arachnid described by Scudder in 1890 under the name of *Kustarachne tenuipes* was placed by me in 1913 in an order of its own, Kustarachnae (=Kustarachnida). The first fossil phalangiids (harvestmen), *Eotrogulus fayoli* and *Nemastomoides elaveris,* were described by Thevenin in 1901 from the Coal Measures of Commentry, France. In 1911 Pocock described the only fossil representative of his order Haptopoda (=Haptopodida) from the Coal Measures of England and named it *Plesiosiro madeleyi.* The only fossil representative of the order Solpugida was described by me in 1913 from the Pennsylvanian of Mazon Creek, under the name of *Protosolpuga carbonaria.*

Although in the middle of the past century several fossils from the Carboniferous of Europe were described as pseudoscorpions, their identification proved to be incorrect. We now know that fossil pseudoscorpions have been found so far only in Cenozoic deposits. They are well represented in the Baltic amber. The only fossil representative of the order Palpigradida was found by Oppenheim in the Jurassic lithographic shale of Germany in 1887. He mistook the fossil for an aquatic bug and called it *Halometra minor.* Its true nature was recognized by Haase in 1890 and as the name *Halometra* was preoccupied, Haase gave it its present name, *Sternarthron zitteli.*

Fossil Acarida were first discovered in Baltic amber. BERENDT & KOCH described several species of them in 1854. The only known Paleozoic species, *Protacarus crani,* was described by HIRST in 1923 from the Old Red Sandstone of Devonian age.

The number of fossil arachnid species discovered since the first Carboniferous scorpion was found has increased steadily at a fairly rapid rate, which slowed down

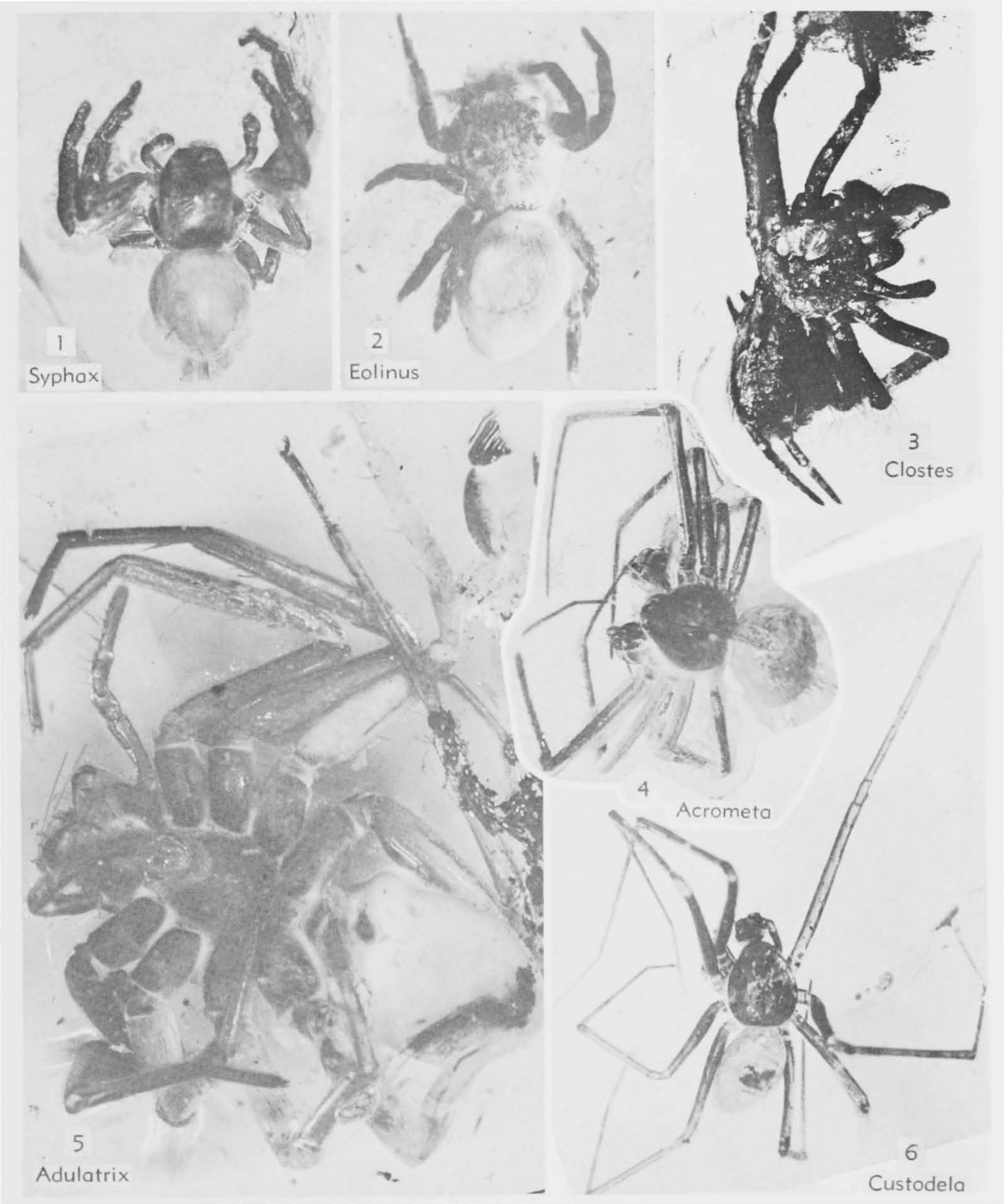

FIG. 31. Spiders (order Araneida) preserved in Oligocene amber of the Baltic region of Europe, photographs. *1, Syphax crassipes,* ×6.3. *2, Eolinus theryi,* ×11. *3, Clostes priscus,* ×8. *4, Acrometa cristata,* ×12. *5, Adulatrix fusca,* ×8.5. *6, Custodela cheiracantha,* ×6 (*76).

only in the second quarter of the present century. By now, every Recent order of Arachnida has one or more fossil representatives and in addition we know 5 Paleozoic orders which became extinct. The total number of species which can be recognized from descriptions and figures has reached about 500 or a few more. One-third of them are Paleozoic. The accompanying table shows their distribution in systematic orders and main geological eras. The table does not include unrecognizable species which were described at a time when indispensable specific characters were not yet understood or by investigators who were not professional arachnologists and who were unfamiliar with the distinctive characters even of orders. The figures given in the table for the number of Recent genera and species are only approximate. It is probable that they will continue to increase for some time to come and at a much more rapid pace than the number of new fossil species.

Numbers of Known Arachnid Genera and Species

Order	Paleozoic		Mesozoic		Tertiary		Quaternary	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
Scorpionida	26	42	2	7	2	2	70	600
Pseudoscorpionida	..	..	..	..	13	18	234	1,000
Phalangiida	2	4	..	..	9	16	640	2,350
Architarbida	14	25	..	..	..	..	..	..
Acarida	1	1	..	..	60	107	1,389	6,000
Haptopodida	1	1	..	..	..	..	..	..
Anthracomartida	11	20	..	..	..	..	..	..
Trigonotarbida	24	38	..	..	..	..	..	..
Palpigradida	..	..	1	1	..	..	4	21
Thelyphonida	2	5	..	..	1	1	10	70
Schizomida	..	..	..	..	2	2	3	28
Kustarachnida	1	3	..	..	..	..	..	..
Phrynichida	3	4	..	..	..	..	18	60
Araneida	16	18	..	..	94	180	2,735	25,000
Solpugida	1	1	..	..	..	..	134	600
Ricinuleida	2	9	..	..	..	..	2	16
Total	102	169	3	8	181	326	5,239	35,745

NOTE. The figures for Tertiary genera include extinct and surviving genera. Extinct Tertiary genera are restricted to the following 4 orders: Pseudoscorpionida, 5; Phalangiida, 1; Acarida, 10; Araneida, 67. Total extinct Tertiary genera, 83; surviving genera included in the Quaternary figures, as well as in the Tertiary ones, 98.

CLASSIFICATION

As explained in the introduction, the classification used in this article is essentially the same as that proposed by me in 1933 for families of spiders and in 1949 for orders of Arachnida. The latter differs only slightly from the generally accepted classification, inasmuch as it omits from the list of orders the name of Pedipalpi because that name stands for an incongruous group which I have divided into 3 natural orders, Thelyphonida, Schizomida, and Phrynichida. It also differs by the substitution of 2 older names, Phalangiida and Solpugida, for Opiliones and Solifugae, names which became more generally used in the 20th century. The definition of all orders takes into account structural differences shown by their fossil representatives, but in orders which survived, is primarily based on characters found in Recent species, the anatomy and embryology of which is by now known in such great detail. In extinct orders the definitions are of necessity limited to their known characters, but when these exhibit trends similar to those observed in living Arachnida, the evidence derived from the latter is taken into account.

The classification of the order Araneida, proposed by me in 1933 and supplemented in 1939 and 1942, is based on a correlation of external characters with comparative anatomy of internal organs. It differs from

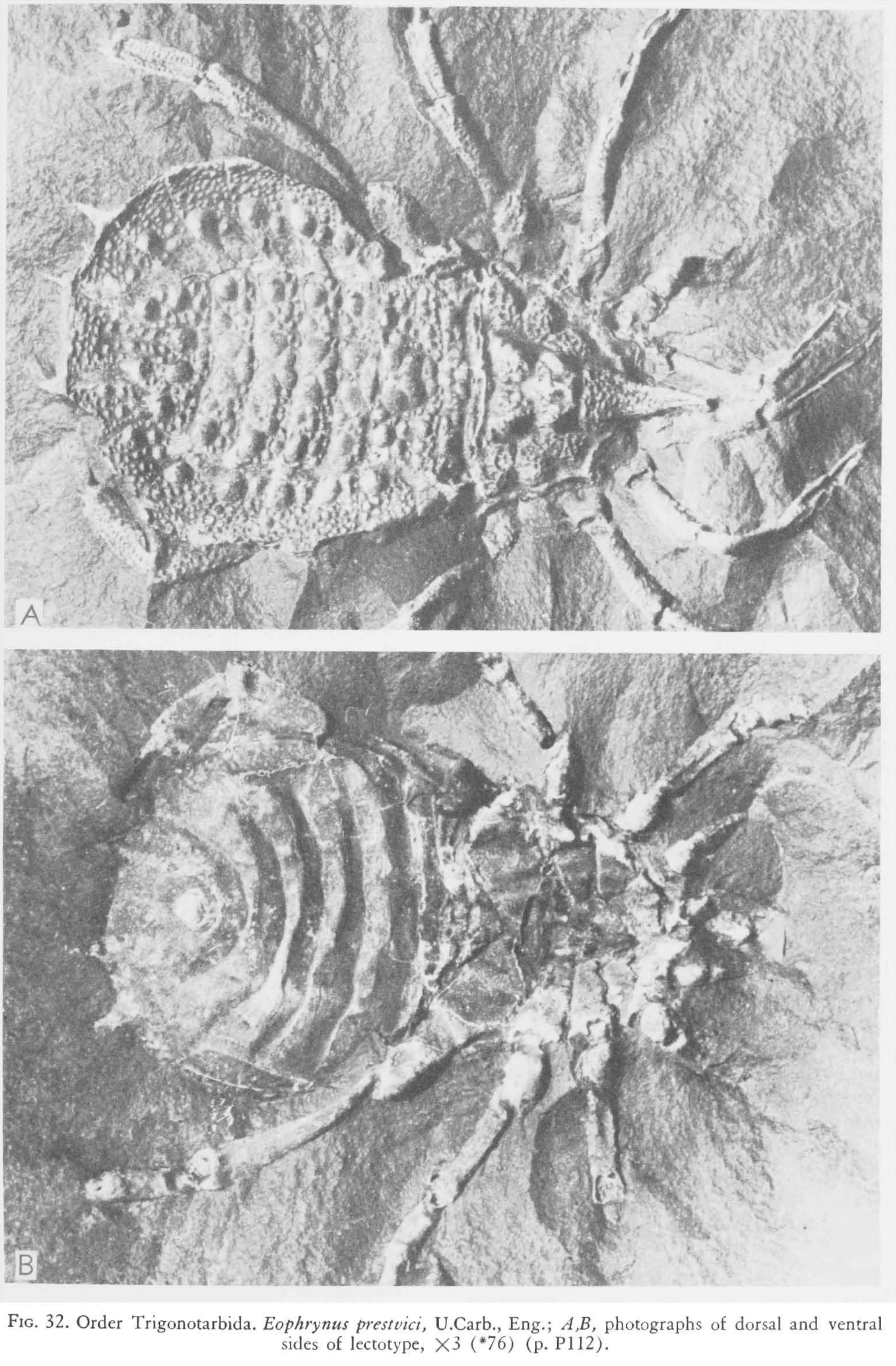

FIG. 32. Order Trigonotarbida. *Eophrynus prestvici*, U.Carb., Eng.; *A,B,* photographs of dorsal and ventral sides of lectotype, ×3 (*76) (p. P112).

other classifications mainly in the grouping of families, in the splitting up of some older families into several independent families for each original one, and in their reassignment to other divisions of the same suborder or even to another suborder. Some features of my classification have been objected to by other arachnologists, but I consider it superior to their own substitute classifications which disregard internal anatomy. The introduction of superfamilies was first proposed by CAPORIACCO in 1938 and I have incorporated them in my present article, but their definitions and groupings had to be somewhat changed to conform with my views.

The classification of scorpions is the same as in my monograph published in 1953. I had however to introduce superfamilies for the purpose of bringing my classification of fossil scorpions in line with the generally accepted classification of Recent scorpions. This presented a difficulty only in the case of the Carboniferous family Eoscorpiidae (=Eoscorpionidae) from which, as I have shown, all Recent families have evolved, until finally I succeeded in establishing the priority of the family Scorpionidae, proposed as a family Scorpionides by LEACH in 1815 and including LINNÉ'*s* genus *Scorpio*. Of course, the definition of the family Scorpionidae as recognized by arachnologists at present is that of POCOCK (1893) and not of LEACH, who recognized but a single family, yet I am given to understand that it is the policy of the *Treatise* to use the *oldest* family name for a superfamily (Fig. 33).

In the classification of pseudoscorpions I followed BEIER. For the order Acarida I used the classification of VITZTHUM, which I prefer to all others, except that I had to change the names of several categories and use older ones in their place. A similar change applies to some other orders, but since the more usual names are mentioned in every case, the reader will have no difficulty in recognizing familiar categories, notwithstanding their old, disused names.

A tabular outline of suprageneric categories of Arachnida is given here with the omission of most of those which contain no known fossil representatives. Taxonomic units with unmentioned genera are distinguished by an asterisk (*)

Suprageneric Divisions of Arachnida

Figures in parentheses indicate number of recognized genera; for the taxa of the class/order group the number includes Recent genera; for the taxa of the family group it refers only to fossil genera. Families represented only by Recent genera are omitted.

- Arachnida (*class*) (5,432) *Sil.-Rec.*
  - Latigastra (*subclass*) (2,394) *Sil.-Rec.*
    - Scorpionida (*order*) (98) *Sil.-Rec.*
      - Protoscorpionina (*suborder*) (4) *Sil.-Penn.*
        - Palaeophonoidea (*superfamily*) (1) *Sil.*
          - Palaeophonidae (1) *Sil.*
        - Mazonioidea (*superfamily*) (3) *Sil.-Penn.*
          - Dolichophonidae (2) *Sil.*
          - Mazoniidae (1) *Penn.*
      - Euscorpionina (*suborder*) (94) *Dev.-Rec.*
        - Palaeoscorpioidea (*superfamily*) (1) *Dev.*
          - Palaeoscorpiidae (1) *Dev.*
        - Archaeoctonoidea (*superfamily*) (2) *Carb.*
          - Archaeoctonidae (2) *Carb.*
        - Scorpionoidea (*superfamily*) (*14) *Carb.-Rec.*
          - Eoscorpiidae (12) *Carb.*
          - Buthidae (*1) *Oligo.-Rec.*
          - Scorpionidae (*1) *Oligo.-Rec.*
        - Cyclophthalmoidea (*superfamily*) (1) *Carb.*
          - Cyclophthalmidae (1) *Carb.*
        - Isobuthoidea (*superfamily*) (3) *Carb.*
          - Isobuthidae (3) *Carb.*
        - Centromachoidea (*superfamily*) (1) *Carb.*
          - Centromachidae (1) *Carb.*
        - Mesophonoidea (*superfamily*) (2) *Trias.*
          - Mesophonidae (2) *Trias.*
        - Incertae sedis (2) *Carb.*
    - Pseudoscorpionida (*order*) (239) *Oligo.-Rec.*
      - Chthoniina (*suborder*) (29) *Oligo.-Rec.*
        - Ditidae (*1) *Oligo.-Rec.*
        - Chthoniidae (*1) *Oligo.-Rec.*
      - Neobisiina (*suborder*) (66) *Oligo.-Rec.*
        - Neobisioidea (*superfamily*) (*1) *Oligo.-Rec.*
          - Neobisiidae (*1) *Oligo.-Rec.*
        - Garypoidea (*superfamily*) (*3) *Oligo.-Rec.*
          - Olpiidae (*1) *Oligo.-Rec.*
          - Garypidae (*2) *Oligo.-Rec.*
        - Feaelloidea (*superfamily*) (*1) *Oligo.-Rec.*
          - Pseudogarypidae (*1) *Oligo.-Rec.*
      - Cheliferina (*suborder*) (144) *Oligo.-Rec.*
        - Cheiridioidea (*superfamily*) (*1) *Oligo.-Rec.*
          - Cheiridiidae (*1) *Olig.-Rec.*
        - Cheliferoidea (*superfamily*) (*5) *Oligo.-Rec.*
          - Cheliferidae (*4) *Oligo.-Rec.*
          - Chernetidae (*1) *Oligo.-Rec.*
    - Phalangiida (*order*) (643) *Carb.-Rec.*
      - Cyphophthalmina (*suborder*) (10) *Rec.*
      - Palpatorina (*suborder*) (133) *Carb.-Rec.*
        - Troguloidea (*superfamily*) (*4) *Carb.-Rec.*
          - Eotrogulidae (1) *Carb.*
          - Nemastomatidae (*1) *Carb.-Rec.*
          - Nemastomoididae (1) *Carb.*
          - Ischyropsalidae (*1) *Oligo.-Rec.*
        - Phalangioidea (*superfamily*) (*6) *Oligo.-Rec.*
          - Phalangiidae (*6) *Oligo.-Rec.*
      - Laniatorina (*suborder*) (500) *Oligo.-Rec.*
        - Gonyleptidae (*superfamily*) (*1) *Oligo.-Rec.*
          - Gonyleptidae (*1) *Oligo.-Rec.*
    - Architarbida (*order*) (14) *Carb.*
      - Architarbidae (12) *Carb.*

Opiliotarbidae (1) *Carb.*
Heterotarbidae (1) *Carb.*
Acarida *(order)* (1,400) *Dev.-Rec.*
Notostigmatina *(suborder)* (3) *Rec.*
Holothyrına *(suborder)* (1) *Rec.*
Trombidiina *(suborder)* (550) *Dev.-Rec.*
Eupodidae (*1) *Dev.-Rec.*
Bdellidae (*1) *Oligo.-Rec.*
Erythraeidae (*2) *Oligo.-Rec.*
Trombidiidae (*1) *Oligo.-Rec.*
Anystidae (*1) *Oligo.-Rec.*
Cheyletidae (*1) *Oligo.-Rec.*
Tetranychidae (*1) *Oligo.-Rec.*
Parasitina *(suborder)* (345) *Oligo.-Rec.*
Parasitoidea *(superfamily)* (*1) *Oligo.-Rec.*
Phytoseiidae (*1) *Oligo.-Rec.*
Ixodoidea *(superfamily)* (*2) *Oligo.-Rec.*
Ixodidae (2) *Oligo.-Rec.*
Acarina *(suborder)* (455) *Oligo.-Rec.*
Acaroidea *(superfamily)* (*2) *Oligo.-Rec.*
Acaridae (2) *Oligo.-Rec.*
Oribatoidea *(superfamily)* (*48) *Oligo.-Rec.*
Belbidae (*3) *Oligo.-Rec.*
Camisiidae (*2) *Oligo.-Rec.*
Carabodidae (*8) *Oligo.-Rec.*
Ceratozetidae (*3) *Oligo.-Rec.*
Cymberemaeidae (*4) *Oligo.-Rec.*
Oribatidae (*10) *Oligo.-Rec.*
Galumnidae (*1) *Oligo.-Rec.*
Haplozetidae (*1) *Oligo.-Rec.*
Hypochthoniidae (*1) *Oligo.-Rec.*
Hermanniellidae (*1) *Oligo.-Rec.*
Liacaridae (*1) *Oligo.-Rec.*
Neoliodidae (*2) *Oligo.-Rec.*
Oribatellidae (*2) *Oligo.-Rec.*
Oribatulidae (*3) *Oligo.-Rec.*
Oripodidae (*1) *Oligo.-Rec.*
Parakalummidae (*1) *Oligo.-Rec.*
Phenopelopidae (*1) *Oligo.-Rec.*
Phthiracaridae (*2) *Oligo.-Rec.*
Tetrapodilina *(suborder)* (46) *Rec.*
Stethostomata *(subclass)* (12) *Carb.*
Haptopodida *(order)* (1) *Carb.*
Plesiosironidae (1) *Carb.*

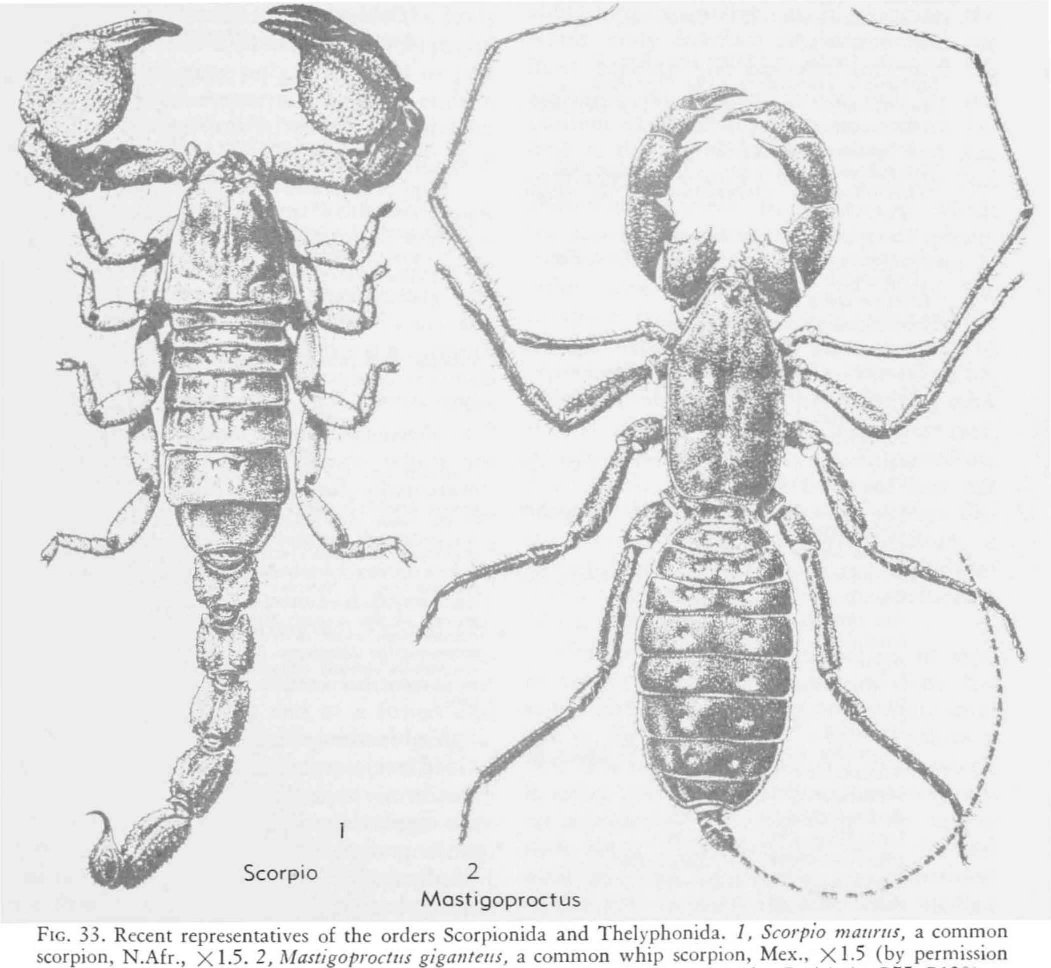

FIG. 33. Recent representatives of the orders Scorpionida and Thelyphonida. *1, Scorpio maurus,* a common scorpion, N.Afr., ×1.5. *2, Mastigoproctus giganteus,* a common whip scorpion, Mex., ×1.5 (by permission from *Traité de Zoologie,* tome 6, sous la direction du PR. GRASSÉ, Masson & Cie., Paris) (p. P75, P120).

  - Anthracomartida *(order)* (11) *Carb.*
    - Anthracomartidae (11) *Carb.*
- Soluta *(subclass)* (24) *Dev.-Carb.*
  - Trigonotarbida *(order)* (24) *Dev.-Carb.*
    - Palaeocharinidae (2) *Dev.*
    - Anthracosironidae (1) *Carb.*
    - Eophrynidae (14) *Carb.*
    - Trigonotarbidae (1) *Carb.*
    - Trigonomartidae (6) *Carb.*
- Caulogastra *(subclass)* (3,002) *Carb.-Rec.*
  - Latisterna *(superorder)* (5) *Jur.-Rec.*
    - Palpigradida *(order)* (5) *Jur.-Rec.*
      - Sternarthronidae (1) *Jur.*
      - Eukoeneniidae (4) *Rec.*
  - Camarostomata *(superorder)* (18) *Carb.-Rec.*
    - Thelyphonida *(order)* (12) *Carb.-Rec.*
      - Thelyphonidae (*2) *Carb.-Rec.*
    - Schizomida *(order)* (5) *?Plio.-Rec.*
      - Schizomidae (*) *?Plio.-Rec.*
      - Calcitronidae (2) *?Plio.*
    - Kustarachnida *(order)* (1) *Carb.*
      - Kustarachnidae (1) *Carb.*
  - Labellata *(superorder)* (2,840) *Carb.-Rec.*
    - Phrynichida *(order)* (21) *Carb.-Rec.*
      - Phrynichidae (*3) *Carb.-Rec.*
    - Araneida *(order)* (2,819) *Dev.-Rec.*
      - Liphistiina *(suborder)* (19) *Dev.-Rec.*
        - Liphistioidea *(superfamily)* (*11) *Dev.-Rec.*
          - Arthromygalidae (9) *Dev.-Rec.*
          - Arthrolycosidae (2) *Carb.*
      - Theraphosina *(suborder)* (370) *Oligo.-Rec.*
        - Theraphosoidea *(superfamily)* (*1) *Oligo.-Rec.*
          - Theraphosidae (1) *Oligo.-Rec.*
        - Atypoidea *(superfamily)* (*1) *Oligo.-Rec.*
          - Dipluridae (*1) *Oligo.-Rec.*
        - Incertae sedis (1) *Eoc.*
      - Hypochilina *(suborder)* (2) *Rec.*
      - Dipneumonina *(suborder)* (2,401) *Oligo.-Rec.*
        - Trionychi *(division)* (1,157) *Oligo.-Rec.*
          - Hersilioidea *(superfamily)* (*2) *Oligo.-Rec.*
            - Urocteidae (*1) *Oligo.-Rec.*
            - Hersiliidae (*1) *Oligo.-Rec.*
          - Scytodoidea *(superfamily)* (*1) *Oligo.-Rec.*
            - Pholcidae (*1) *Oligo.-Rec.*
          - Zodarioidea *(superfamily)* (*3) *Oligo.-Rec.*
            - Zodariidae (*1) *Oligo.-Rec.*
            - Spatiatoridae (2) *Oligo.*
          - Lycosoidea *(superfamily)* (*10) *Oligo.-Rec.*
            - Eresidae (*1) *Oligo.-Rec.*
            - Amaurobiidae (*2) *Oligo.-Rec.*
            - Psechridae (*1) *Oligo.-Rec.*
            - Agelenidae (*3) *Oligo.-Rec.*
            - Insecutoridae (1) *Oligo.*
            - Pisauridae (*1) *Oligo.-Rec.*
            - Lycosidae (*1) *Oligo.-Rec.*
          - Araneoidea *(superfamily)* (*34) *Oligo.-Rec.*
            - Archaeidae (*1) *Oligo.-Rec.*
            - Mimetidae (*1) *Oligo.-Rec.*
            - Arthrodictynidae (1) *Oligo.*
            - Dictynidae (*1) *Oligo.-Rec.*
            - Micryphantidae (*1) *Oligo.-Rec.*
            - Theridiidae (*7) *Oligo.-Rec.*
            - Adjutoridae (3) *Oligo.*
            - Ephalmatoridae (1) *Oligo.*
            - Linyphiidae (*9) *Oligo.-Rec.*
            - Araneidae (*11) *Oligo.-Rec.*
          - Archaeometoidea *(superfamily)* (3) *Carb.*
            - Archaeometidae (3) *Carb.*
        - Dionychi *(division)* (1,117) *?Carb., Oligo.-Rec.*
          - Zoropsoidea *(superfamily)* (*1) *Oligo.-Rec.*
            - Zoropsidae (*1) *Oligo.-Rec.*
          - Thomisoidea *(superfamily)* (*12) *Oligo.-Rec.*
            - Eusparassidae (*6) *Oligo.-Rec.*
            - Thomisidae (*6) *Oligo.-Rec.*
          - Clubionoidea *(superfamily)* (*11) *Oligo.-Rec.*
            - Drassodidae (*2) *Oligo.-Rec.*
            - Inceptoridae (1) *Oligo.*
            - Clubionidae (*2) *Oligo.-Rec.*
            - Parattidae (1) *Oligo.*
          - Salticoidea *(superfamily)* (*6) *Oligo.-Rec.*
            - Salticidae (*6) *Oligo.-Rec.*
          - Pyritaraneoidea *(superfamily)* (2) *Carb.*
            - Pyritaraneidae (2) *Carb.*
        - Quadrostiati *(division)* (127) *Oligo.-Rec.*
          - Dysderoidea *(superfamily)* (*5) *Oligo.-Rec.*
            - Segestriidae (*1) *Oligo.-Rec.*
            - Dysderidae (*3) *Oligo.-Rec.*
            - Oonopidae (*1) *Oligo.-Rec.*
          - Anyphaenoidea *(superfamily)* (*1) *Oligo.-Rec.*
            - Anyphaenidae (*1) *Oligo.-Rec.*
          - Argyronetoidea *(superfamily)* (*1) *Mio.-Rec.*
            - Argyronetidae (*1) *Mio.-Rec.*
      - Apneumonina *(suborder)* (16) *Rec.*
  - Rostrata *(superorder)* (135) *Carb.-Rec.*
    - Solpugida *(order)* (135) *Carb.-Rec.*
      - Galeodidae (*1) *Carb.-Rec.*
  - Podogona *(superorder)* (4) *Carb.-Rec.*
    - Ricinuleida *(order)* (4) *Carb.-Rec.*
      - Poliocheridae (*1) *Carb.*
      - Curculioididae (*1) *Carb.*

Class ARACHNIDA Lamarck, 1801

[*nom. correct. auctt.* (*pro.* Arachnidae LAMARCK, 1801, *emend.* STØRMER, 1944]

[=Embolobranchiata LANKESTER, 1905; Arachnida PETRUNKEVITCH, 1945]

[LAMARCK was the first to set aside LINNÉ's 7th order, Aptera, of the class Insecta as a separate class which he named Arachnidae, later accepting LATREILLE's modification of the name into Arachnides. For many years the class Arachnides still included all wingless insects, myriapods, crustaceans, horseshoe crabs, pycnogonids and arachnids. The present spelling "Arachnida" seems to have been used for the first time by NEWPORT in 1830, but the horseshoe crabs and the pycnogonids were retained in the class until the beginning of this century. Meanwhile, Tardigrada and Pentastomida were added to it by LEUCKART, and trilobites and eurypterids by LANKESTER. Only new evidence furnished by comparative anatomy and embryology finally made it possible to give the class Arachnida its present definition, adopted here.]

Air-breathing chelicerates with body divided into a cephalothorax and an abdomen, the former typically with 6 pairs of uniramous appendages. First pair (chelicerae) always preoral, 2- or 3-jointed. Second pair (pedipalpi) variously developed, but usually, typically 6-jointed. Correlated with the modification of structure, the function of the pedipalpi varies considerably from order to order. Third to 6th pairs typically 7-

jointed and usually developed as legs, although the 3rd pair is invariably modified as organs of chemotactile perception in some orders and the 5th pair as organs of copulation in the order Ricinuleida. Abdomen composed of a maximum of 12 segments and is either broadly joined to the cephalothorax or else the 1st abdominal segment is greatly constricted and forms a cone-shaped cylindrical pedicel (petiolus). Abdominal appendages present in the adult only in scorpions as a pair of combs (pectines) and in spiders as spinnerets.

Mouth parts vary considerably in structure and composition from order to order. They are formed by the chelicerae, upper lip (rostrum), lower lip (labium) and pedipalpal coxae or, as in scorpions, 1st and 2nd pedal coxae. Predigestion outside the body is the rule, with a preoral or a pharyngeal strainer permitting only fluid food to pass into the digestive system. The latter ends in an anus always situated on the last abdominal segment, which is closed either by a sphincter or an operculum.

Respiration by means of book lungs, tracheal tubes, or a combination of both, except in some cases of complete loss of organs of respiration in Acarida. Respiratory pigment always haemocyanin. Circulatory system composed of a dorsal heart, a complex arterial system and predetermined channels for the return of the blood to the heart through lateral ostia. Excretory system of 2 types of organs: coxal glands which are modified nephridia, and malpighian tubes which open into the digestive tract at the end of the mid-gut. Nervous system always with a dorsal brain characterized by a lack of a deutocerebrum, which is presumably fused with the protocerebrum. Ventral nervous chain of paired ganglia always exhibiting a trend to a forward displacement of abdominal ganglia and to a fusion and loss of some posterior abdominal ganglia. Eyes always of the simple type (ocelli). Organs of reproduction situated in the abdomen, with genital opening on the sternite of the embryologically 2nd abdominal segment, except in some Acarida in which it is secondarily displaced in the male. Sexes always separate. Females oviparous or ovoviviparous, rarely parthenogenetic.

Size varies from a fraction of a millimeter in some mites to 200 mm. in the largest scorpions. Habits terrestrial or secondarily aquatic, with complex inherited patterns of behavior. Most arachnids are carnivorous, but many mites are herbivorous. The great majority of arachnids are free-living, but many species of mites are temporarily or permanently parasitic. *Sil.-Rec.*

EXTERNAL CHARACTERS

CEPHALOTHORAX

The **head** is always fused with the 5 **thoracic segments,** forming a single unit or **tagma** always distinct from the **abdomen,** even when the latter is broadly joined with the last thoracic segment. Only when the segmentation of the abdomen also becomes obliterated by fusion, as in Acarida, the whole body forms a single unit and the limit between the **cephalothorax** and the abdomen can be determined only by the position of the 4th pair of legs, which belong to the last thoracic segment, and that of the genital opening which is on the 2nd abdominal segment. In all cases in which the abdomen is not fused with the cephalothorax, the dorsal surface of the latter is either covered with a single shield, the **carapace (peltidium),** which often shows its composition by the presence of a pair of **cephalothoracic sulci** outlining the limits between the head and the thorax, or else with several distinct plates. In the latter case, which is characteristic of Palpigradida, Schizomida and Solpugida and does not occur in other orders, one can always distinguish a single, large **propeltidium,** a paired (very rarely single) **mesopeltidium** and a single (rarely paired) **metapeltidium** (Figs. 83,*1b,2a;* 86,*1;* 112,*2a,3*).

The **eyes** of all arachnids are of the type of simple **ocelli,** with a corneal lens, the outer surface of which may be either convex or flat, a glass body which produces a new lens in each instar, and a retina which is either post- or prebacillar, depending upon whether the corresponding eyes receive their nerve supply from the 1st or the 2nd optic ganglia. The number and disposition of the eyes vary. One pair is often median in position, the others, of which there may be up to 5 pairs, as in some scorpions, are lateral. In many cases the eyes are elevated either on a common **eye tubercle** or on separate tubercles. In other cases they are sessile, i.e., their base is on a level with the surface of the carapace. The configuration of the **eye group** and the number of eyes furnish valuable systematic characters, but their value must not be exaggerated, as was often done in the past. Palpigradida, Anthracomartida and Ricinuleida have no eyes. In Schizomida the **median eyes** are wanting and the **lateral** eyes are rudimentary. Blind genera occur almost in all orders which normally possess well-developed eyes. **Compound eyes,** such as are found in Xiphosura, Eurypterida, Crustacea and Hexapoda, are never present in any Arachnida. The organs of scorpions belonging to the Triassic family Mesophonidae and those of the Palaeocharinidae (Devonian members of the order Trigonotarbida) claimed to be compound eyes are unlike true compound eyes and are probably sense organs of some unknown function.

The shape and proportions of the carapace are of importance in classification, but there are many cases in which the carapace of the male differs considerably from that of the female of the same species. A real "doublure" comparable to that in Xiphosura and Eurypterida is present only in the carapace of Thelyphonida (Fig. 84,*2*). In the order Ricinuleida a movable plate **(cucullus)** is always present at the anterior end of the carapace (Figs. 113-116). When flexed, the cucullus hides and protects the chelicerae.

VENTRAL SURFACE

The ventral surface of the cephalothorax is occupied by the **coxae** of the 6 pairs of appendages and the **thoracic sternites,** if such exist. The configuration of the coxosternal region is a very important taxonomic character of the highest order. In each case it presents a clear picture of the evolutionary changes which the cephalothorax of the particular order has undergone, changes involving partial or complete loss of thoracic sternites and displacement of the coxae from their original lateral position to the respective position which they now occupy. The extent of movability of the coxae is determined by the way of their articulation and the degree of their fusion with the ventral wall of the body. The movability of the coxae varies a great deal within the same order and even within the same species. Thus, in scorpions the anterior 2 pairs of coxae are movable individually, while the 3rd and 4th coxae are longitudinally fused together on each side of the body and possess jointly only very limited freedom of motion, being to all practical purposes immobile. The use of the degree of mobility of coxae has therefore a very limited systematic value.

ABDOMEN

The abdomen, which in the early embryological stages is always composed of 12 segments, may retain its segmentation in the adult or undergo various changes during development, masking or seriously changing its external appearance. Consequently external segmentation, even when present and well visible, does not necessarily represent the original segmentation. Theoretically, each abdominal segment should have a **tergite** and a **sternite** connected with each other laterally by a soft pleura and with the preceding and succeeding tergite and sternite by an intersegmental membrane. When the abdomen is distended, the tergites and sternites appear as independent plates, but in a normally **contracted abdomen** the intersegmental membrane of all segments becomes infolded under the posterior edge of the preceding tergite and sternite, so that the latter overlap the outer surface of the anterior edge of the succeeding tergite and sternite. In some segments, as in the 5 segments of the so-called postabdomen or "tail" of scorpions, the body wall of each segment forms a solid chitinous ring at the expense of the lateral pleurae, which are therefore wanting. In some cases, as in Anthracomartida and some Trigonotarbida, the last tergite is folded and forms the last plate on the ventral surface. A regular feature of the Anthracomartida is the fusion of the 2nd and 3rd tergites into a single plate, while the corresponding sternites remain separate (Fig. 66,*2a,b*). In the family Curculioididae of the order Ricinuleida, the 4 tergites visible as separate plates in the family Poliocheridae (Fig. 115,*1a*) are fused into a single plate (Fig. 116,*3b*). In Arachnida with a globular or ellipsoidal abdomen, the number of tergites visible in any position of the animal is always smaller than the total number (Figs. 97,*A,D,F*). The 1st tergite in Arachnida with a more or less flat abdomen is often concealed under the posterior edge of the carapace, as in Anthracomartida and Ricinuleida (Figs. 67, *1,5,7;* 68,*1,4*). Usually the tergites and sternites of Arachnida are entire, but in Anthracomartida the tergites are subdivided into 5 plates each and the sternites into 3 plates each. This is also the case in Architarbida and in one family of Ricinuleida. The tergites of some pseudoscorpions and of Haptopodida are subdivided into a pair of plates each. The 1st abdominal segment has completely disappeared in all Euscorpionina, Phalangiida and Ricinuleida. In the former, the first visible tergite is therefore the tergite of the 2nd embryonic segment, while in Ricinuleida it is the tergite of the 3rd segment, because the tergite of the 2nd segment, although present, is concealed under the carapace. All this shows clearly how misleading it would be, as it was done in the past, to number the *visible* tergites and sternites without taking into account their actual numerical order revealed by anatomical and embryological studies.

JUNCTURE BETWEEN CEPHALOTHORAX AND ABDOMEN

The juncture between the cephalothorax and the abdomen in Arachnida is of the greatest importance, but the outward appearance may be very misleading, as can be readily understood from what was just stated concerning the 1st *visible* tergite in Ricinuleida. In the case of the subclasses Latigastra and Stethostomata, the juncture is said to be "broad," which means that the carapace is connected with the abdomen by an intersegmental membrane of the full width of the posterior edge of the carapace and anterior edge of the abdomen. Because a broad connection is practically rigid, permitting but a very slight motion of the abdomen as a whole, the line of connection is usually more or less curved in a transverse

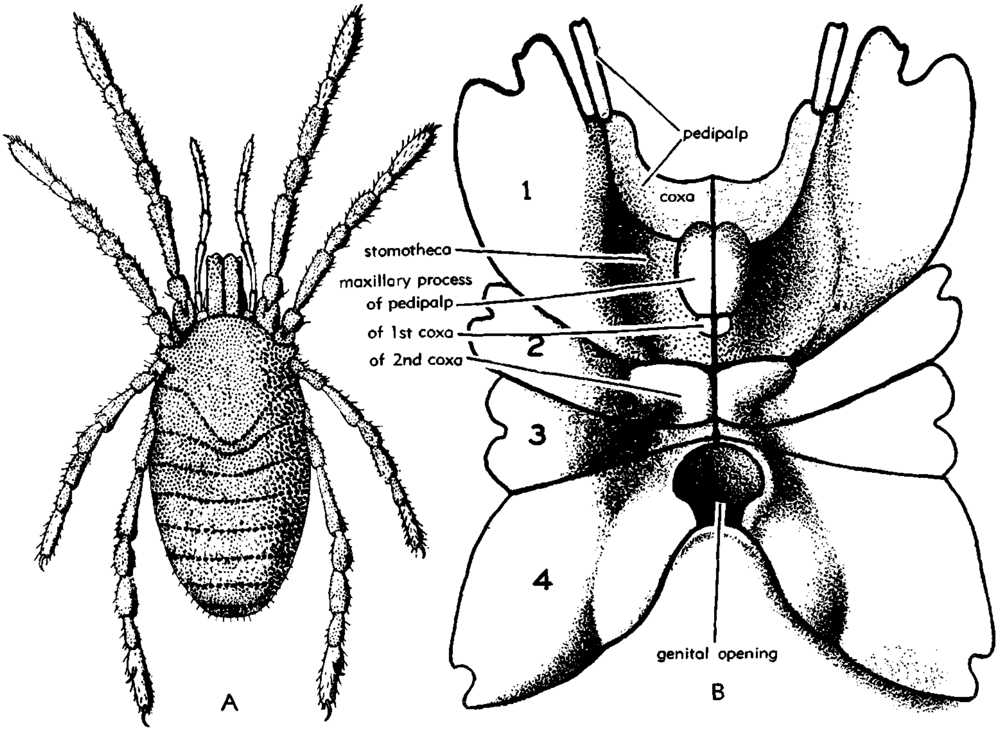

FIG. 34. Order Phalangiida; a Recent representative of the suborder Cyphophthalmina, *Siro duricorius,* Austria, ×18, and coxosternal region enlarged (68) (p. P85).

plane to the body, even when it has the appearance of a perfectly straight line when viewed from above. A similar connection is also found in the families Anthracosironidae and Trigonotarbidae in the order Trigonotarbida. In the family Eophrynidae of the same order, the connection is restricted to about the middle 3rd of the width of the carapace. In all Latigastra, Stethostomata and Soluta, the ventral connection between the cephalothorax and abdomen is more or less angular, because the anterior edge of the 1st sternite (or 2nd, when the 1st segment is lost) is triangular, as is also the diaphragm separating the cavity of the cephalothorax from that of the abdomen. In the subclass Caulogastra, the connection between the cephalothorax and the abdomen is considerably narrower than the width of the posterior edge of the carapace. In typical cases, such as presented by common spiders (Araneida), the 1st abdominal segment is reduced to a thin cylinder the anterior half of which is invaginated into the cavity of the cephalothorax with the entire connecting, cylindrical membrane. The dorsal portion of the wall of the 1st segment is of hard chitin. It is the tergite and is called **lorum pediculi.** The ventral wall remains usually soft, membranous, lacking a scleritized sternite. In less typical cases, such as presented by the whip scorpions (Thelyphonida), the dorsal tergite of the 1st segment is almost as wide as the posterior edge of the carapace, while the sternite is much narrower and quite short. In alcoholic speci-

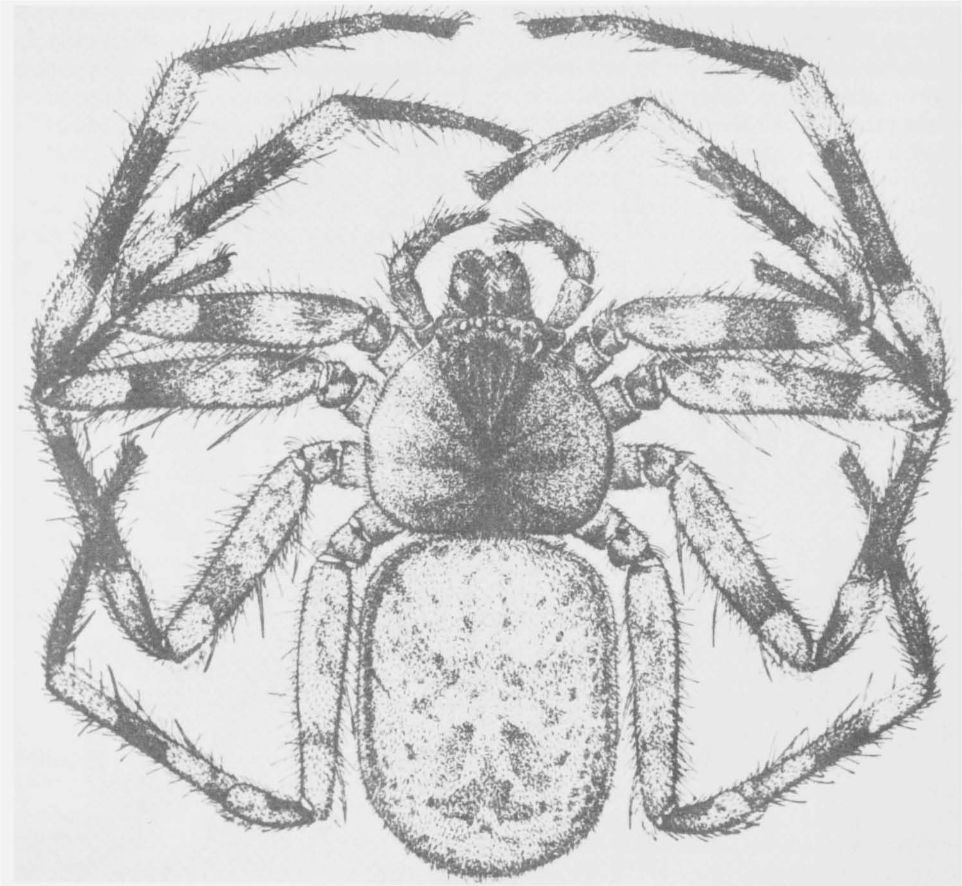

FIG. 35. *Selenops* sp., a laterigrade spider (order Araneida) of the superfamily Thomisoidea, family Selenopidae, from tropical Africa, ×6 (by permission from *Traité de Zoologie,* tome 6, sous la direction du PR. GRASSÉ, Masson & Cie., Paris) (p. P146).

mens of Recent species of caulogastric Arachnida, the abdomen breaks off easily, usually leaving the pedicel attached to the cephalothorax. In Arachnida with a broad juncture the abdomen remains firmly attached to the cephalothorax, from which it can be separated only by a sharp knife. But when, as in Anthracomartida, the abdomen is hard and its segments are firmly connected with each other, the soft membrane between the cephalothorax and the abdomen may disintegrate or break before fossilization is completed, with the result that the entire abdomen becomes severed in a single piece and may be the only portion of the animal preserved as a fossil (Figs. 34, 35).

CEPHALOTHORACIC APPENDAGES

The structure of the cephalothoracic appendages varies considerably from order to order and the terminology of their segments is often confusing, owing to the fact that different names have been given by specialists to the same segments in different orders of Arachnida. Moreover, the homology of the segments is not yet fully agreed upon. The greatest modifications occur in Acarida, and interested persons are referred to special articles on Recent representatives of that order.

The 1st pair of appendages in Arachnida was often termed antennae or mandibles in the past and even in the beginning of the present century. Now they are always called **chelicerae.** They are 3-jointed in Scorpionida, Phalangiida, Architarbida, Haptopodida, Anthracomartida and Palpigradida, but 2-jointed in all other orders. In both types they may be **retrovert** or **chelate,** but in the latter case one of the fingers of the chela is always immobile, being nothing but a rigid process of the segment proximal to the movable finger which forms the last segment (Fig. 112,*2c*). Phylogenetically and embryologically, the movable finger should be dorsal to the immobile one. But torsion is the cause of modification found in different orders and suborders. Thus, the movable finger is lateral in Scorpionida, Pseudoscorpionida and Palpigradida, medial in Haptopodida, ventral in Solpugida and Acarida.

The 2nd pair of appendages was sometimes called mandibles or maxillae in the past, but is now always termed **pedipalpi.** With the exception of the order Acarida, in which the number of pedipalpal segments varies from 7 in the Devonian *Protacarus* to 2 in some Recent species, the pedipalpi in all other orders are composed of 6 segments and may be **pediform** or **raptorial.** In the latter case they may be retrovert, as in Phrynichida, subchelate, as in some Thelyphonida, or chelate, as in Scorpionida and Pseudoscorpionida (Figs. 33, 36, 48). In Palpigradida (Fig. 82,*2d*) they are pediform and are used for walking, hence the name of the order in general use at present. In Araneida, they are usually much smaller than the legs and are used as sense organs by the young of both sexes and by adult females. Adult male spiders have their organs of copulation on the 6th joint of the pedipalpi. The basal joint, i.e., the coxa of the pedipalp, is usually participating in the process of ingestion, the exception being Scorpionida, Palpigradida and Solpugida, in all of which it has nothing to do with ingestion. In Schizomida, Thelyphonida, Kustarachnida and Ricinuleida, the pair of pedipalpal coxae are firmly grown together in the median line. Their common wall facing the body is deeply concave and covered with short, chitinous, fine spines. The convex **rostrum** (upper lip), covered with similar spines, fills out the concavity, the spines of the rostrum forming together with the spines of the coxae a perfect filtering apparatus. Into this concave filtering space (Fig. 84,*2*), called **"camarostome,"** the true mouth opens. In Araneida the pedipalpal coxae harbor so-called maxillary glands which produce digestive enzymes. For their accommodation these coxae are provided with maxillary lobes, conveniently termed **maxillae,** and either individual openings for each separate gland or a perforated disc on which all ducts open. The 6th, i.e., the terminal joint of the pedipalpi, is in many cases provided with a claw and, as a unique exception, is subdivided in Palpigradida, giving the impression that their pedipalp is composed of more than 6 segments.

The **legs,** of which there are never more than 4 pairs, are typically 7-jointed, but subsegmentation is common and this gives rise to some terminological confusion. In Araneida, 7 segments is the rule. They are called **coxa, trochanter, femur, patella, tibia,**

metatarsus and **tarsus.** Only the tarsus is subsegmented in a few species with slender and long legs. The trochanter serves as a pivot for the motion of the leg in any direction, thus physiologically corresponding to the hip joint of a vertebrate. The articulation between the femur and the patella is such that only flexion and extension are possible. This articulation corresponds physiologically to our knee. In some orders the coxa, trochanter and metatarsus may be subdivided into 2 segments each. The patella may be permanently fused with the tibia, leaving no trace of its existence. This composite segment is then called tibia. True homologies of the segments in the legs of various orders of Arachnida can be established only by a study of the type of their articulation, attachment of individual muscles and planes of possible motion. The tarsus is usually provided at its end with from 1 to 3 movable **claws,** which are either articulated directly with the tarsus or else with a terminal subsegment of the latter, called **onychium or posttarsus.** In legs which are modified as tactile organs, as in the case of the 1st pair of legs in Thelyphonida and especially in Phrynichida, claws are wanting. In legs of Arachnida accustomed to climbing on smooth surfaces, only 2 claws are present, but they are accompanied by some organ comparable to a sucker and called **arolium,** or by tufts of flattened hairs which function as a sucker owing to their peculiar structure permitting such close apposition to each other that the wall of the cup produced by them is as impermeable to air as if it were formed by a continuous membrane. The legs are often clothed with hair of various kinds, simple, clavate, plumose, etc. Movable spines are also present in many cases and their arrangement is often of systematic value. Thus, the spider family Mimetidae can be at once recognized by a row of special spines on their 1st and 2nd tibia and metatarsus, (Fig. 101,*3b*), while the most characteristic feature of the family Theridiidae is the presence of the so-called **comb** (Fig. 105,*5*) formed by a row of serrated bristles on the 4th tarsi.

ABDOMINAL APPENDAGES

Abdominal appendages are present only in scorpions and spiders, in the former in the shape of combs or pectines on the 3rd sternite (Figs. 37, 47), in spiders as **spinnerets** (mamillae) on that portion of the abdominal wall which belongs to the 4th and 5th segments.

ECDYSIS

In molting or ecdysis, not only the entire chitinous external skeleton is shed, but the chitinous lining of the book lungs, tracheal tubes, fore-gut and hind-gut is completely withdrawn from the inside of the corresponding organs. Such exuviae are common in amber, but some have been found even in the Carboniferous.

INTERNAL ANATOMY

Because internal organs are rarely preserved in fossil Arachnida they are here discussed only briefly. More detailed information may be found in various books listed at the end of this article.

DIGESTIVE SYSTEM

The digestive system follows more or less the same plan in all orders, but presents many interesting variations. Thus, in Araneida the filtering apparatus is located in the pharynx; in Scorpionida the filtering is accomplished in the channels formed by the adjoining maxillary lobes of the 1st and 2nd pairs of legs; in Schizomida, Thelyphonida and Ricinuleida by the camarostome. Phalangiida have no filter comparable to that in other Arachnida and are capable of ingesting larger particles. The esophagus is more or less similar in all orders. But a pumping gizzard is highly developed in several orders and very poorly in other orders. The mid-gut combines the functions of an organ producing enzymes and resorbing liquefied food. Usually it forms a system of blind, tubular sacs in the cephalothorax, for which I proposed the now generally accepted term **thoracenteron,** and a still more complicated system of branched ramifications in the abdomen. The abdominal system of branches used to be called "liver" in the past, but on my initiative is now called **chylenteron.** A large stercoral pouch in which the excrements are formed and temporarily stored, is usually present at the end of the median tube of the mid-gut, dorsal to it. The hind-gut is always short. The anus is at the end of the abdomen, ventral. In several orders a round anal operculum is present. In fossils, a clear impression of it is usually visible on the last tergite as well as on the last sternite, a circumstance which must be remembered when only one surface of the fossil is preserved. In many orders an operculum is lacking and the anus is closed by the contraction of a sphincter.

EXCRETORY SYSTEM

The excretory system consists of a pair of coxal glands which are modified nephridia, and a pair of malpighian tubes. The former are in the cephalothorax, the latter in the abdomen. The coxal glands open by 1 or 2 pairs of openings situated behind the coxae. The malpighian tubes open into the digestive system at the end of the mid-gut. The white crystals in the excreta of Arachnida are guanin.

CIRCULATORY SYSTEM

The circulatory system of arachnids may be very complex, as in scorpions and spiders, or subject to considerable reduction and even complete disappearance in some Acarida. Even in its highest development it is an "open" system, but the channels for the return of the blood to the heart are always predetermined. The heart, dorsal to the mid-gut in position, is restricted to the abdomen, except in Thelyphonida and Solpugida, in which a portion of it is in the cephalothorax. In fossil Arachnida, the heart has been found in only 2 specimens, one an amber spider, the other a Pennsylvanian architarbid. The blood in all Recent arachnids is propelled forward through the anterior aorta and backward through 3 posterior arteries. In scorpions the heart has 7 pairs of lateral ostia for the return of the blood; in spiders from maximum 5 pairs in Liphistiidae to 2 pairs in Quadrostiati and Apneumonina. All blood corpuscles are of the leucocyte type. The blood plasma is of a semitranslucent white color, turning rap-

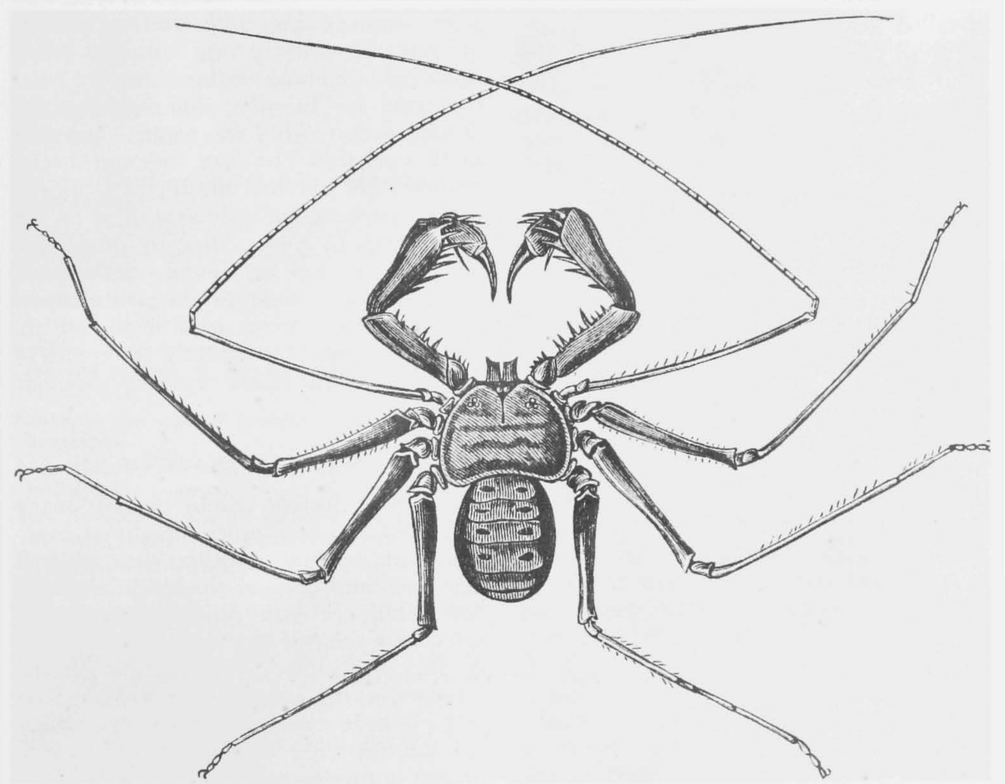

FIG. 36. Order Phrynichida; *Phrynichus reniformis*, Ceylon, ×1 (from Cuvier's Regne animal) (p. P126).

idly blue at exposure to air. The respiratory pigment of the blood is hemocyanin.

RESPIRATORY SYSTEM

The respiratory system consists of book lungs, tracheal tubes, or a combination of both types. It is lacking in many Acarida; in Araneida both types are present in the Dipneumonina, only book lungs in the Liphistiina, Theraphosina and Hypochilina, and only tracheal tubes in the Apneumonina. In all other orders either book lungs or tracheal tubes are present, but never both in the same order. Ventral evertible sacs, supposed to have respiratory function, are present in Palpigradida, some Phrynichida and Architarbida. The number and position of the respiratory stigmata varies from order to order, but is always a fixed one for each order.

NERVOUS SYSTEM

The main plan of the nervous system is remarkably uniform in all arachnids, but its detail structure varies considerably. The so-called deutocerebrum is always lacking, as in all Chelicerata. The chelicerae receive their nerves from the tritocerebrum, the pedipalpi from the 1st ventral pair of ganglia. The thoracic subesophageal ganglionic mass with a distinct pair of ganglia for each pair of thoracic appendages usually includes also several pairs of distinct abdominal ganglia, which have been drawn into the thorax from the abdomen during the embryological development by a process of contraction of the longitudinal connectives. The 1st pair of abdominal ganglia incorporated in the thoracic mass remains distinct even when the 1st abdominal segment is completely lost. In some orders, as for example in scorpions and whip scorpions, some of the abdominal ganglia remain in the abdomen even when they move forward out of their original position. In other orders, such as spiders, all abdominal ganglia are drawn into the cephalothorax in development and only their nerves remain in the abdomen. In all cases the maximum number of abdominal ganglia is 12, but with the loss of posterior segments the number of remaining ganglia may be smaller. A sympathetic nervous system has been described in several orders of Arachnida.

SENSE ORGANS

Only eyes, tactile and chemoreceptive organs are more or less well known. Although some arachnids produce sounds by organs of stridulation, no organs of hearing have yet been discovered. The eyes are always on the carapace and their number varies even within the same order. The maximum number of 6 pairs is found only in scorpions. Although presenting many differences in the structure of their lens, iris, vitreous body and retina, all arachnid eyes are of the type of simple ocelli. The corneal lens produced by the vitreous body may be disc-shaped in a transverse section, ellipsoidal or even triangular, with a flat or convex external surface. Some eyes have a retina with a tapetum which reflects light, making them luminous when a ray strikes them at night.

Tactile organs represented by sensory hairs of various types, are situated on the pedipalpi and legs. So-called trichobothria, at one time believed to be organs of hearing, are now known to be sensitive only to very slow motion of air or very light touch. They are very thin hairs arising from the center of a small membranous disc. They are more numerous in "hairy" species than in those devoid of hair. They are present, however, in all arachnids. The most common chemoreceptors are so-called slit organs found on various parts of the body as well as on the appendages. In spiders they are called lyriform organs and are found on the pedipalpi and legs close to the articulations. There are also various sense organs of unknown function, among them the combs of scorpions and the racket organs of solpugids (Fig. 112,*2b*).

REPRODUCTIVE SYSTEM

The reproductive system presents many variations. In some orders organs of copulation are wanting, in others they are well developed and peculiar to the different orders. Thus, the male copulatory organs of spiders are situated on the terminal segment of the pedipalpi; in Ricinuleida on the metatarsi of the 3rd pair of legs. Male Phalangiida have a penis on their 2nd abdominal sternite, their females possess an ovipositor in the corresponding place. In Acarida a penis is also present, but its position varies greatly. In scorpions a pair of so-called paraxial organs, connected with the vasa deferentia and capable of slight protrusion through the genital opening between the opercula, serve as organs of copulation. Correlated with the differences of structure of the reproductive organs the mating instincts also present great differences and reach the maximum of complexity in spiders.

GLOSSARY OF MORPHOLOGICAL TERMS

The following alphabetically arranged glossary of morphological terms applied to arachnids and used by specialists in the description of species and in keys for their identification, is designed to be of help to those who are not familiar with them. No distinction is made between different terms as to their systematic value because such distinction would be misleading. Alternative terms, used by different arachnologists but synonymous inasmuch as they refer to the same or homologous structures, are given in italics and their synonyms indicated. Obsolete terms, now out of use but common in publications of the past century, are marked with an asterisk (*).

abdomen. Complete portion of body following upon cephalothorax.

****antennae.*** Obsolete term for chelicerae, used in the past to emphasize their homology with the antennae of crustaceans and insects.

apodeme. Invagination of the body wall for attachment of muscles.

arolium. Trumpet-shaped membranous structure at the end of tarsi in Pseudoscorpionida and some Phrynichida.

basitarsus. Leg segment preceding tarsus (protarsus, metatarsus).

beak. Hollow tube with mouth opening at its end in Solpugida (rostrum).

boss. Swelling at base of chelicerae for accommodation of muscles in spiders (condyle).

calamistrum. Row of special bristles on 4th metatarsi of spiders possessing a cribellum; used for drawing out a band of special silk from the latter (Fig. 103,*1b,2c*).

camarostome. Concave space formed by a depression in the common wall of fused pedipalpal coxae and the convex rostrum fitting into it; serves as filter of liquefied food before it reaches the mouth (found in Schizomida, Thelyphonida and Ricinuleida).

****capitulum.*** Anterior portion of body in Acarida bearing mouth parts (gnathosoma).

carapace. Dorsal covering of cephalothorax in all arachnids, formed by fusion of cephalic and thoracic tergites; called entire when forming a single plate; when composed of several plates (as in Schizomida, Palpigradida and Solpugida) called segmented (peltidium).

caruncle. Sucker-like membrane at the end of tarsi in many Acarida.

cephalothoracic sulci. Pair of grooves separating the cephalic from thoracic portion of the carapace.

cephalothorax. Anterior portion of the body bearing 6 pairs of appendages (prosoma).

chela. Pincers of an appendage formed by a rigid process of the penultimate joint and a movable last joint.

chelicerae. Preoral appendages of all Chelicerata, corresponding to 2nd antennae of Crustacea, but modified for biting or piercing; composed of 3 or 2 segments (Figs. 70,*1d;* 82,*2c;* 112,*2c*).

chylenteron. Abdominal portion of enzyme-producing digestive diverticles of mid-gut.

clypeus. Portion of carapace between its anterior edge and the eyes.

comb. Term applied to 2 totally different structures. In Araneida, a row of serrated bristles on the 4th tarsi, found only in the family Theridiidae. In scorpions, a pair of abdominal appendages situated on the sternite following upon the genital opercula, present in all scorpions, but not in any other arachnids.

coxa. Basal segment of all cephalothoracic appendages, but name rarely used in the case of the chelicerae.

coxal glands. Modified nephridia situated in cephalothorax and opening to exterior by 1 or 2 pairs of lateral orifices behind the coxae.

cribellum. Single or paired perforated plate in a small group of spiders, corresponding to the anteromedial spinnerets of Liphistiina and serving as outlet for special silk glands.

cucullus. Term properly applied only to the movable plate, articulated to the front of the carapace in Ricinuleida; erroneously applied to part of carapace, anterior to the eyes in Pseudoscorpionida.

deutonymph. Second developmental stage in Acarida.

diaxial. Type of chelicerae in Araneida, in which the fangs move more or less in and out in a plane transverse to the longitudinal plane of symmetry of the body (labidognathous).

doublure. Ventral fold of anterior edge of carapace, present only in Thelyphonida.

drum. Small disclike sense organ of unknown function, situated on dorsal surface of tarsi in Araneida ("tarsal organ" of BLUMENTHAL).

empodium. Modified structure at end of tarsus in Acarida, taking place of the 3rd claw (pulvillus).

epigynum. Chitinous external structure in front of genital opening in female spiders of the suborders Dipneumonina and Apneumonina.

femur. Third segment of leg, forming the "hip" articulation with the preceding and the "knee" articulation with the following segment.

finger, immobile. Anterior, finger-like, rigid process of a chela.

finger, movable. Finger-like, movable last segment of a chela.

galea. Spinning tube on movable finger of chelicerae in Pseudoscorpionida.

gizzard. Last portion of the fore-gut developed as a pumping organ; its dorsal dilator muscle is attached to an apodeme visible on external surface of carapace and called thoracic groove.

gnathosoma. Anterior portion of body in Acarida, bearing the mouth parts; formerly called capitulum.

hand. Common appellation of pedipalpal chela; in restricted sense, the main part of the segment less its immobile finger, comparable to human palm.

hysterosoma. Section of body in Acarida, following upon 2nd pair of legs.

labidognathous. Alternative term for diaxial.

lorum pediculi. Dorsal sclerite of pedicel in Araneida.

malleoli. Racket organs of Solpugida on ventral surface of 4th pair of legs.

**mandible.* Obsolete term used in the past by some arachnologists for chelicerae and by others for pedipalpal coxae.

maxilla. Common name for coxa of pedipalp.

mesopeltidium. Single, more commonly paired, sclerites in arachnids with segmented carapace, situated immediately behind propeltidium.

metapeltidium. Usually single, rarely paired, last sclerite of a segmented carapace, following upon mesopeltidium.

metapodosoma. Section of body in Acarida, bearing the 3rd and 4th pairs of legs.

metatarsus. Typically 6th segment of a leg, following upon tibia and preceding tarsus (basitarsus, protarsus).

notogaster. Dorsal shield of hysterosoma in Acarida.

ocellus. Simple eye, as distinct from compound or facetted eye; only type of eyes found in arachnids.

onychium. Distal subsegment of tarsus carrying claws, found in some arachnids, but wanting in others (posttarsus).

operculum. Lid closing an opening, such as the anus or genital opening; usually disclike and flat, solid or composed of 2 parts, present only in some orders. Genital opercula in scorpions always paired, meeting in a median longitudinal line. Anal operculum of Anthracomartida composed of a larger anterior and a smaller posterior plate meeting in a transverse line.

opisthosoma. Posterior portion of body, following upon the 4th pair of legs (abdomen).

orthognathous. Type of chelicerae with fangs moving in a plane parallel to the plane of symmetry of the body (alternative term for paraxial).

palpi. Term applied either to pedipalpi including pedipalpal coxae, or more properly to the 5 segments following the coxa.

paraxial. Type of chelicerae in which the fangs move in a plane parallel to the plane of symmetry of the body, original, more primitive type (orthognathous, prognathous).

paracymbium. Basal apophysis of terminal segment of pedipalp in male spiders of the families Erigonidae and Linyphiidae.

patella. Fourth segment of a typical leg, following upon and forming the "knee" articulation with the femur; fused with tibia in some orders and then completely losing its identity.

pedicel. Greatly modified 1st segment of abdomen in Caulogastra, reaching its extreme development in spiders.

pedipalpi. Second pair of cephalothoracic appendages, subject to many variations in structure; largest and most conspicuous appendages in scorpions and pseudoscorpions, ending in a powerful chela; stout and conspicuous in whip scorpions and Phrynichida, but ending in a pointed joint; least conspicuous appendages in Architarbida. Terminal segment in male spiders bears at the time of maturity the organs of copulation.

peltidium. Latin name for carapace.

petiolus. Latin name for pedicel.

plagula sternalis. Ventral plate of pedicel, present in some genera of spiders.

postabdomen. Attenuated portion of abdomen in scorpions, composed of 5 segments and a telson modified as a poison gland (tail).

posttarsus. Distal subsegment of tarsus, bearing claws (onychium).

preabdomen. Anterior portion of abdomen in scorpions, composed of 7 segments, considerably wider than the tail.

pretarsus. Rarely used alternative of posttarsus.

prognathous. Alternative term for paraxial.

propeltidium. Anterior sclerite of a segmented carapace.

propodosoma. Section of body in Acarida, bearing the 1st and 2nd pairs of legs.

prosoma. Alternative term for cephalothorax.

protarsus. Alternative term for metatarsus.

proterosoma. Anterior section of body in Acarida, ending behind 2nd pair of legs.

protonymph. First postembryonic stage of Acarida.

pteromorph. Winglike outgrowth of body wall in Acarida.

pulvillus. Special structure at end of tarsus in Acarida (empodium).

quadrangle of eyes (or simply **quadrangle**). Rectangle formed by outer tangent lines to 4 median eyes of spiders.

racket organs. Special sense organs of Solpugida, situated on 4th pair of legs (malleoli).

rostrum. Term applied to totally different structures in different orders of Arachnida—in spiders, upper lip; in Solpugida, tubelike "beak"; in Eophrynidae, anterior spike of carapace, similar to the rostrum of a lobster.

sclerite. Hardened chitinous portion of any part of external skeleton.

scopula. Brush of short hair on any appendage; common on metatarsi and tarsi of many spiders.

serrula. Sawlike chitinous keel on aterior edge of maxillae in spiders; toothed keel on cheliceral fingers in pseudoscorpions.

somite. Body segment.

spinneret. Abdominal appendage of spiders, with spinning tubes at the end; maximum, 4 pairs, in Liphistiina; minimum, 1 pair, in a few genera of 4 different families (mamillae). In pseudoscorpions, a special spinning organ on the movable finger of chelicerae, called galea.

spiracle. Opening of tracheal tube or book lung (stigma).

sternite. Scleritized plate of ventral wall of a segment of the body.

sternum. Scleritized sternal plate of a single thoracic segment or more often of several thoracic segments, as in scorpions and spiders.

stigma. Opening of a book lung, or of a tracheal tube (spiracle).

stylophore. Fused base of chelicerae in some Acarida.

syngnathous. Same as diaxial.

tarsus. Last segment of leg, sometimes subsegmented.

tectopodium. Leaflike extension near base of coxa in Acarida.

telson. Dorsal, postanal extension of body, articulated to last abdominal segment; in scorpions, harbors poison glands and ends in a sting; in whip scorpions, developed as a multijointed flagellum; in Schizomida, rodlike in females, knoblike in males.

tergite. Hardened chitinous plate on the dorsal surface of a body segment.

thoracenteron. Thoracic diverticles of mid-gut.

thoracic groove. External indentation of dorsal cephalothoracic apodeme serving for attachment of dilator muscles of gizzard.

tibia. Fifth segment of typical leg or pedipalp, following upon patella which may be completely fused with it, in which case the resulting segment retains the name tibia.

trichobothrium. Sensory hair arising from the center of a disclike membrane on legs or pedipalpi and serving for perception of currents of air; number and distribution of trichobothria have value in taxonomy.

tritonymph. Third nymphal stage of Acarida.

trochanter. Second segment of pedipalp or leg, so articulated to coxa and femur as to permit motion of the entire leg in any direction; physiologically corresponds to vertebrate hip articulation.

ONTOGENETIC DEVELOPMENT

Most Arachnids are oviparous. Scorpions are ovoviviparous. Normal parthenogenesis occurs in some Acarida. Eggs are usually taken care of by the mother, either enclosed in a cocoon, as in the majority of spiders; or guarded inside a nest, as in Schizomida, until the embryological development is completed; or attached to the underside of a rock or loose bark and left to themselves. In almost all orders, including even scorpions in which development takes place inside the mother's body, the emerging 1st instar is unable to ingest food, because the development of the mid-gut is not completed at that time and the embryonic yolk, serving for nourishment, fills completely the mid-gut, which still lacks direct connection with the fore- and hind-gut. With few exceptions, ingestion of external food begins in the 2nd instar. Sexual maturity is reached after several molts, although in a few exceptional cases development is so abbreviated that adult males emerge from the eggs with fully developed reproductive organs, as has been shown for an Australian and an American species of spiders belonging to the family of orb weavers. In some families of spiders and in scorpions, the 1st instar is spent on the back of the mother. Except in the case of Acarida and Ricinuleida, in which the 1st instar differs from the following ones by having only 3 pairs of legs, the young of all other Arachnida possess 4 pairs of legs already in the 1st instar, though the proportions of body and appendages differ greatly from those in later stages. Because of their inability to ingest external food and lack of the sensation of hunger, young of the same batch of eggs keep together during the 1st instar. Dispersal coincides with the completion of digestion of the embryonic yolk, establishment of direct connection between the 3 sections of the digestive tract and the consequent awakening of the sensation of hunger. Young taken care of by their mother leave her and run away; young which spend their 1st instar in close association with each other, but without parental care, disperse similarly. Gregarious species are known only in a few spiders and some mites. In all carnivorous arachnids dispersal is a prerequisite check to cannibalism, which takes place invariably in confinement. Only in plant-eating mites is cannibalism nonexistent.

HABITAT AND GEOGRAPHICAL DISTRIBUTION

Most arachnids are free-living, terrestrial and carnivorous. Aquatic species occur only in a few genera of spiders and in several families of marine and fresh-water mites. Apart from the question of climate, food supply and extermination by enemies, geographical distribution is determined by the physically possible methods of transportation of eggs, young and adults in a viable condition. The most striking of such methods is the aerial transportation of spiderlings and small adult spiders on gossamer threads through dozens and hundreds of miles. Stronger winds carry to considerable distances dead leaves with attached egg cocoons of spiders and galls filled with mites. Parasitic Acarida depend partly upon the habits of their own nymphs and adults and partly upon the habits of their hosts.

Several orders of arachnids are found only in tropical and subtropical regions, the widest horizontal and vertical distribution being found in spiders and Acarida which exceed other orders in number of species. The smallest orders are Palpigradida, Schizomida and Ricinuleida. Very few species of Recent arachnids are cosmopolitan in their distribution, but many genera are represented in widely separated regions of the world. Thus, in the family Scorpionidae, the genus *Opisthophthalmus* is restricted to South Africa, *Opisthacanthus* is represented in Africa and America, and *Diplocentrus* only in America. Most families of spiders are represented on all continents, but many genera have a restricted distribution as have also 2 or 3 families. On the other hand, of the only 2 genera comprising the very clearly defined family Hypochilidae, the genus *Hypochilus* is found only in America, the genus *Ectatosticta* in China and Tasmania.

GEOLOGICAL RECORD AND EVOLUTION

As a class, the Arachnida were a richer group in the past than at present. Of the 16 known orders of Arachnida, only 11 survived, 5 became extinct in the late Paleozoic. At present the scorpions represent the oldest order because they are the only arachnids so far found in the Silurian. The first representatives of Acarida, Trigonotarbida and Araneida (the latter not quite certain) have been discovered in the Devonian. Presumably on account of their small size, no Acarida have been found in any later formation until the Oligocene (Baltic amber), but of the known 16 orders of Arachnida, 12 are represented in the Carboniferous. The only fossil representative of the order Palpigradida was found in the Jurassic; several genera of the order Pseudoscorpionida in the Oligocene (Baltic amber); and of the order Schizomida in the ?Pliocene (onyx marble). The fossil record of Arachnida is therefore very incomplete, with a big gap between the late Paleozoic and the Oligocene. A single fossil scorpion is known from the Devonian, none from the Permian, 2 genera from the Triassic and none again until the Oligocene. The order Phalangiida is represented by only 3 genera in the Carboniferous and none in later formations until the Oligocene. (Some have been reported and figured in the Lebanon Cretaceous, but not yet described.) The order Araneida, except for the doubtful representative described from the Devonian, is represented only in the Carboniferous and the Oligocene. But in their case we know at least definitely that fossil spiders have been finally found in the Cretaceous, because 3 collections of them have been placed in my hands for study.

Of the 5 extinct orders of Arachnida, Trigonotarbida are represented in the Devonian and were common in the Carboniferous, but have never been found in any later formation. The other 4 orders, namely Anthracomartida, Haptopodida, Kustarachnida and Architarbida have been found only in the Carboniferous. These 4 orders, while in some regards of great importance for understanding of the evolution of the orders of Arachnida, are themselves so distinct from all other orders that they can be regarded only as end products of macroevolution and not as intermediate stages. The unraveling of the process of evolution in Arachnida has to depend therefore on the tracing of the direction in evolutionary trends common to all of them and appearing also in the ontogeny of living representatives. In this respect, HAECKEL's biogenetic law, postulating that ontogeny is a recapitulation of phylogeny, is of great help, for it prevents making the mistake of assuming a reverse direction in certain trends. At the same time one must be on guard against the possibility that a trend which persisted through so many millennia and is still operative, may have remained latent at times and active at other times, being continuous in direction, yet discontinuous in operation, and therefore not necessarily synchronous with geological sequence.

Keeping these principles in mind we will not be astonished in finding that, for example, Recent scorpions do not represent the end of their macroevolutionary trend, consisting in a gradual loss of posterior thoracic sternites, but a middle stage which proved to be viable, while the extremes became extinct in the Carboniferous. Whether Recent scorpions still possess this trend in a latent stage or have completely lost it, we do not know and nothing but an experiment or a lucky monstrosity could give an answer to this question. But one fact remains unquestionable and that is that with the appearance of the first representatives of the Carboniferous superfamily Scorpionoidea this trend was arrested and all further morphological changes were of a smaller and different type.

Something similar may be observed in the displacement of the mouth opening backward from its original position at the end of the 1st cephalic segment. That process, as in all trends, is unidirectional. It reaches its maximum in Xiphosura and Stethostomata (among the Arachnida), but was arrested in all other Arachnida at a stage when the mouth reached the 1st postcheliceral segment, i.e., the pedipalpal segment. It is in that position in the Silurian protoscorpions, as well as in all Recent scorpions and other arachnids. In this single respect the Paleozoic Stethostomata are more advanced than now-living arachnids.

The most conspicuous trend, common to all Arthropoda and clearly operative in all Arachnida, is the one involving fusion of anterior abdominal segments with the cephalothorax and the gradual loss of posterior segments. Perhaps it would be more appropriate to treat them as 2 different trends, for they proceed in the opposite direction and are both, of course, irreversible. But the mechanics of both are essentially the same and consist either in a shortening of a segment without changing its transverse area or in a reduction of its transverse area by peripheral constriction without changing its length, until the segment disappears completely. At the anterior end of the abdomen, the 1st segment is the first to be affected. It disappears completely in scorpions, harvestmen and mites by the first method and in Ricinuleida by the second, i.e., by peripheral constriction. But in both cases, the 1st abdominal neuromere remains distinct and the same applies to the neuromeres of the following segments when they become fused with the cephalothorax, as in some harvestmen and mites.

Both methods of disappearance are also at work at the posterior end of the abdomen. But in all cases the last segment is the first to go, then the penultimate, then the antepenultimate and so on, the maximum involving 7 posterior segments in some spiders. In scorpions, 5 segments were involved, but, instead of being lost, they became attenuated and permanently retained in the form of a "tail." The gradual attenuation of these segments can be easily seen in the embryonic stages of any Recent scorpion and undoubtedly underwent a similar change in the Ordovician Eurypterida. In Phrynichida only the 12th segment became attenuated and remains as a single-jointed pygidium. In Thelyphonida and Ricinuleida, the 3 last segments underwent similar attenuation and these orders are characterized by the possession of a 3-jointed pygidium. In spiders one can see 12 abdominal segments in the early embryo and follow the attenuation of posterior segments forming an "evanescent" tail similar to that of scorpions, but then gradually lost, leaving only 1 to 3 anteriormost tergites which become the so-called anal tubercle of the adult spider. HOLM, who gave an excellent description of this process, was misled by the similarity between the araneid evanescent postabdomen and that of scorpions and, assuming that scorpions are primitive arachnids in every respect because they were present in the Silurian, reached the erroneous conclusion that the spider *Segestria* is more primitive than a scorpion inasmuch as the scorpion has 5 postabdominal segments, whereas *Segestria* has 7. The reverse is, of course, the only possible interpretation. Scorpions are in several respects less primitive than some other Arachnida, as, for example, Palpigradida and segmented spiders of the suborder Liphistiina. In other respects they exhibit more primitive characters as, for example, in the presence of 7 pairs of cardiac ostia and 4 pairs of book lungs. Even *Liphistius* has only 5 pairs of

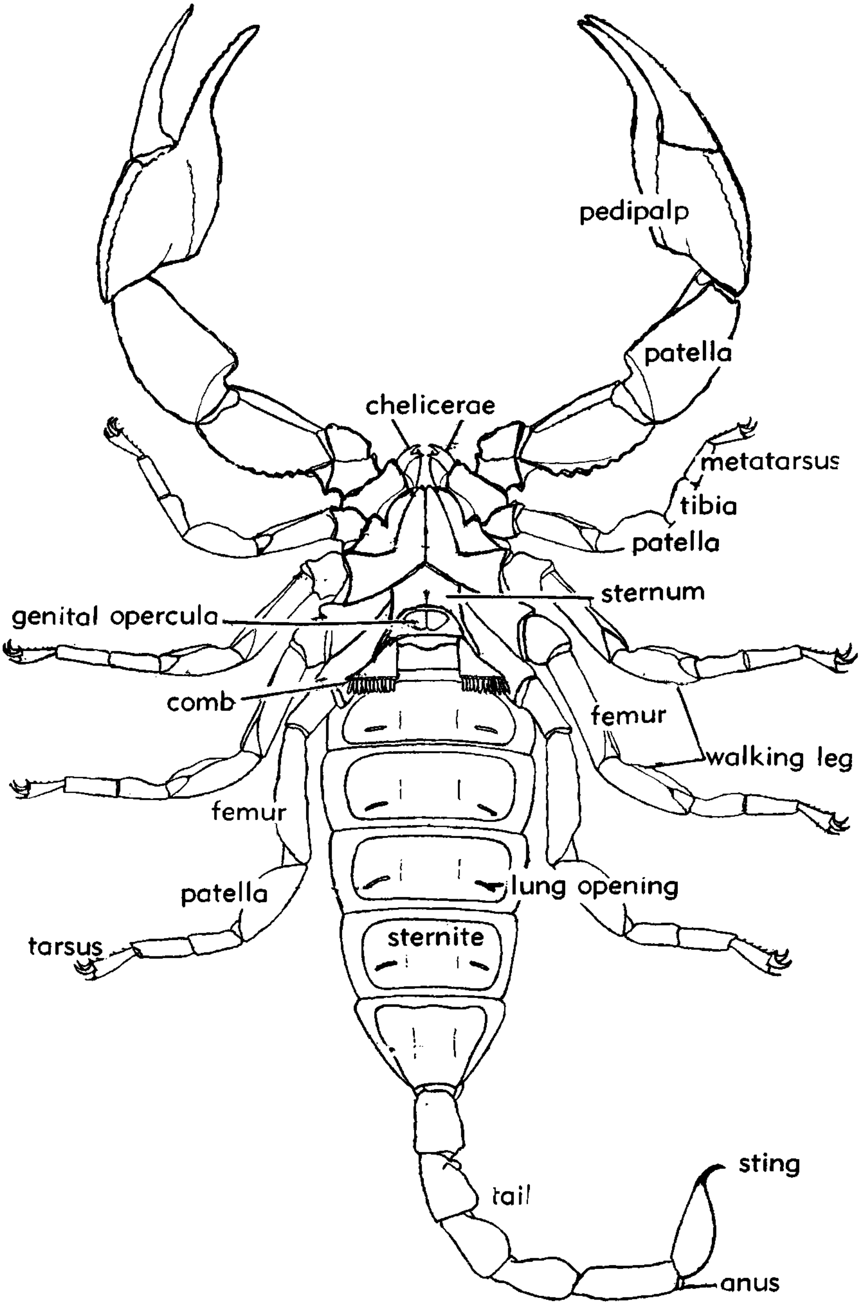

Fig. 37. External morphology of scorpions; *Opisthacanthus lepturus,* Panama, viewed from ventral side, ×2 (76).

ostia and 2 pairs of book lungs, while *Segestria* has 2 pairs of ostia and is in some respects one of the most advanced spiders.

The loss of segments may appear at first sight to be a trend involving only loss and not an increase in complexity of structure, which one associates with the idea of progressive evolution. But one must remember that Arthropoda developed from more primitive segmented animals, Recent relatives of which are the Annelida. In Annelida the segmentation of the body is still anomomeristic, the number of segments in many species increasing with age. The segregation of segments into tagmata of a definite number of segments was accomplished at a loss of segments and of the ability to increase the number of segments during life, but resulted in greater compactness of the body and in improved functional efficiency of its entire mechanism. This is certainly progressive evolution.

The tempo of evolution in Arachnida varies considerably from order to order. The most stable order seems to be the Thelyphonida. The Carboniferous *Prothelyphonus* and *Geralinura* present the same fundamental structures as the Recent genera. The macroevolution of the scorpions began in the Silurian and came to its end in the Carboniferous. Except for a belated straggler in the Triassic, all Recent scorpions can be readily traced to a single superfamily produced in the Carboniferous, along with several other, extinct superfamilies. Later formation of scorpion families involved only minor modifications. In Ricinuleida, the Recent family Ricinoididae has a different arrangement of coxae compared with the Carboniferous family Poliocheridae and produced by a trend similar to that which was responsible for the formation of Carboniferous superfamilies. But the paucity of material makes it impossible to say whether the family Ricinoididae was only recently produced or had its origin in the Carboniferous. The spiders began to split up into superfamilies already in the Carboniferous, but for some reason not yet clear continued to produce new families at least in the Oligocene. Only the Acarida exceeded the spiders in the lability of their organization and produced more than twice as many families for about a quarter of as many species.

One of the most interesting problems of relationship, and therefore of evolution, is presented by the harvestmen. This order Phalangiida is always divided into 3 suborders—Cyphophthalmina, Palpatorina and Laniatorina—on the basis of external characters which are clearly visible, but not in themselves of fundamental importance. However, important anatomical differences exist and, as HANSEN & SØRENSEN have pointed out, Cyphophthalmina differ in many respects from the other 2 suborders, which have more features in common with each other. On the other hand Cyphophthalmina resemble Architarbida in many respects and it is not impossible that if we knew the internal anatomy of the latter, a still closer relationship between them could be established. Points of similarity between the Cyphophthalmina and some Acarida have also been discussed by various authors and it seems possible that Architarbida, Cyphophthalmina and Acarida represent 3 branches of a single ancestral group. For the present it is safer to consider them as separate orders.

Subclass LATIGASTRA Petrunkevitch, 1949

[Type: *Scorpio* LINNÉ, 1758]

Arachnida with broad juncture between cephalothorax and abdomen. Basal joint of chelicerae anterior to pedipalpal coxae. Abdomen with distinct trend toward shortening of anterior segments, loss of 1st segment in Scorpionida and Phalangiida and fusion with cephalothorax in Phalangiida and Acarida. *Sil.-Rec.*

Order SCORPIONIDA Latreille, 1817

[*nom. correct.* PEARSE, 1936 (*pro* Scorpionides LATREILLE, 1817)] [=Scorpiones HEMPRICH & EHRENBERG, 1826; Scorpiides C.L.KOCH, 1837; Scorpiones *auctt.*] [Type: *Scorpio* LINNÉ, 1758]

Abdomen segmented, clearly divided into a stout preabdomen (composed of 8 segments in Protoscorpionina, 7 segments in Euscorpionina) and a more slender postabdomen or "tail" composed in both suborders of 5 segments. At end of tail a dorsal telson, which has the shape of a bulb drawn out into a more or less curved sting and harbors within the bulb a pair of poison glands (Figs. 33, 37). Carapace entire, with a pair of median and 2 to 5 pairs of lateral eyes. Chelicerae 3-jointed, chelate (Fig. 44,*6*); their movable finger lateral. Pedipalpi 6-jointed, powerful, chelate; their movable finger ventrolateral (Fig. 37). Legs 7-jointed, with pair of claws and a spur at end, except in *Palaeophonus,* in which tarsi are simply pointed (the spur is often rated as a rudimentary 8th segment, "praetarsus" of BÖRNER, "posttarsus" of VACHON). First and 2nd coxae usually with maxillary glands harbored in maxillary processes. Single sternal plate followed by a pair of genital opercula, behind which are a pair of combs. Four pairs of book lungs with stigmata on 4 sternites following the combs. Anus terminal, at end of "tail." Ovoviviparous. *Sil.-Rec.*

DISCUSSION

Embryology of Recent scorpions shows that the 1st abdominal segment disappears, retaining in the adult only its neuromere, which becomes incorporated into the thoracic ganglionic mass as the 6th pair of its ganglia. The 1st visible tergite and the genital opercula on the 1st visible sternite in even just-born scorpions belong therefore to the 2nd embryonic segment. The original number (12) of abdominal segments is restored in the course of embryological development by subsegmentation of the 8th embryonic segment. The 1st segment does not disappear, but persists in the adult only in Protoscorpionina, which have consequently 8 preabdominal tergites and as many "tail" segments (5) as Recent scorpions. The corresponding 1st sternite is, however, not known in Protoscorpionina, because all 4 specimens, the only ones now known, present their dorsal surface with only some ventral lines impressed on it from below. All preabdominal tergites are connected with their sternites by a soft lateral pleural membrane. The last preabdominal segment is considerably narrowed posteriorly to the width of the "tail." The 5 segments of the latter have the shape of complete polygonal prisms with hard walls, lateral pleural membranes being absent. The intersegmental membranes of the tail are very short and the segments are so articulated that they never separate, unless forcibly torn apart. On the other hand, the tergites and sternites of the preabdomen, when the latter is distended by eggs or by any other cause, appear as individual plates well separated from each other by the soft intersegmental membrane. Granular or smooth keels are usually present on all tail segments and on the last preabdominal tergite.

The configuration of the coxosternal region (Figs. 38,*1c*; 40) is of suprafamilial value and is due to loss of certain thoracic sternites. All Recent families of scorpions have the same configuration of their coxosternal region as the Paleozoic family Eoscorpiidae. The coxa of the pedipalpi has never a maxillary lobe, nor does it harbor any maxillary gland. The size and shape of the pedipalpal "hand" varies greatly within each family and has therefore at best only generic value. The arrangement of granules on the hand, especially on the cutting edge of both fingers, is of a similar systematic value. The legs increase in length from the 1st to the 4th. In the superfamily Scorpionoidea, to which the Recent families also belong, the maxillary lobes of the 1st and 2nd pair of coxae harbor maxillary glands secreting digestive enzymes. The outer walls of the maxillary lobes of the 2nd pair, which are enclosed between the maxillary lobes of the 1st pair, and the medial walls of the latter are covered with small spines. The channel between the lobes functions as a filter allowing only fluid food to enter the mouth, drawn in by the suction of the powerful pumping pharynx. These coxae are independently movable, but the 3rd and 4th pedal coxae are permanently grown together, can move only jointly, and that motion is practically negligible. The proportions of the individual leg segments in Palaeophonidae are very different from those of all other scorpions, each segment being almost as wide as long, and their tarsi end in a point instead of in a pair of claws.

The mouth is situated between the bases of the pedipalpal coxae. In front of it is an anterior lip, behind it a posterior lip. The gizzard is scarcely different from the esophagus. The thoracenteron has only 2 pairs of diverticles, the chylenteron 5 pairs. The hind-gut is short and ends in an anus which is closed by a sphincter. The heart is restricted to the preabdomen and has 7 pairs of ostia. The openings of the coxal glands are at the base of the 3rd pedal coxae. Four abdominal neuromeres are incorporated in the thoracic ganglionic mass, 8 are in the abdomen and of these the 12th is fused with the 11th. The reproductive glands are in both sexes of the fenestrated type. The male has a pair of copulatory organs (so-called paraxial organs, connected with the vasa deferentia) which can be protruded through the genital opening. The latter is closed by a pair of opercula in both sexes. Secondary sexual characters are not conspicuous. Males are often more slender and have a longer tail than the females. The newly born young climb on the back of their mother and stay there until their first skin is shed, when they disperse. The size of adult scorpions varies from 13 to 200 mm.

Suborder PROTOSCORPIONINA Petrunkevitch, 1949

[*nom. correct.* PETR., herein (*pro* Protoscorpiones PETR., 1949)] [Type: *Palaeophonus* THORELL & LINDSTRÖM, 1885]

Scorpions with 1st abdominal segment persisting in the adult and preabdomen with 8 tergites (43). *Sil.-U.Carb.*

Superfamily PALAEOPHONOIDEA Thorell & Lindström, 1885

[*nom. transl.* PETR., herein (*ex* Palaeophonoidae THORELL-L., 1885)] [=Apoxypodes THORELL-L., 1885 (suborder)]

Legs with segments almost as wide as or even wider than long. Tarsi terminating in a point, without claws. *Sil.*

Family PALAEOPHONIDAE Thorell & Lindström, 1885

[*nom correct.* FRITSCH, 1904 (*pro* Palaeophonoidae THORELL-L., 1885); *emend.* PETR., 1953]

First abdominal tergite concealed under carapace, its anterior edge indicated by a transverse furrow. First pair of coxae wide apart, without maxillary lobes (Fig. 38,*1c*). *Sil.*

Palaeophonus THORELL & LINDSTRÖM, 1884 [*nom. correct.* THORELL-L., 1885 (*pro Paleophoneus* LINDSTRÖM, 1884)[1]] [**Palaeophoneus nuncius* THORELL-L., 1884]. Carapace subquadrate, with concave anterior edge. Hand, to base of fingers, almost as wide as long, with strongly convex ventral edge (45). *Sil.*, Eu.—FIG. 38,*1*. **P. nuncius* THORELL-L., Gotl.; *1a*, specimen as preserved in matrix, ×1.9; *1b*, distal half of 2nd leg, showing tibial spur and pointed tarsus, ×7; *1c*, outline of carapace with coxae and genital opercula superposed, ×3.2 (76).—FIGS. 38,*2*; 39*B*. *P. caledonicus* HUNTER, Scot.; 38,*2*, dorsal surface of specimen, showing eyes, ×3; 39*B*, photograph of holotype, ×7 (76*).

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[1] Owing to an unfortunate *lapsus calami* the name of the genus was first misspelled with *-eus* instead of *-us* at the end, and the names of its 2 authors printed not immediately following the name of the species, but in a footnote on the same page 985 of the Comptes Rendus Acad. Sci. Paris, 1884, in the abstract of the letter written by LINDSTRÖM to MILNE-EDWARDS, informing him of the important discovery of a Silurian scorpion. That the spelling of the name was a *lapsus calami* and its subsequent correction by the authors themselves not an attempt to *change* the name, but to restore its original spelling is quite clear from the statements of the authors in their joint paper of 1885 (*On a Silurian Scorpion from Gotland:* K.Svensk. Akad., Band 21, No. 9). They say (1885) on p. 7: "Owing to various hindrances no opportunity was found to make this discovery known before November the 12th 1884, when it was announced at the evening meeting of the Royal Swedish Academy of Sciences. A photograph, double the size of the original, was sent abroad to several museums and zoologists, after we had agreed jointly to undertake this memoir and had named the animal *Palaeophonus nuncius.* This new species was first mentioned in print in the 'Comptes Rendus de l'Académie des Sciences,' Paris, 1884, Dec. 1, p. 984, in an article 'Sur un Scorpion du terrain Silurien de Suède.' And (1885) on p. 9 the authors say (*in footnote 2*): "The name of the genus should be written, as it is here, *Palaeophonus*, not *Palaeophoneus*." The name is spelled correctly in the Glasgow *Herald* of December 19, 1884, and on the original label accompanying the specimen in the Stockholm Museum. It is therefore quite wrong to assign the authorship of the name to LINDSTRÖM alone and to revert to the first, incorrectly spelled name, merely on the purely formal basis of priority of its publication and in disregard of the authors' own explanation, as the Editor of the *Treatise* suggested in his correspondence with me concerning this subject. LINDSTRÖM himself acknowledged the joint authorship in the above letter; and neither he, nor THORELL, nor anybody else has ever used the wrong spelling.

(Prof. PETRUNKEVITCH's foregoing note presents adequate statement of THORELL & LINDSTRÖM's intentions, making clear at the same time that evidence of a *lapsus* is not contained in the original publication of 1884. Accordingly, the only legal way to validate the universally accepted spelling, which is that here used, is through application to ICZN to place *Palaeophonus* THORELL & LINDSTRÖM, 1884, on the "Official List of Generic Names in Zoology" and to place the name *nuncius* THORELL & LINDSTRÖM, 1884, as published in the combination *Palaeophonus nuncius*, on the "Official List of Specific Names in Zoology"; also to place the name *Palaeophoneus* THORELL & LINDSTRÖM, 1884, on the "Official List of Rejected and Invalid Generic Names in Zoology" and to place the name *nuncius* THORELL & LINDSTRÖM, 1884, as published in the combination *Palaeophoneus nuncius*, on the "Official List of Rejected and Invalid Specific Names in Zoology." If this seems cumbersome, it is only needful to point out that until this is done, under the Rules nomenclatural instability relating to these names will continue to exist, being not removable by lengthened years of usage or expressions of individual opinion.—EDITOR)

(Subsequently to notes given above, Prof. PETRUNKEVITCH has been informed by Mr. FRANCIS HEMMING, Secretary of ICZN, that action recommended by the Editor should be taken; hence application has been made to designate *Palaeophonus* THORELL & LINDSTRÖM and *Palaeophonus nuncius* THORELL & LINDSTRÖM as *nomina conservanda* by use of the plenary powers of ICZN.—EDITOR)

Superfamily MAZONIOIDEA Petrunkevitch, 1913

[*nom. transl.* PETR., herein (*ex* Mazoniidae PETR., 1913)]

Legs with segments distinctly longer than wide, their proportions similar to those of Euscorpionina. Tarsi not preserved, but presumably ending in a pair of claws (38). *Sil.-U.Carb.*

Family DOLICHOPHONIDAE Petrunkevitch, 1953

First abdominal tergite concealed under carapace. Coxosternal region and armature of legs unknown. *Sil.*

Dolichophonus PETRUNKEVITCH, 1949 [**Palaeophonus loudonensis* LAURIE, 1889]. Carapace much longer than wide, with concave anterior edge. Eyes lacking. Hand longer than fingers (43,45). *Sil.(Wenlock.)*, Scot.—FIG. 38,*4*. **D. loudonensis* (LAURIE); dorsal surface of holotype, ×1 (76).

Proscorpius WHITFIELD, 1885 [**Palaeophonus osborni* WHITF., 1885]. Carapace as wide as long, convex in front, with flat ocular tubercle, but no eyes. Hand shorter than fingers (45). *U.Sil.*, N. Am.—FIGS. 38,*3;* 39*A*. **P. osborni* (WHITF.), N.Y.; 38,*3*, dorsal surface, ×2.3; 39*A*, photograph of holotype ×2.8 (76).

Family MAZONIIDAE Petrunkevitch, 1913

[Correctly spelled on p. 35; misspelled Mazonidae on p. 54]

First abdominal tergite fully visible. *Penn.*

Mazonia MEEK & WORTHEN, 1868 [**M. woodiana*]. Carapace about as long as wide, with a pointed projection in front and a pair of eyes on an oval tubercle close behind anterior end (36). *Penn.*, N.Am.—FIG. 38,*5*. **M. woodiana*, Ill.; ×1 (76).

Suborder EUSCORPIONINA Petrunkevitch, 1949

[*nom. correct.* PETR., herein (*pro* Euscorpiones PETR., 1949] [Type: *Scorpio* LINNÉ, 1758] [=Dionychopodes THORELL, 1885 (rejected because used in different arachnid orders at various times)]

Scorpions in which the 1st abdominal segment, present in the early embryo, disappears in the course of development and becomes reduced to its neuromere incorporated in the thoracic ganglionic mass as its 6th pair of ganglia. First tergite of even 1st instar is really that of 2nd embryonic segment. Leg segments distinctly longer than wide, tarsi with a pair of claws. First coxae always with maxillary lobes, 2nd coxae with maxillary lobes in all Recent and most fossil genera, but lacking in some fossil ones. Maxillary lobes of 2nd pair contiguous along median line and wedged in between those of 1st coxae (45). *Dev.-Rec.*

DISCUSSION

The subdivision of Euscorpionina into families, as recently proposed by me and used here for subdivision into superfamilies, is based on differences in the configuration of the coxosternal region. These differences are caused by the disappearance of a portion of the sternum and the shifting into the vacated place of 1 or 2 pairs of coxae. Only in the case of the Palaeoscorpioidea a different character had to be used for separation from the other superfamilies because their coxosternal region is unknown. In the Archaeoctonoidea (Fig. 40,*2*) the anterior quarter of the sternum disappeared and the 1st coxae occupy the vacant place, while the next 3 pairs are in their original position. In the Scorpionoidea (Fig. 40,*1*) the sternum lost its anterior half and the 1st and 2nd pair of coxae occupy the vacant place. In the Mesophonoidea (Fig. 40,*6*) the arrangement of the coxae is essentially the same as in the Scorpionoidea, but only the 1st coxae have maxillary lobes. In the Cyclophthalmoidea (Fig. 40,*3*) the sternum lost its anterior ¾, the vacated space is occupied by 3 pairs of coxae and only the 4th pair is in its original position. In the Isobuthoidea (Fig. 40,*5*) the space vacated by the disappearance of the anterior ¾ of the sternum is occupied by the 2 anterior pairs of coxae and by the last quarter of the sternum, which moved forward, followed by the genital opercula which occupied its place. In the Centromachoidea (Fig. 40,*4*) the remnant of the sternum and the genital opercula moved still one segment further, with the result that the 3rd and 4th pairs of coxae are abutting against the genital opercula.

Superfamily PALAEOSCORPIOIDEA Lehmann, 1944

[*nom. transl.* PETRUNKEVITCH, herein (*ex* Palaeoscorpiidae, *nom. correct.* PETR., herein, *pro* Palaeoscorpionidae LEHMANN, 1944)]

Preabdomen with median longitudinal fold continuous with tail and resembling it. *Dev.*

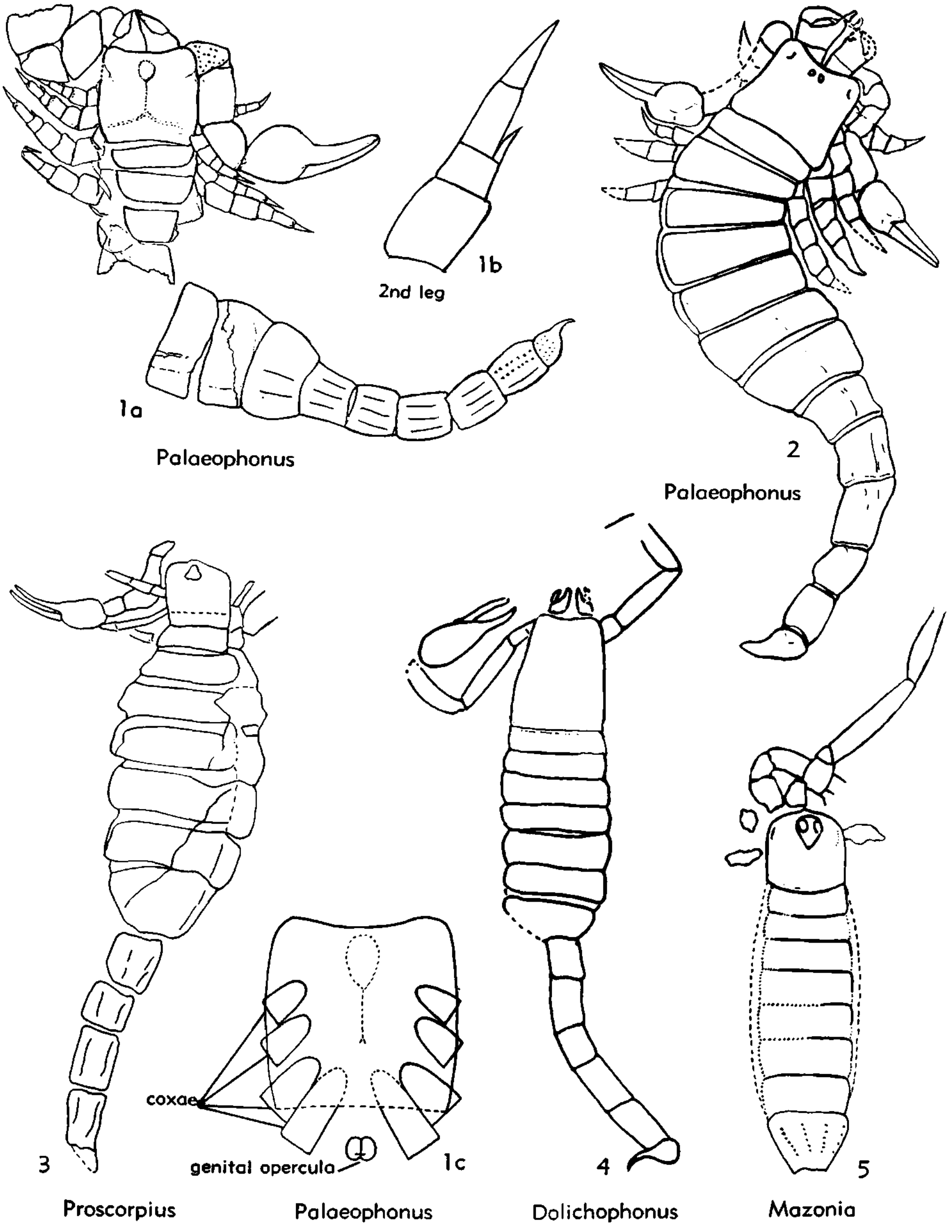

FIG. 38. Order Scorpionida, suborder Protoscorpionina (76). *1, Palaeophonus nuncius,* Sil., Swed.; *1a,* ×1.9; *1b,* 2nd leg showing pointed tarsus, ×7; *1c,* coxosternal region with outline of carapace, ×3.2. *2, Palaeophonus caledonicus,* Sil., Eng.; ×3. *3, Protoscorpius osborni,* Sil., N.Y.; ×2.3. *4, Dolichophonus loudonensis,* Sil., Scot.; ×1.5, *Mazonia woodiana,* Penn., Ill.; ×1 (p. P69-P70).

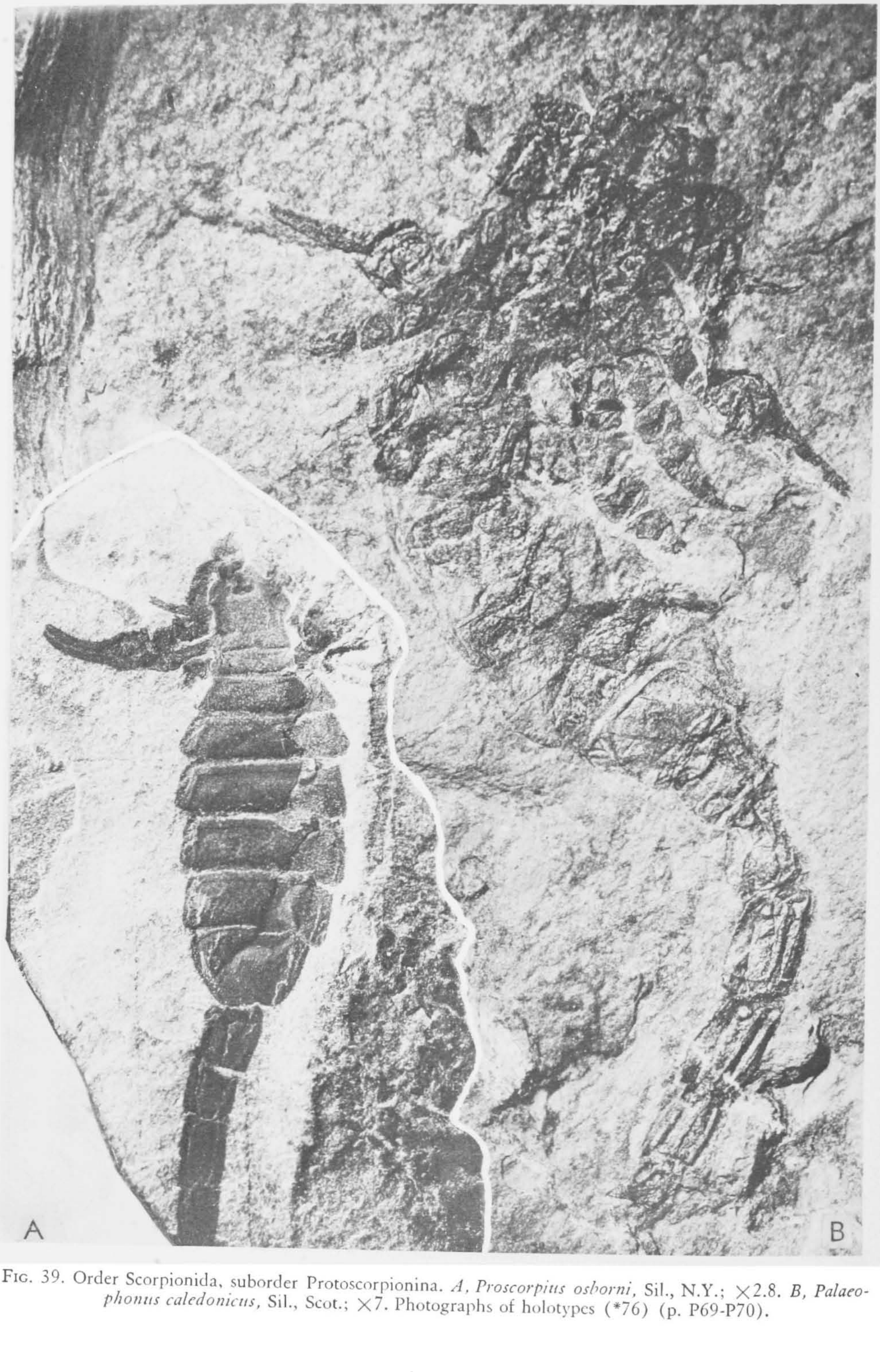

FIG. 39. Order Scorpionida, suborder Protoscorpionina. *A, Proscorpius osborni,* Sil., N.Y.; ×2.8. *B, Palaeophonus caledonicus,* Sil., Scot.; ×7. Photographs of holotypes (*76) (p. P69-P70).

Family PALAEOSCORPIIDAE Lehmann, 1944

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Palaeoscorpionidae LEHMANN, 1944)]

Median eyes situated behind middle of carapace, lateral eyes not known. Tarsi with 2 claws. Coxosternal region unknown (23, 45). *Dev.*

Palaeoscorpius LEHMANN, 1944 [**P. devonicus*] (23). *Dev.,* Ger.

Superfamily ARCHAEOCTONOIDEA Petrunkevitch, 1949

[*nom. transl.* PETR., herein (*ex* Archaeoctonidae PETR., 1949)]

First pair of coxae meeting in median line in front of sternum, the other 3 pairs abutting against sternum. *Carb.*

Family ARCHAEOCTONIDAE Petrunkevitch, 1949

[*emend.* PETR., 1953]

Only 1st pair of coxae with maxillary lobes (43, 45) (Fig. 40,*2*). *Carb.*

Archaeoctonus POCOCK, 1911 [**Eoscorpius glaber* PEACH, 1883]. Sternum with slightly converging sides, truncated at both ends. Carapace as wide in front as behind with a slight anterior median projection, much wider than long. Eyes seemingly wanting. Hand shorter than fingers, which curve toward each other (45). *Carb.,* Eu.—FIG. 41,*1*. **A. glaber* (PEACH), Scot.; ventral view, ×1.4 (76).

Eoctonus PETRUNKEVITCH, 1913 [*emend.* PETR., 1953] [**E. miniatus*]. Carapace wider than long, with distinctly converging sides. Pair of eyes ¼ length of carapace behind anterior edge (34). *Penn.,* N.Am.—FIG. 41,*2*. **E. miniatus,* Ill.; dorsal side, ×4.6 (76).

Superfamily SCORPIONOIDEA Leach, 1815

[*nom. transl.* PETRUNKEVITCH, herein (*ex* "family" Scorpionides LEACH, 1815[1])]

First and 2nd pairs of coxae with well-developed maxillary lobes (Fig. 40,*1*), those of 2nd pair meeting in median line and wedged in between maxillary lobes of 1st pair; 3d and 4th pairs of coxae abutting against sternum (45). *Carb.-Rec.*

Family EOSCORPIIDAE Scudder, 1884

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Eoscorpioidae SCUDDER, 1884)] [=Eoscorpionidae *auctt.*]

Coxae of 3d and 4th pairs of legs not much longer than those of 1st and 2nd pairs and probably not yet grown together along their line of contact, retaining independent motion. *Carb.*

Eoscorpius MEEK & WORTHEN, 1868 [**E. carbonarius*]. Carapace rectangular, median eyes situated at considerable distance from anterior edge (38). *U.Carb.,* N.Am.-Eu.—FIG. 42. **E. carbonarius,* Ill.; dorsal side, ×1.4 (73).

Alloscorpius PETRUNKEVITCH, 1949 [**Eoscorpius granulosus* PETR., 1913]. Carapace rectangular, median eyes not far behind anterior edge (45). *U.Carb.,* N.Am.-Eu.—FIG. 43,*1*. **A. granulosus* (PETR.), Ill.; dorsal side, ×0.7 (76).

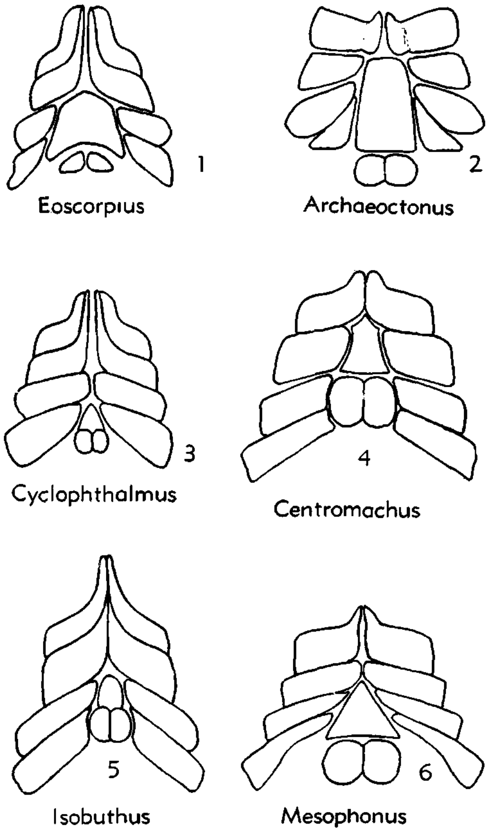

FIG. 40. Coxosternal region of fossil scorpions belonging to 6 families of the suborder Euscorpionina: *1,* Eoscorpiidae; *2,* Archaeoctonidae; *3,* Cyclophthalmidae; *4,* Centromachidae; *5,* Isobuthidae; *6,* Mesophonidae (76) (p. P73-P78).

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[1] The name Scorpionides was proposed by LATREILLE as name for an order. LEACH was the first to use it as a *family* name, with *Scorpio* LINNÉ as type, but like LATREILLE's order, LEACH's family still included pseudoscorpions besides scorpions.

Trigonoscorpio Petrunkevitch, 1913 [**T. americanus*]. Carapace triangular, with truncated apex; median eyes close to anterior edge. Hand slender, with long fingers. Tail slender (34). *U.Carb.*, N. Am.-Eu.—Fig. 43,*2*. **T. americanus*, Ill.; dorsal side, ×2 (76).

Buthiscorpius Petrunkevitch, 1953 [**Anthracoscorpio buthiformis* Pocock, 1911]. Carapace with convex converging sides and convex anterior edge, median eyes on tubercle about ⅓ from anterior edge. Fingers considerably longer than hand (45). *U.Carb.*, Eu.—Fig. 43,*3*. **B. buthiformis* (Pocock), Eng.; carapace, ×6.5 (76).

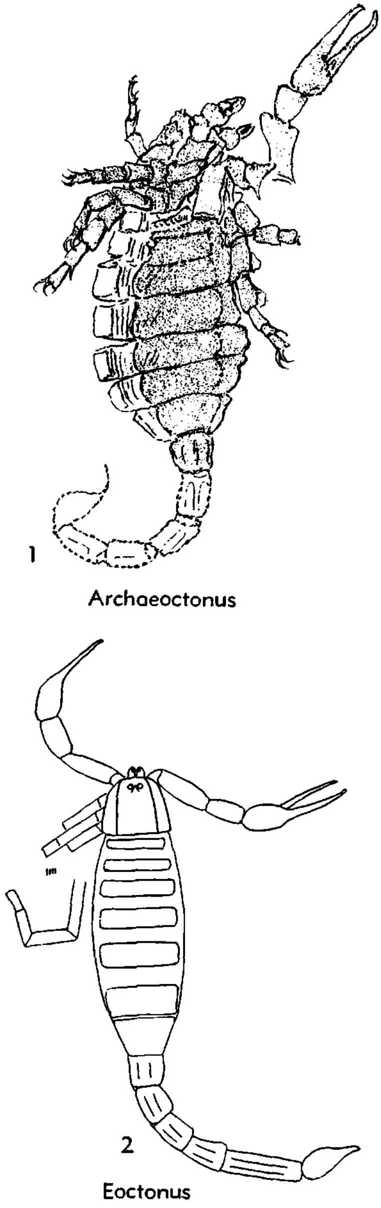


Fig. 41. Family Archaeoctonidae: *1, Archaeoctonus glaber*, U.Carb., Scot., ×1.4; *2, Eoctonus miniatus*, Penn., Ill., ×4.6 (76) (p. P73).

Fig. 42. Family Eoscorpiidae: *Eoscorpius carbonarius*, Penn., Ill., ×1.4 (80) (p. P73).

Anthracoscorpio Kušta, 1888 (**Cyclophthalmus juvenis* Kušta, 1885] [=*Lichnoscorpius* Petrunkevitch, 1949]. Carapace semicircular, with slightly concave posterior edge; median eyes sessile, situated in advance of middle (45). *Carb.*, Eng.-Czech.—Fig. 43,*4*. **A. juvenis* (Kušta), Czech.; carapace, ×20 (76).

Lichnophthalmus Petrunkevitch, 1949 [**L. pulcher*]. Carapace trapezoidal, wider than long, with cephalic portion distinctly elevated and posterior edge margined; eyes ellipsoidal, on tubercle not far from anterior edge (43). *Carb.*, Eng.—Fig. 43,*7*. **L. pulcher;* carapace, ×2.7 (76).

Typhlopisthacanthus Petrunkevitch, 1949 (**Palaeopisthacanthus mazonensis* Petr., 1913]. Tail very short and slender. Carapace much longer than wide, flat, with converging sides. No eyes (43). *Carb.*, N.-Am.-Eu.—Fig. 43,*5*. **P. mazonensis* (Petr.), Ill.; dorsal side, ×2 (76).

Palaeopisthacanthus Petrunkevitch, 1913 [**P. schucherti*]. Tail very short and slender. Carapace wider than long, trapezoidal; median eyes on tubercle ⅓ from anterior edge (38). *Carb.*, N. Am.—Fig. 43,*6*. **P. schucherti*, Ill.; dorsal side, ×2.7 (76).

Compsoscorpius Petrunkevitch, 1949 [**C. elegans*]. Carapace subtriangular, with rounded front; sides and posterior edge margined; median eyes on large longitudinally elliptic tubercle situated on well-developed cephalic portion; 3 pairs of lateral eyes close to edge, slightly anterior to median ones. Hand slender, with long curved fingers (43). *Carb.*, Eu.—Fig. 44,*1*. **C. elegans*, Eng.; carapace, ×5.5 (76).

Typhloscorpius Petrunkevitch, 1949 [**T. distinctus*]. Carapace wider than long, with cephalic portion strikingly elevated, posterior edge straight, margined; front almost as wide as posterior edge. Other parts unknown (43). *Carb.*, Eu.—Fig. 44,*2*. **T. distinctus*, Eng.; carapace, ×3.3 (76).

Europhthalmus Petrunkevitch, 1949 [**E. longimanus*]. Carapace elliptic, with straight posterior edge; median eyes close to anterior edge. Pedipalpi ⅔ length of body (43). *Carb.*, Eu.—Fig. 45,*1*. **E. longimanus*, Eng.; dorsal side, ×1.5 (76).

Garnettius Petrunkevitch, 1953 [**Mazonia hungerfordi* Elias, 1936]. Carapace rectangular, with pointed anterior projection; median eyes on tubercle close to anterior edge. Hand stout, shorter than fingers, which are also stout; 3rd leg with dorsal spurs on tibia and metatarsus (43). *U.Carb.*, N. Am.—Fig. 44,*8*. **G. hungerfordi* (Elias), Kans.; ×0.5 (76).

Family SCORPIONIDAE Leach, 1815

[*nom. transl.* Pocock, 1893 (*ex* Scorpionini Peters, 1861, *nom. correct. pro* Scorpionides Leach, 1815, *non* Scorpionides C.L. Koch, 1837]

Third and 4th pairs of coxae grown together along line of contact and much longer than 1st and 2nd pairs. Sternum pentagonal. Single spur in intersegmental membrane between metatarsus and tarsus of 1st and 2nd pairs of legs, no such spur on 3rd and 4th pairs. Three pairs of lateral eyes. *Oligo.-Rec.*

Scorpio Linné, 1758 (**S. maurus* = *S. europaeus* Linné 1758, *non* 1754). Median eyes in middle of carapace. Last preabdominal sternite and ventral

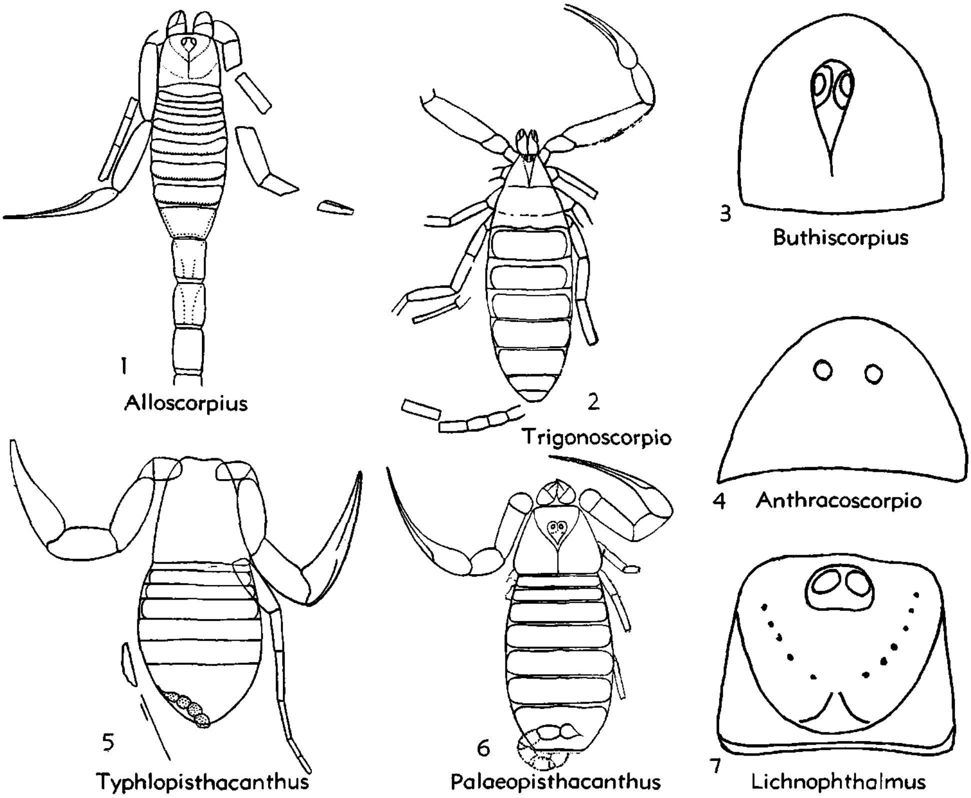


Fig. 43. Family Eoscorpiidae: *1, Alloscorpius granulosus*, Penn., Ill., ×0.7; *2, Trigonoscorpio americanus*, Penn., Ill., ×2; *3, Buthiscorpius buthiformis*, U.Carb., Eng., carapace, ×6.5; *4, Anthracoscorpio juvenis*, U.Carb., Czech., carapace, ×20; *5, Typhlopisthacanthus mazonensis*, Penn., Ill., ×2; *6, Palaeopisthacanthus schucherti*, Penn., Ill., ×2.7; *7, Lichnophthalmus pulcher*, U.Carb., Eng., carapace, ×2.7 (76) (p. P73-P74).

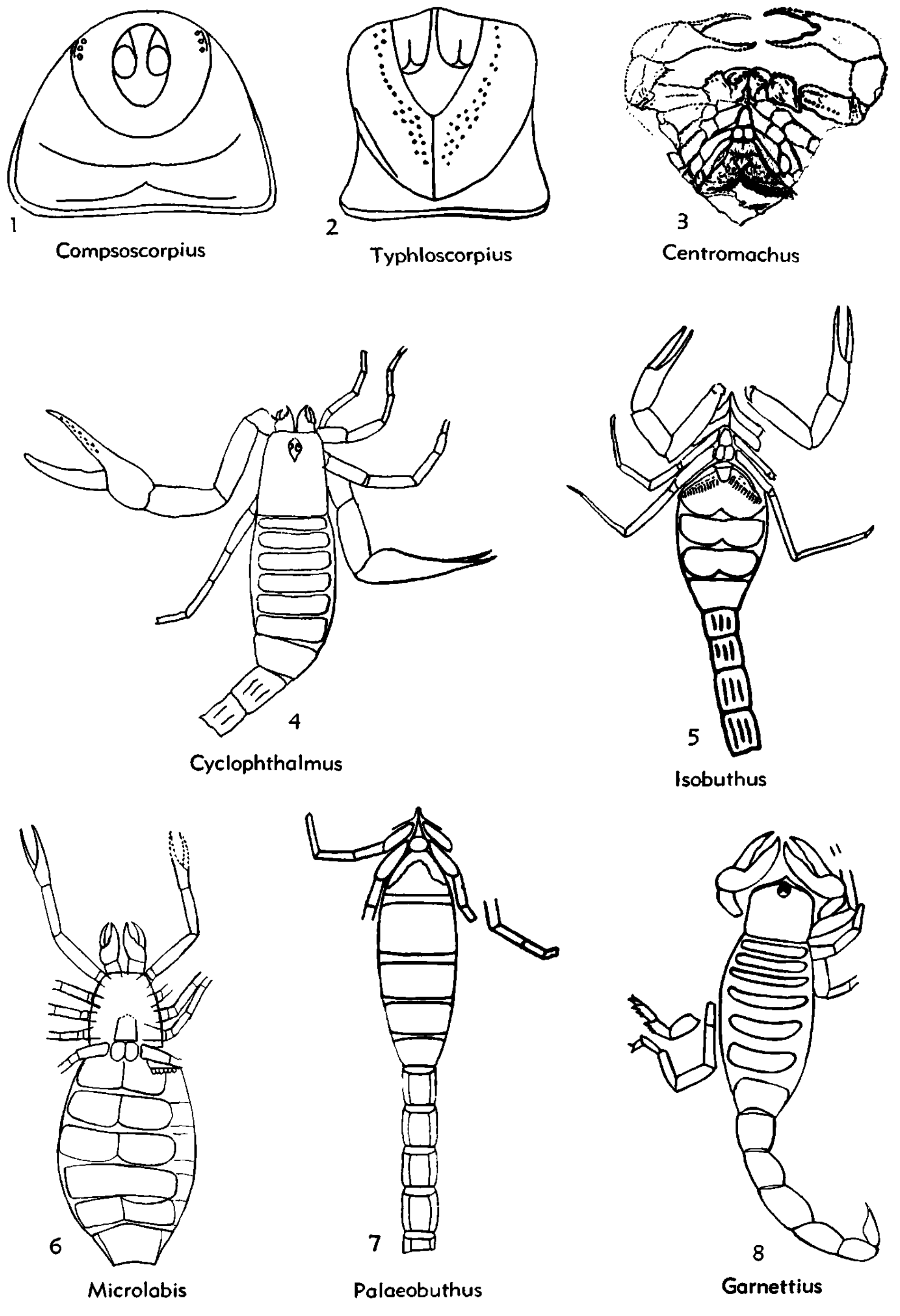


FIG. 44. Eoscorpiidae: *1, Compsoscorpius elegans,* U.Carb., Eng., carapace, ×5.5; *2, Typhloscorpius distinctus,* U.Carb., Eng., carapace, ×3.3; *7, Garnettius hungerfordi,* Penn., Kans., ×0.5. Centromachidae: *3, Centromachus euglyptus,* U.Carb., Scot., ×2. Cyclophthalmidae: *4, Cyclophthalmus senior,* U.Carb., Czech., ×0.6. Isobuthidae: *5, Isobuthus kralupensis,* U.Carb., Czech., ×0.4; *6, Microlabis sternbergii,* U.Carb., Czech., ×1.5 (76) (p. P75-P78).

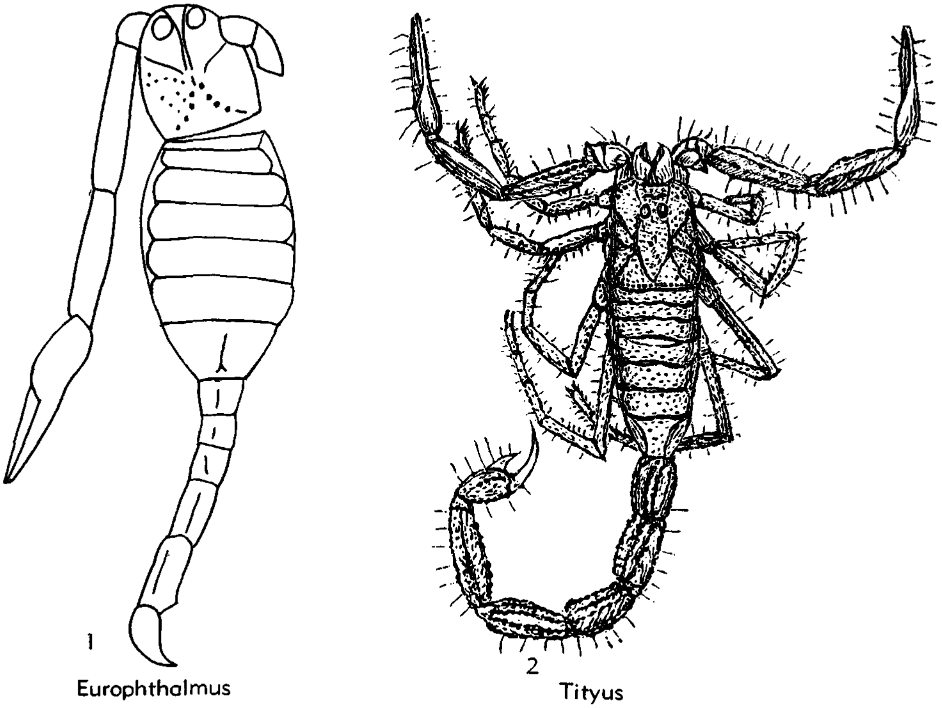


FIG. 45. Eoscorpiidae: *1, Europhthalmus longimanus,* U.Carb., Eng., ×1.5 (76). Buthidae: 2, *Tityus eogenus,* Oligo., Balt., ×7 (74) (p. P75-P77).

surface of 1st tail segment with 4 keels (31). *Oligo.-Rec.* (*S. schweiggeri* HOLL, *Oligo.*, Balt.; *S. zeuneri* HADZI, *Mio.*, Ger.).—FIG. 33,*1*. **S. maurus, Rec.,* N.Afr.; dorsal view, male, ×1.5 (*75*a*).

Family BUTHIDAE C. L. Koch, 1837

[*nom. correct.* SIMON, 1864 (*pro* Buthides C.L. KOCH, 1837)]

Third and 4th coxae as in Scorpionidae. Sternum triangular. Two spurs in intersegmental membrane between metatarsus and tarsus. Three or 5 pairs of lateral eyes. *Oligo.-Rec.*

Tityus C.L. KOCH, 1836 [*Scorpio bahiensis* PERTY, 1833]. *Oligo.-Rec.*—FIG. 45,*2*. *T. eogenus* MENGE, *Oligo.*, Balt.; dorsal side, ×7 (74).

Superfamily CYCLOPHTHALMOIDEA Petrunkevitch, 1913

[*nom. transl.* PETR., herein (*ex* Cyclophthalmidae PETR., 1913)]

Three pairs of coxae in front of sternum, 4th pair abutting against sternum; 1st and 2nd pairs with maxillary lobes (34) (Fig. 40,*3*). *Carb.*

Family CYCLOPHTHALMIDAE Petrunkevitch, 1913

Characters of superfamily. *Carb.*

Cyclophthalmus CORDA, 1835 [**C. senior*]. Carapace much longer than wide, with slightly converging sides, anterior edge slightly concave, posterior edge straight; median eyes on tubercle, not far from anterior edge. Hand shorter than fingers (34,35). *Carb.*, Eu.—FIG. 44,*4*. **C. senior,* Czech.; dorsal side, ×0.6 (76).

Superfamily ISOBUTHOIDEA Petrunkevitch, 1913

[*nom. transl.* PETR., herein (*ex* Isobuthidae PETR., 1913]

Two pairs of coxae in front of sternum, 3rd pair abutting against sternum, 4th pair against genital opercula (34, 45) (Fig. 40, *5*). *Carb.*

Family ISOBUTHIDAE Petrunkevitch, 1913

Characters of superfamily. *Carb.*

Isobuthus FRITSCH, 1904 [**Cyclophthalmus kralupensis* THORELL, 1885] [=*Eobuthus, Feistmantelia* FRITSCH, 1904]. Abdominal sternites distinctly bilobed. Carapace as wide as long. Hand longer than wide, with long fingers. Comb with more than 20 teeth (34, 45). *U.Carb.*, Eu.-N.Am.—FIG. 44,*5*. **I. kralupensis* (THORELL), Czech.; ventral side, ×0.4 (76).—FIG. 46. *I. rakovnicensis* (FRITSCH); specimen and counterpart, ×0.85 (76).

Microlabis CORDA, 1839 [**M. sternbergii*]. Abdominal sternites with slight median indentation and ridge. Carapace much narrower in front than behind. Sternum with parallel sides, ?pentagonal. Comb with less than 10 teeth (45). *Carb.*, Eu.—FIG. 44,*6*. **M. sternbergii*, Czech.; ventral side, ×1.5 (76).

Palaeobuthus PETRUNKEVITCH, 1915 [**P. distinctus*]. Abdominal sternites with straight posterior edge without indentation or median ridge. Sternum triangular (34, 45). *Penn.*, N.Am.—FIG. 44,*7*. **P. distinctus*, Ill.; ventral side, ×1.35 (76).

Superfamily CENTROMACHOIDEA Petrunkevitch, 1953

[*nom. transl.* PETR., herein (*ex* Centromachidae PETR., 1953)]

First pair of coxae in front of sternum, 2nd pair abutting against sternum, 3rd and 4th pairs abutting against genital opercula (45) Fig. 40,*4*). *Carb.*

Family CENTROMACHIDAE Petrunkevitch, 1953

Sternum pentagonal. Other characters of superfamily. *Carb.*

Centromachus THORELL, 1885 [**Eoscorpius euglyptus* PEACH, 1883]. Comb massive, with many intermediate plates and about 40 teeth. Hand stout, with short fingers curving toward each other (45). *Carb.*, Eu.—FIG. 44,*3*. **C. euglyptus* (PEACH), Scot.; ventral side of cephalothorax, ×2 (76).

Superfamily MESOPHONOIDEA Wills, 1910

[*nom. transl.* PETRUNKEVITCH, herein (*ex* Mesophonidae WILLS, 1910)]

Two pairs of coxae in front of sternum, but only 1st pair with maxillary lobes; 3rd and 4th pairs abutting against sternum (Fig. 40,*6*). Stigmata of book lungs at posterior edge of sternites (not on the sternites themselves), with a row of thorns on both lips (45, 61). *Trias.*

Family MESOPHONIDAE Wills, 1910

Combs with 8 to 17 teeth. Other characters of superfamily. *Trias.*

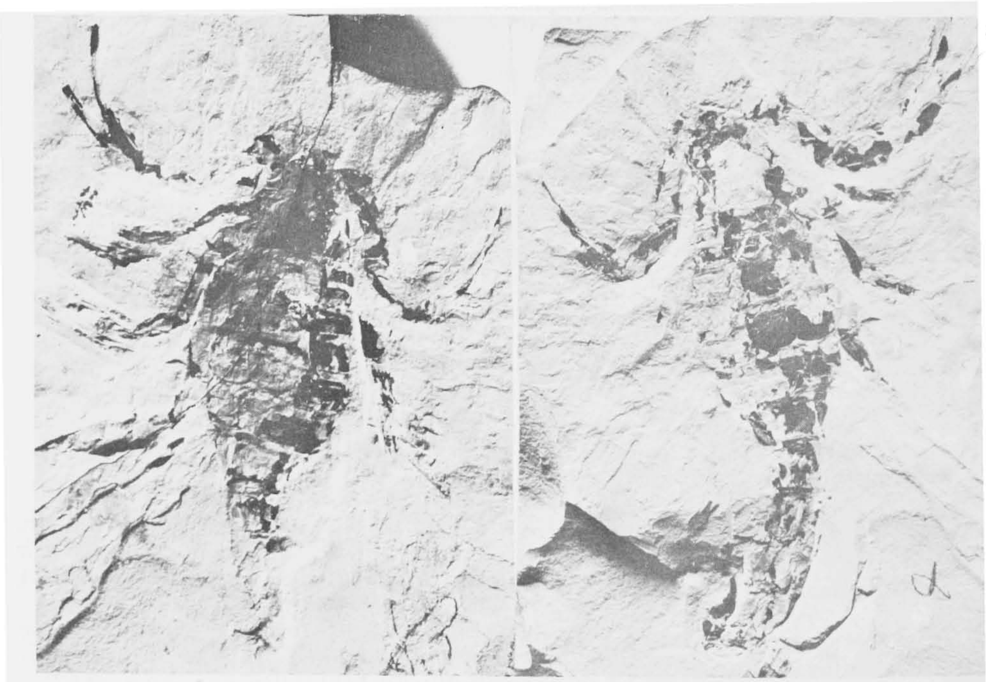


FIG. 46. Isobuthidae: *Isobuthus rakovnicensis*, U.Carb., Czech., photographs of both pieces, ×0.85 (*76).

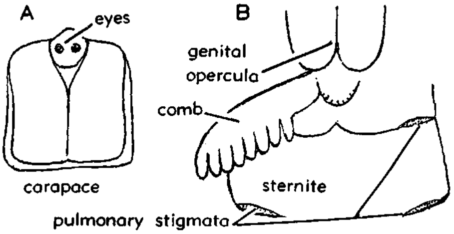


FIG. 47. Mesophonidae: *Mesophonus gracilis,* U. Trias., Eng.; *A,* carapace of male, ×7.7; *B,* genital opercula, comb and stigmata, ×7.7 (82).

Mesophonus WILLS, 1910 [**M. perornatus*]. Carapace rectangular, with anterior median process; pair of median eyes almost in line with anterior edge (Fig. 47*A*). Carapace presumably dimorphic: in presumptive male squarish and without organs described as "compound facetted eyes," in presumptive female transversely oblong and having such "eyes." Hand narrow, with long slender fingers. Sternum pentagonal (45, 61). *U.Trias.,* Eu. —FIG. 47. *M. gracilis* WILLS, L.Keuper, Eng.; *A,* carapace of male; *B,* genital opercula, right comb, sternite and stigmata, ×7.7 (82).

Spongiotarsus WILLS, 1947 [**S. pustulosus*]. Sternum an equilateral triangle. Cuticle of segments with polygonal texture and pustulose surface (61). *Trias.,* Eng.

Genera Incertae Sedis

Lissoscorpionides BODE, 1951 [**L. schmidti*]. Tail short and slender. Poorly known (?related to *Palaeopisthacanthus* or *Typhlopisthacanthus*). *L. Jur.,* Ger.

Palaeomachus POCOCK, 1911 (**Eoscorpius anglicus* WOODWARD, 1876). Only a pedipalp known. *U. Carb.,* Eng.

Order PSEUDOSCORPIONIDA Latreille, 1817

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Pseudoscorpiones LATREILLE, 1817)] [=*Chernetes* SIMON, 1879; Chelonethi THORELL, 1882] [Type: *Chelifer* GEOFFROY, 1763]

Latigastra with segmented abdomen composed of 12 segments, but the 12th rudimentary and so small that it is easily overlooked and the end of the abdomen looks evenly rounded. Carapace entire. Coxosternal region without true sternum, coxae contiguous in median line or with a "pseudosternum" or with rudimentary sternal plates. Chelicerae 2-jointed, chelate, with movable finger lateral in position, supplied with a serrula and a galea (spinneret). Coxa of pedipalp with maxillary lobe; pedipalpi 6-jointed, chelate, powerful. Movable finger of hand ventral in position. Legs 6- or 7-jointed, ending in a pretarsus which forms 7th or 8th joint and is armed with a pair of claws and an arolium. Gizzard and malpighian tubes wanting. Respiration by tracheal tubes with pair of stigmata on the 1st abdominal sternite and another pair on 3rd sternite. Poison glands, if present, situated in the hand and opening either on one of the fingers, or, in case of a pair of glands, on both fingers. Male reproductive organs with an atrium (*uterus masculinus externus* of German authors) and a pair of eversible "ram's-horn organs," but without organs of copulation. Female with a single median ovary and a pair of tubular sperm receptacles. Ventral nervous system concentrated in the cephalothorax. Oviparous (3, 7, 52, 56). *Oligo.-Rec.*

DISCUSSION

The pseudoscorpions are small arachnids which resemble scorpions on account of their powerful chelate pedipalpi. They can be easily distinguished from scorpions by the absence of a "tail." Fossil pseudoscorpions can be recognized by the presence of 11 plainly visible abdominal tergites whereas a scorpion with a broken-off tail has only 7 tergites. Both tergites and sternites may be entire or divided by a median longitudinal line, those of the 12th segment (between which the slitlike anus opens) being very narrow and having the appearance of a pygidium when protruded. The carapace is always entire, but may be impressed transversely by 1 or 2 furrows; commonly it bears 1 or 2 pairs of eyes, but some genera are blind (Fig. 48).

The mouth, situated between the pedipalpal coxae, has an anterior and a posterior lip. The lips are covered with fine hair which serves as a filter. The lips and the pedipalpal coxae form together a prebuccal cone. The pharynx is a powerful pumping organ. The esophagus opens directly into the mid-gut without a gizzard. The mid-gut has an extensive system of diverticles forming a chylenteron. It has a stercoral pouch at its end. The hind-gut is a short rectum.

The heart is limited to the abdomen and has a maximum of 3 pairs of ostia in some genera and a minimum of a single pair in others. The tracheal tubes are highly branched, the 1st pair supplies the cephalothorax, the 2nd pair the abdomen. The eggs develop in a ventral brood pouch on the abdomen.

About 1,000 species are known, ranging in size from 0.8 to 6 mm. Although several fossils from the Carboniferous and one from the Jurassic were classed by their discoverers as representatives of the order Pseudoscorpionida, such identification proved to be erroneous. The Carboniferous species are scorpions, the Jurassic form is a malacostracan. True pseudoscorpions are fairly common in Oligocene and Miocene deposits; of 19 families recognized in living forms, 9 are represented by fossils described from Baltic amber (Oligocene). They include 12 genera and 18 species (Figs. 49, 50).

Suborder CHTHONIINA Beier, 1932

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Chthoniinea BEIER, 1932)] [=Chthonioidea CHAMBERLIN, 1929] [Type: *Chthonius* C.L. KOCH, 1843]

First and 2nd pairs of legs without basitarsus, 3rd and 4th pairs with basitarsus (3). *Oligo.-Rec.*

Family CHTHONIIDAE Hansen, 1894

Spiracles transverse. Epigynal area nonsclerotic. *Oligo.-Rec.*

Chthonius C. L. KOCH, 1843 [**Obisium orthodactylum* LEACH, 1815]. Spurs present on 1st, 2nd, and 3rd coxae. *Oligo.-Rec.* [*C. mengei* BEIER, Oligo., Balt.].

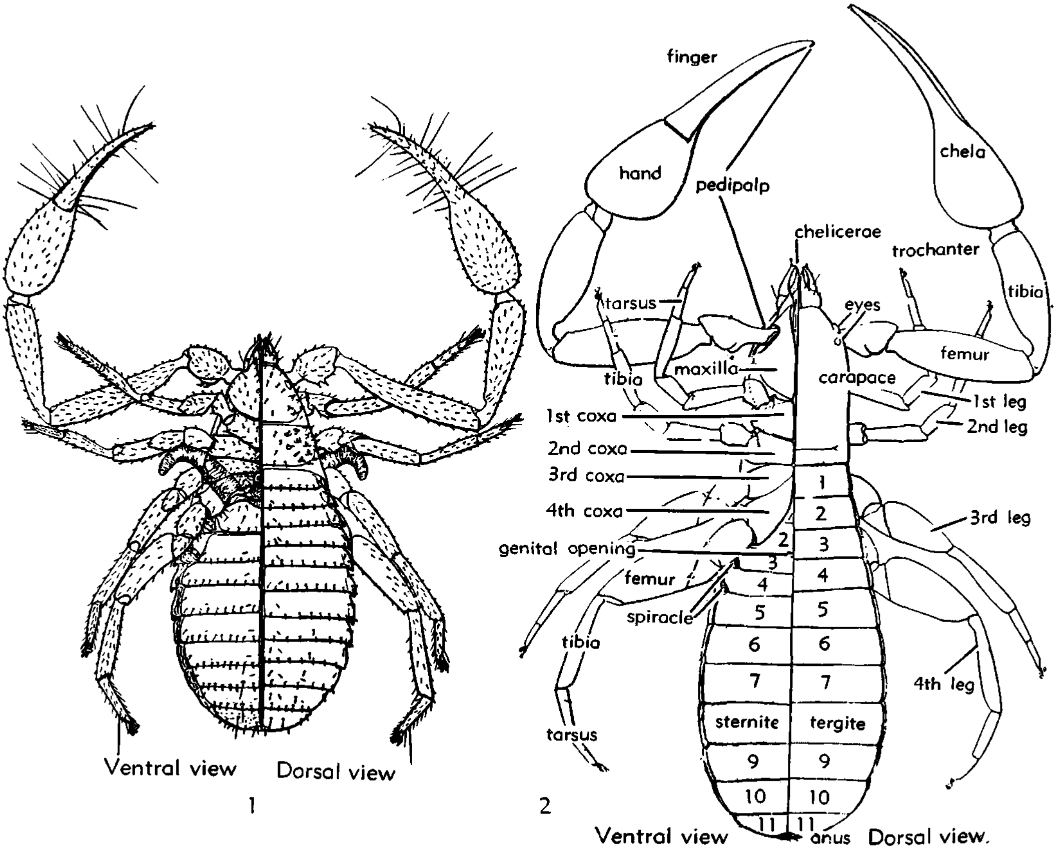


FIG. 48. External morphology of Recent pseudoscorpions, ventral (left half) and dorsal (right half): *1, Chelifer cancroides; 2, Hesperolpium slevini* (66).

Family DITHIDAE Chamberlin, 1931

Spiracles obliquely oriented. Epigynal area sclerotized. *Oligo.-Rec.*

Heterolophus TÖMÖSVARY, 1884 [**H. guttiger*]. Carapace smooth. Two pairs of eyes of equal size. Pedipalpal fingers with teeth. *Oligo.-Rec.*—FIG. 49,*2*. *H. kochii* (MENGE), Oligo., Balt.; dorsal side ×20 (74).

Suborder NEOBISIINA Beier, 1932

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Neobisinea BEIER, 1932)] [Type: *Neobisium* CHAMBERLIN, 1930]

Basitarsus present in all legs. *Oligo.-Rec.*

Superfamily NEOBISIOIDEA Beier, 1932

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Neobisiides BEIER, 1932)]

Movable finger of chelicerae with teeth. *Oligo.-Rec.*

Family NEOBISIIDAE Chamberlin, 1930

Poison gland only in immobile finger of pedipalp. Opisthosomal pleura granular. *Oligo.-Rec.*

Neobisium CHAMBERLIN, 1930 [**Obisium muscorum* LEACH]. *Oligo.-Rec.*—FIG. 49,*1*. *N. rathkii* (KOCH & BERENDT), Oligo., Balt.; dorsal side, ×18 (71).

Superfamily GARYPOIDEA Beier, 1932

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Garypides BEIER, 1932)]

Movable finger of chelicerae smooth. *Oligo.-Rec.*

Family OLPIIDAE Chamberlin, 1930

Poison glands in both fingers of pedipalp. Opisthosomal pleura smooth. *Oligo.-Rec.*

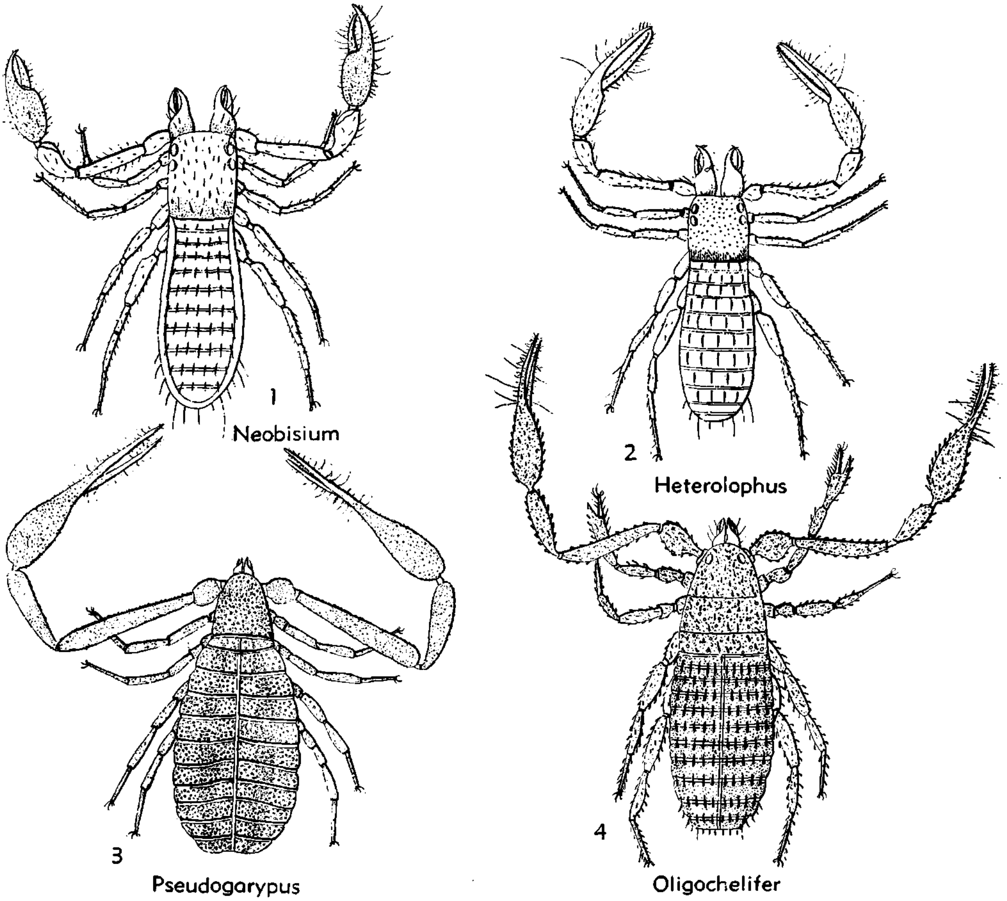
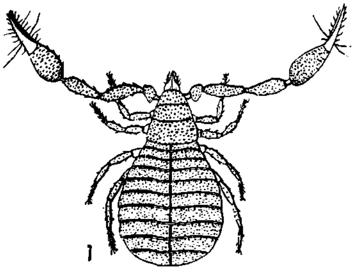


FIG. 49. Pseudoscorpions from the Oligocene Baltic amber: *1, Neobisium rathkii,* ×18; *2, Heterolophus kochii,* ×20; *3, Pseudogarypus hemprichii,* ×30; *4, Oligochelifer berendtii,* ×37 (71, 74) (p. P81-P82).



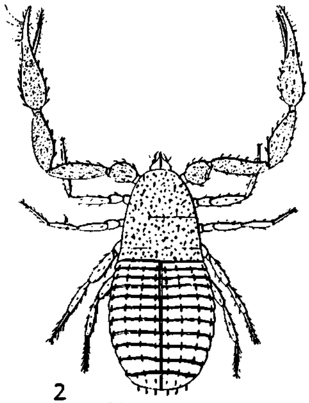


Fig. 50. Pseudoscorpions from the Oligocene Baltic amber: *1, Cheiridium hartmanni,* ×33; *2, Oligochernes weigandi,* ×25 (74) (p. P82).

Garypinus Daday, 1888 [**Olpium dimidiatum* L. Koch, 1873]. *Oligo.-Rec.* [*G. electri* Beier, Oligo., Balt.].

Family GARYPIDAE Hansen, 1894

Poison glands as in Olpiidae. Opisthosomal pleura granular. *Oligo.-Rec.*

Garypus L. Koch, 1873 [**Obisium beauvoisii* Savigny, 1829]. *Mio.-Rec.* [*G. burmiticus* Cockerell, Mio., Burma].

Geogarypus Chamberlin, 1930 [**Garypus minor* L. Koch, 1873]. *Oligo.-Rec.* [*G. macrodactylus* Beier, Oligo., Balt.].

Superfamily FEAELLOIDEA Beier, 1932

[*nom. correct.* Petrunkevitch, herein (*pro* Feaellides Beier, 1932)]

All tarsi with a single segment. *Oligo.-Rec.*

Family PSEUDOGARYPIDAE Chamberlin, 1923

Two pairs of eyes. *Oligo.-Rec.*

Pseudogarypus Ellingsen, 1909 [**Garypus bicornis* Banks, 1895]. *Oligo.-Rec.*—Fig. 49,*3. P. hemprichii* (Koch & Berendt), Oligo., Balt.; dorsal side, ×30 (71).

Suborder CHELIFERINA Hagen, 1878

[*nom. correct.* Petrunkevitch, herein (*pro* Cheliferinea Beier, 1932)]
[Type: *Chelifer* Geoffroy, 1763]

All legs without basitarsus. One pair of eyes or none. *Oligo.-Rec.*

Superfamily CHEIRIDIOIDEA Chamberlin, 1931

Femoral articulations of all legs of same morphological type, vestigial, functionless. *Oligo.-Rec.*

Family CHEIRIDIIDAE Chamberlin, 1924

All legs 5-jointed. Poison glands only in immobile fingers of pedipalpi. *Oligo.-Rec.*

Cheiridium Menge, 1855 [**Chelifer muscorum* Leach, 1817]. *Oligo.-Rec.*—Fig. 50,*1. C. hartmanni* (Menge), Oligo., Balt.; dorsal side, ×33 (74).

Superfamily CHELIFEROIDEA Chamberlin, 1931

[*nom. transl.* Chamberlin, 1931 (*ex* Cheliferidae Stecker, 1874)]

Femoral articulations heteromorph, of one type in legs 1 and 2, of another type in legs 3 and 4. *Oligo.-Rec.*

Family CHERNETIDAE Menge, 1855

All legs 6-jointed. Poison glands only in movable fingers of pedipalpi. *Oligo.-Rec.*

Oligochernes Beier, 1937 [**O. bachofeni*]. *Oligo.*, Balt.—Fig. 50,*2. O. weigandi* (Menge); ×25 (74).

Family CHELIFERIDAE Stecker, 1874

[*nom. transl.* Hagen, 1879 (*ex* Cheliferinae Stecker, 1874)]

Poison glands in both fingers of pedipalpi. *Oligo.-Rec.*

Electrochelifer Beier, 1937 [**E. mengei*]. *Oligo.*, Balt.

Oligochelifer Beier, 1937 [**Dichela berendtii* Menge, 1854]. *Oligo.*, Eu.—Fig. 49,*4.* **O. berendtii* (Menge), Balt.; ×37.

Oligowithius Beier, 1937 [**Obisium sieboldi* Menge, 1854]. *Oligo.*, Balt.

Pycnochelifer Beier, 1937 [**Chelifer kleemanni* Koch & Berendt, 1854]. *Oligo.*, Balt.

Order PHALANGIIDA Perty, 1833

[*nom. correct.* Petrunkevitch, herein (*pro* Phalangida Perty, 1833, *nom. transl.* Perty *ex* family Phalangides Leach, 1815)] [=Opiliones Sundevall, 1833] [The name Opiliones was proposed as a substitute for Phalangides because it limited the order to arachnids of the same group, whereas the name Phalangides did not originally have such a restricted meaning either in its French vernacular form used by Latreille or in its Latin form used by both Latreille and Lamarck. Leach was the first to restrict the name to a "family." As the name of an order, Phalangida was in common use up to 1909 and has not only priority over Opiliones, but also the advantage that the type of the order is *Phalangium* Linné]

Latigastra with compact body 1 to 22 mm. in length, usually with slender legs which are in some species 200 mm. long. First abdominal segment lost, its neuromere incorporated in the thoracic ganglionic mass. Maximum number of abdominal segments 10 (if anal operculum is counted as 10th tergite). Carapace entire, but the last 2 thoracic tergites, corresponding to the segments bearing the 3rd and 4th pairs of legs, may be clearly outlined by transverse furrows. Three to 8 abdominal tergites usually fused with carapace, forming dorsal scutum, but the tergites may remain recognizable by transverse furrows between them. Configuration of coxosternal region subject to several structural variations. All coxae movable in Phalangioidea and some other groups; immobile in Nemastomatidae and Trogulidae. First pair of coxae movable, other pairs immobile and coalesced in Laniatorina. Sternum may be present or wanting. Chelicerae 3-jointed, chelate. Pedipalpi 6-jointed, pediform or raptorial, with or without a claw at end. Legs 7-jointed, tarsi often subsegmented and flexible, those of 1st and 2nd pairs always with a single claw, those of 3rd and 4th pairs either with a single claw or with 2 claws. Coxae of pedipalpi and of 1st pair of legs with maxillary lobes, those of 2nd legs usually without lobes, but in some groups with lobes (Fig. 51).

Mouth opens either directly to the outside or into a stomotheca formed by the inner surface of the 1st coxae. Pharynx hexagonal, lacking an apparatus for filtering

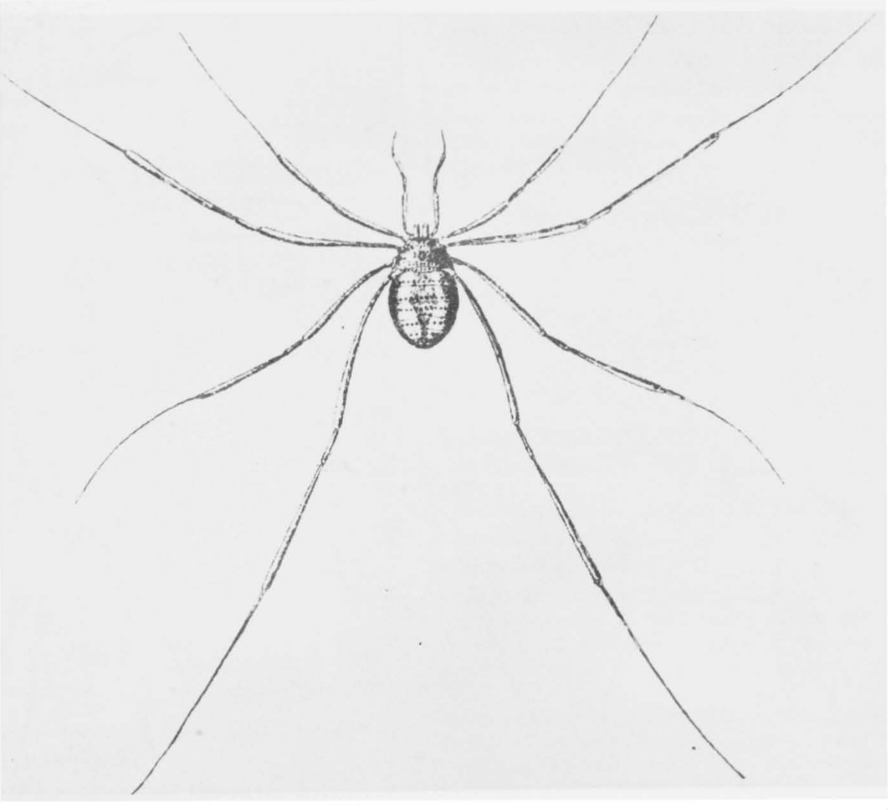


Fig. 51. *Phalangium opilio,* a common harvestman of Europe and North America, ×2 (after Blanchard).

food, so that coarse particles are regularly ingested. Mid-gut with spacious diverticles occupying major portion of body cavity. Hind-gut quite short, anus with an operculum. Respiration by means of a pair of highly ramified tracheal tubes with a pair of spiracles on 2nd abdominal sternite, behind 4th pair of coxae. A pair of coxal glands with openings behind 3rd pair of coxae. Heart with only 2 pairs of ostia. Arterial system lacking. A pair of odoriferous glands in the cephalothorax, with openings close to 2nd or 4th coxae, dorsal to them. Pair of median eyes, usually elevated on a tubercle, but sessile and wide apart in Cyphophthalmina. Reproductive organs of male with testes fused into a single U-shaped organ, with protrusible penis. Females with a U-shaped ovary and protrusible ovipositor. Oviparous (4, 21, 35, 51). *Penn.-Rec.*

DISCUSSION

Recent Phalangiida are divided into 3 suborders—Cyphophthalmina, Palpatorina and Laniatorina—with more than 2,350 species. Owing to poor preservation, the few known Paleozoic Phalangiida cannot be assigned unreservedly to any of the Recent suborders,

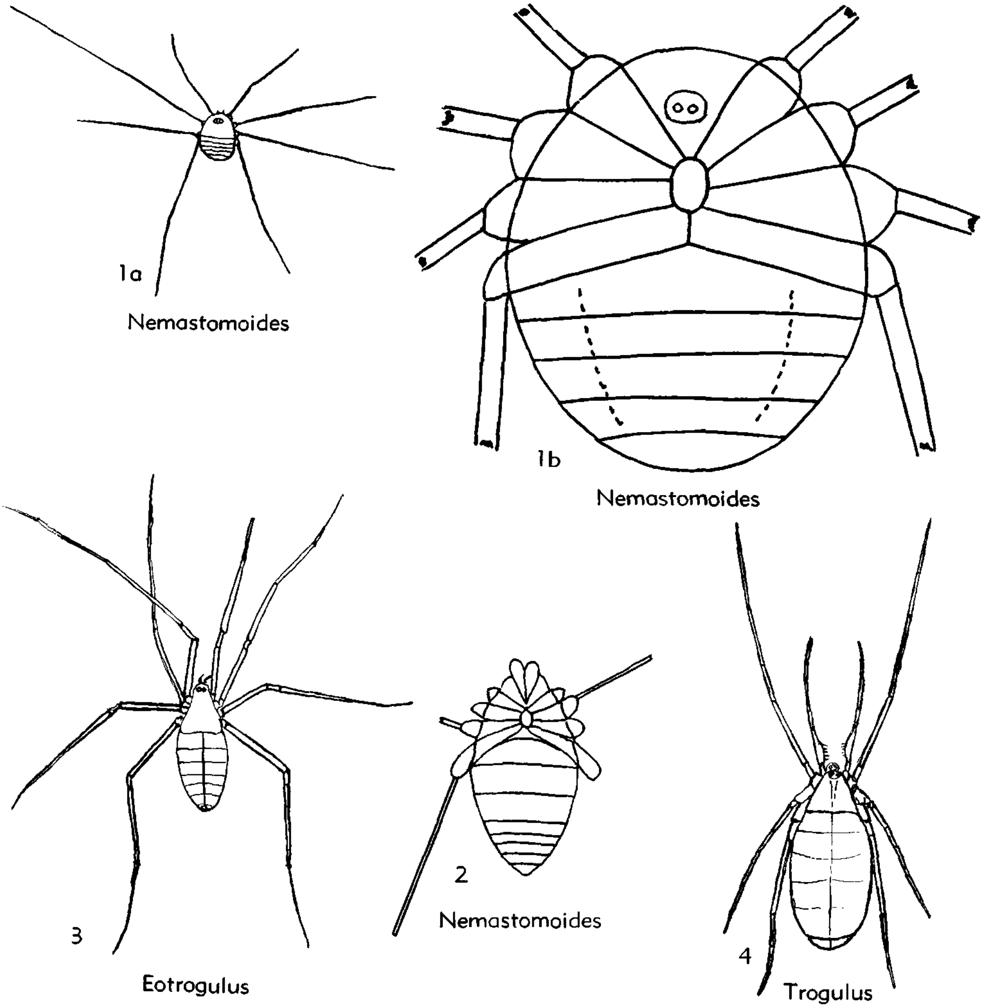


FIG. 52. Phalangiida. *1, Nemastomoides elaveris,* U.Carb., Fr.; *1a,* dorsal side, ×2.2; *1b,* ventral side of body, ×20. *2, Nemastomoides longipes,* Penn., Ill.; ventral side, ×2.7. *3, Eotrogulus fayoli,* U.Carb., Fr., ×3. *4, Trogulus gypseus,* representative of the suborder Cyphophthalmina, Rec., Morocco, ×1.8 (76) (p. P85).

but their general appearance favors placing them in the Palpatorina. A Jurassic fossil, *Hasseltides primigenius* (WEYENBERGH), which formerly (45) was considered to be a phalangiid, recently has been shown by VAN REGTEREN ALTENA, on the basis of other specimens, to be a distorted incomplete crinoid *(Saccocoma)*. Most Tertiary Phalangiida belong to the Palpatorina but at least one representative of the Laniatorina has been found.

Suborder CYPHOPHTHALMINA Simon, 1879

[*nom. correct.* PEARSE, 1936 (*pro* Cyphophthalmi SIMON, 1879)] [=Anepignathi THORELL, 1882] [Type: *Siro* LATREILLE, 1796 (=*Cyphophthalmus* JOSEPH, 1868)]

Openings of stink glands at end of a pair of lateral conic protuberances of cephalothorax. Genital opening without an operculum. *Rec.*

Suborder PALPATORINA Thorell, 1876

[*nom. correct.* PEARSE, 1936 (*pro.* Palpatores THORELL, 1876)] [=Plagiostethi SIMON, 1879] [Type: *Phalangium* LINNÉ, 1758]

Openings of stink glands not on protuberances. Pedipalpi slender. All tarsi with a single, simple claw. *Carb.-Rec.*

Superfamily TROGULOIDEA Sundevall, 1833

[*nom. transl.* PETRUNKEVITCH, herein (*ex* Trogulides SUNDEVALL, 1833)] [=Dyspnoi HANSEN & SÖRENSEN, 1904]

Terminal joint of pedipalpi shorter than tibia. *Carb.-Rec.*

Family EOTROGULIDAE Petrunkevitch, nov.

Coxae free, arranged in 2 nearly parallel rows. *Carb.*

Eotrogulus THEVENIN, 1901 [**E. fayoli*]. Carapace longer than wide, subtriangular, with rounded apex and slightly concave sides. Pair of sessile eyes close to anterior end. Abdominal tergites bisected by median line. Legs not exceeding 2.5 times body length. *Carb.*, Fr.—FIG. 52,*3*. **E. fayoli;* dorsal side, ×3 (76).

Family TROGULIDAE Sundevall, 1833

[*nom. correct.* SIMON, 1879 (*pro* Trogulides SUNDEVALL, 1833)]

Carapace forms a bifurcated "hood" in front of the eyes. *Rec.*

Trogulus LATREILLE, 1802 [**Acarus nepaeformis* SCOPOLI, 1763]. *Rec.*—FIG. 52,*4*. *T. gypseus* SIMON, Rec., Morocco; dorsal side, ×1.8 (76).

Family NEMASTOMATIDAE Simon, 1872

Sternum fused with arculi genitales separating posterior coxae. Dorsal scutum composed of carapace and 5 abdominal tergites grown together. *Carb.-Rec.*

Nemastoma C.L. KOCH, 1836 [**Phalangium lugubre* MÜLLER, 1776]. Abdominal tergites of scutum firmly grown together, *Oligo.-Rec.* [*N. denticulatum* KOCH & BERENDT, Oligo., Balt.].

Family NEMASTOMOIDIDAE Petrunkevitch, nov.

Sternum oval, separated from 1st abdominal sternite by 4th coxae meeting in median line. *Carb.*

Nemastomoides THEVENIN, 1901 [**N. elaveris*] [=*Protopilio* PETR., 1913]. Carapace wider than long, with evenly rounded front and sides. Eyes on tubercle considerably in front of middle. *U. Carb.*, Eu.-N.Am.—FIG. 52,*1*. **N. elaveris,* Fr. (Commentry); *1a,* dorsal side, ×2.2; *1b,* ventral side, ×20 (76).—FIG. 52,*2*. *N. longipes* (PETR.), Ill.; ventral side, ×2.7 (76).

Family ISCHYROPSALIDAE Simon, 1879

Carapace separated from abdominal scutum by a transverse line. *Oligo.-Rec.*

Sabacon SIMON, 1879 [**S. paradoxus*]. All femora lacking false articulations. All coxae movable. *Oligo.-Rec.* [*S. bachofeni* RÖWER, Oligo., Balt.].

Superfamily PHALANGIOIDEA Thorell, 1876

[*nom. transl.* PETRUNKEVITCH, herein (*ex* Phalangiidae SIMON, 1879, *nom correct. pro* Phalangioidae THORELL, 1876] [=Eupnoi HANSEN & SÖRENSEN, 1904]

Terminal joint of pedipalpi longer than tibia. Maxillary lobe of 2nd coxae long and slender. *Oligo.-Rec.*

Family PHALANGIIDAE Thorell, 1876

[*nom. correct.* SIMON, 1879 (*pro* Phalangioidae THORELL, 1876)]

Body soft. Eyes on tubercle in middle of carapace. Tarsi with numerous segments, flexible. *Oligo.-Rec.*

Caddo BANKS, 1892 [**C. agilis*]. Eyes very large, occupying almost entire carapace. *Oligo.-Rec.*—FIG. 53,*1*. *C. dentipalpus* (KOCH & BERENDT); oblique dorsal view, ends of legs omitted, ×7 (71).

Cheiromachus MENGE, 1854 [**C. coriaceus*]. Trochanter of pedipalp short, cone-shaped, wider in front than at base; femur very stout, dorsally convex, laterally compressed, with fairly long ventral thorns; patella much thinner and half as long as femur, wider in front than at base; tibia

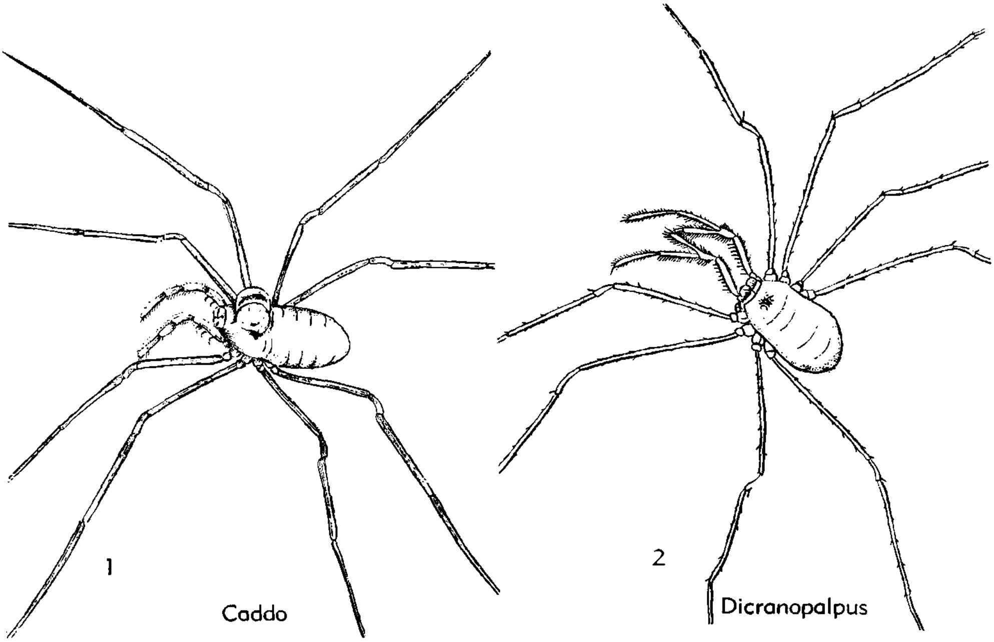


FIG. 53. Phalangiida from the Oligocene Baltic amber: *1, Caddo dentipalpus,* ×7; 2, *Dicranopalpus ramiger,* ×5.4 (71) (p. P85-P86).

short, spindle-shaped; terminal joint cylindrical, short. Ocular tubercle with strong thorns. *Oligo.,* Balt.

Dicranopalpus DOLESCHALL, 1852 [**D. gasteinensis*]. Patella of pedipalp with long apophysis. *Oligo.-Rec.*—FIG. 53,*2*. *D. ramiger* (KOCH & BERENDT), Oligo., Balt.; dorsal side, ends of legs omitted, ×5.4 (71).

Liobunum C.L. KOCH (**Phalangium rotundum* LATREILLE, 1798). Palpal claw denticulate. Femur of 1st leg longer than body. *Oligo.-Rec.* [*L. longipes* MENGE, Oligo., Balt.].

Opilio HERBST, 1798 [**Phalangium parietinum* DEGEER, 1778]. Middle joint of chelicerae without dorsal spur in male. *Oligo.-Rec.* [*O. ovalis* KOCH & BERENDT, Oligo., Balt.]

Phalangium LINNÉ, 1758 [**P. opilio*]. Middle joint of pedipalp with dorsal spur in male. *Oligo.-Rec.* FIG. 51. **P. opilio,* Rec., Eu.-N.Am.(cosmop.); ×2 (76).—FIG. 54. *P. oculatum* PETRUNKEVITCH, Oligo., Colo.; ×6.5 (76).

Suborder LANIATORINA Thorell, 1876

[*nom. correct.* PEARSE, 1936 (*pro* Laniatores THORELL, 1876)] [=Mecostethi SIMON, 1879] [Type: *Gonyleptes* KIRBY, 1819]

Pedipalpi raptorial, powerful. Tarsi of 1st and 2nd legs with single claw, those of 3rd and 4th with 2 claws or a trident claw (4). *Oligo.-Rec.*

Family GONYLEPTIDAE Sundevall, 1833

Third and 4th tarsi with 2 claws. Carapace fused with 5 abdominal tergites into a solid scutum. Fourth coxae very large and immobile. *Oligo.-Rec.*

Gonyleptes KIRBY, 1819 [**G. horridus*]. First tarsus 6-jointed. Femur of pedipalp with spine. Ocular tubercle with pair of thorns. *Oligo.-Rec.* [*G. nemastomoides* KOCH & BERENDT, Oligo., Balt.].

Order ARCHITARBIDA Petrunkevitch, 1945

[*nom. correct.* PETR., herein (*pro* Architarbi PETR., 1945)] [=Phalangiotarbi HAASE, 1890] [Type: *Architarbus* SCUDDER, 1868]

Latigastra with segmented abdomen, 5 or 6 anterior tergites of which are distinctly abbreviated. Carapace entire, with either a pair of sessile eyes (Fig. 56,*8*) or 3 pairs of eyes on a flat, trifoliate tubercle (Figs. 55, 58, 59) or without eyes. Abdomen composed of not more than 11, more commonly of 10 segments. Abbreviated tergites thickened and longitudinally bisected by a median line (Fig. 55,*7a*). Owing to fusion, number of sternites always smaller than that of tergites, but not less than 7 nor more than 9, and always divided by a pair of longitudinal lines (Fig. 55,*6*). Last sternite with circular anal operculum. Lateral pleural membrane not segmented. Except in Heterotarbidae, coxosternal region has typically only 4 pairs of more or less triangular coxae radiating from a small sternum. Pedipalpal coxae hidden from view by 1st pedal coxae, above which they are situated; they become occasionally partly visible when the 1st coxae are not in full contact with each other, as usual (Figs. 55,*6;* 58,*4b*). Laterally, on each side of sternum, the 4 pedal coxae are in contact with each other. The triangular space between the 4th coxae is oc-

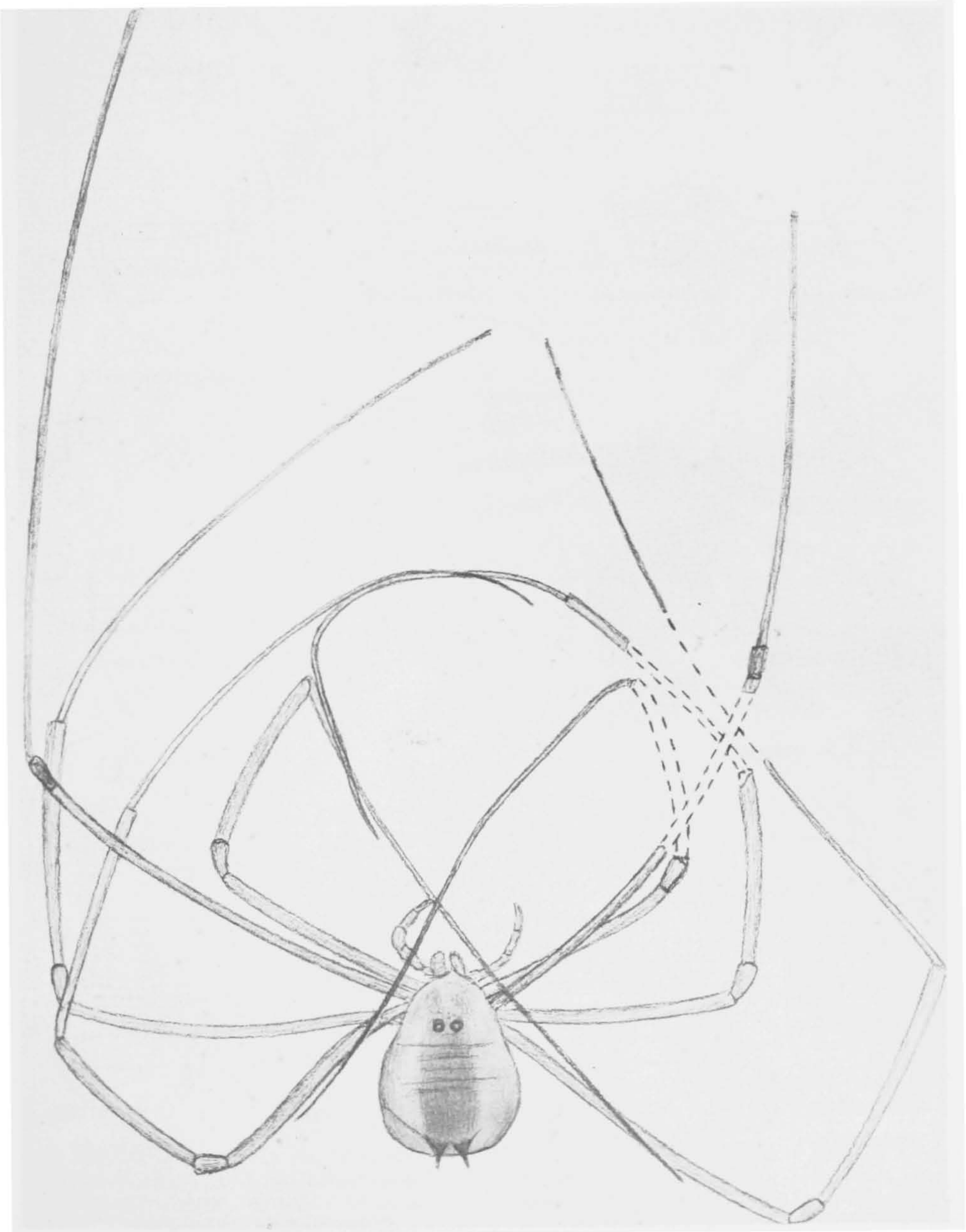


FIG. 54. *Phalangium oculatum*, Oligo., Colo. (Florissant), ×6.5 (76) (p. P86).

cupied by the 1st and 2nd abdominal sternites. Sternum small, consisting of 3 (Fig. 55,*6*) or 4 sclerites (Fig. 58,*4b*), or completely wanting (Fig. 56,*2b*). Chelicerae 3-jointed, chelate, small. Pedipalpi 6-jointed, slender, short. Legs 7-jointed, except in Opiliotarbidae in which trochanters of 3rd and 4th pairs of legs are 2-jointed, making these legs 8-jointed.

Mouth concealed, presumably opening

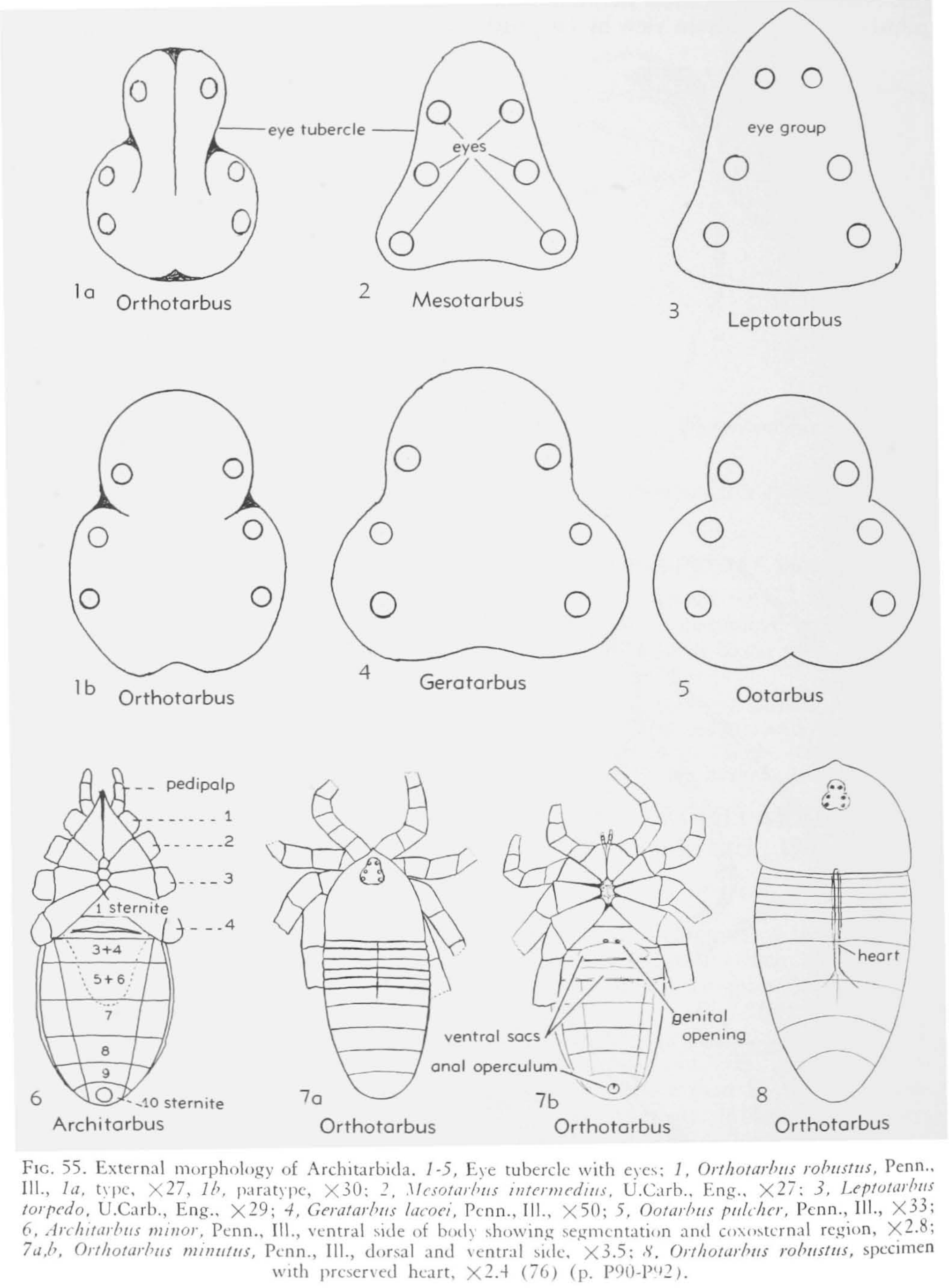


FIG. 55. External morphology of Architarbida. *1-5*, Eye tubercle with eyes; *1*, *Orthotarbus robustus*, Penn., Ill., *1a*, type, ×27, *1b*, paratype, ×30; *2*, *Mesotarbus intermedius*, U.Carb., Eng., ×27; *3*, *Leptotarbus torpedo*, U.Carb., Eng., ×29; *4*, *Geratarbus lacoei*, Penn., Ill., ×50; *5*, *Ootarbus pulcher*, Penn., Ill., ×33; *6*, *Architarbus minor*, Penn., Ill., ventral side of body showing segmentation and coxosternal region, ×2.8; *7a,b*, *Orthotarbus minutus*, Penn., Ill., dorsal and ventral side, ×3.5; *8*, *Orthotarbus robustus*, specimen with preserved heart, ×2.4 (76) (p. P90-P92).

into a stomotheca as in Recent Cyphophthalmina of the order Phalangiida, formed by medial walls of 1st coxae. A pair of round genital openings, usually present on 2nd abdominal sternite, probably are openings of sperm receptacles (Fig. 55,*7b*). Book lungs wanting, but 1 to 4 ventral sacs are present, one sac per segment on 3rd to 6th abdominal sternites, which presumably are organs of respiration. The presence of

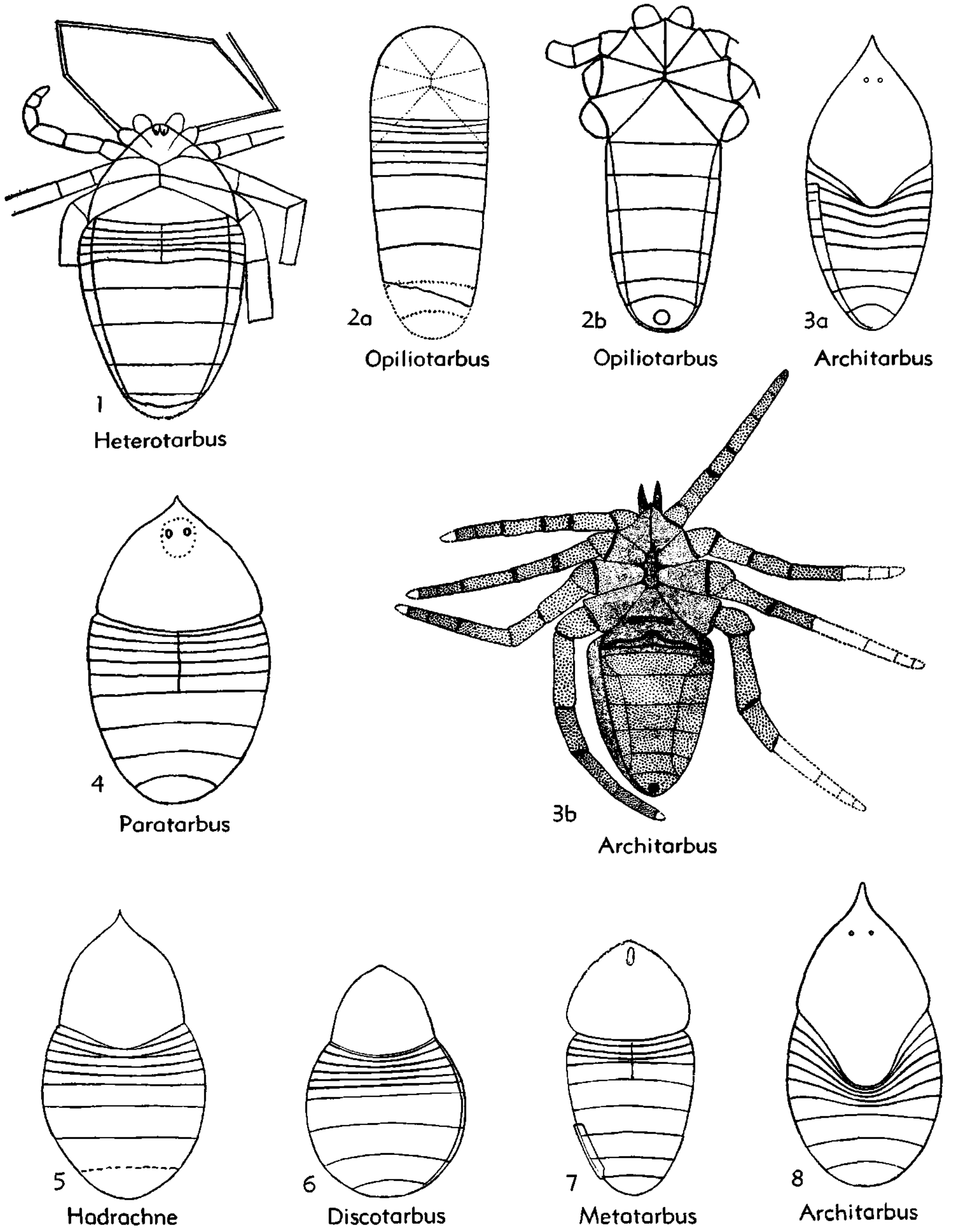


Fig. 56. Architarbida. *1, Heterotarbus ovatus,* Penn., Ill., ×2.7; *2, Opiliotarbus elongatus,* Penn., Ill.; *2a,b,* dorsal and ventral side, ×2.7; *3, Architarbus rotundatus,* Penn., Ill.; *3a,b,* dorsal and ventral side, ×1.65; *4, Paratarbus carbonarius,* Penn., Ill., ×2.1; *5, Hadrachne horribilis,* Penn., Ill., ×1; *6, Discotarbus deplanatus,* Penn., Ill., ×2.7; *7, Metatarbus triangularis,* Penn., Ill., ×2; *8, Architarbus minor,* Penn., Ill., ×2.7 (76) (p. P90-P93).

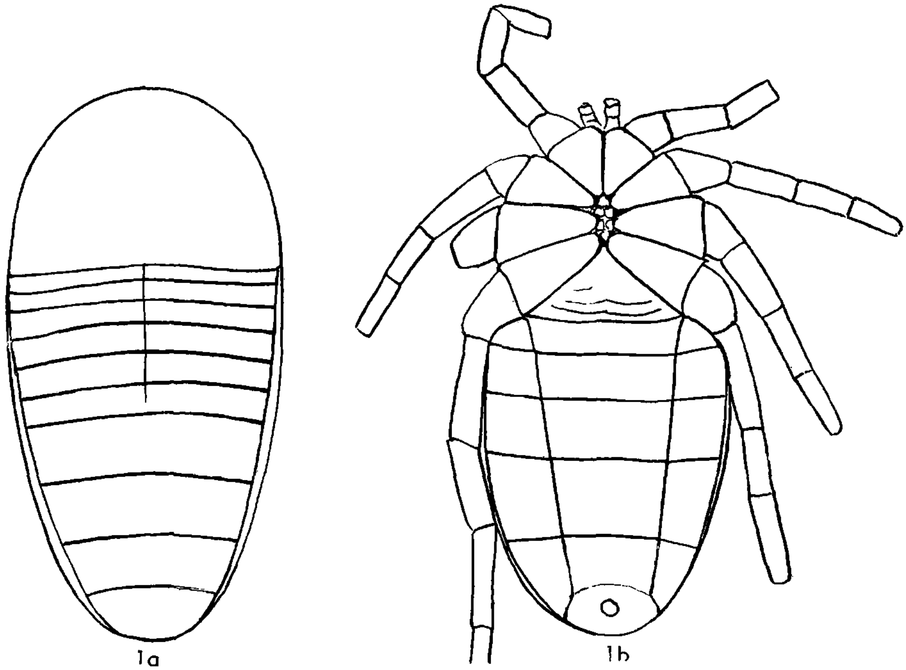


FIG. 57. *Phalangiotarbus subovalis,* U.Carb., Eng.; *1a,b,* dorsal and ventral sides of lectotype, ×9 (76).

tracheal tubes cannot be demonstrated, but is not excluded, because tracheal tubes cannot be seen in fossils which undoubtedly possessed them. Heart, enclosed in its pericardium and ending in 3 posterior arteries, is preserved in one specimen (Fig. 55,*1c*) and seems to be limited to abdomen. Nothing known of other internal organs. (14, 34, 43, 45.) *Carb.*

Family ARCHITARBIDAE Karsch, 1882

[=Phalangiotarbidae HAASE, 1890]

Abdomen with 10 tergites and 8 or 9 sternites. All coxae triangular, trochanters single-jointed, legs similar, 7-jointed (45). *Carb.*

Architarbus SCUDDER, 1868 [**A. rotundatus*] [=*Geraphrynus* SCUDDER, 1884]. Carapace rhomboidal, pointed in front, rounded behind, longer than wide, with pair of sessile eyes; sides of posterior portion of carapace concave; abbreviated abdominal tergites sigmoidal. Order of legs 4321 (34, 38, 43, 45). *Penn.,* N.Am.—FIG. 56,*3.* **A. rotundatus,* Ill.;*3a,* dorsal side, ×1.65; *3b,* ventral side, ×1.65 (76).—FIGS. 55,*6;* 56,*8. A minor* PETR., Ill.; 55,*6,* ventral side showing position of posterior edge of carapace by dotted line reaching beyond 6th sternite, ×2.8; 56,*8,* dorsal side, ×2.7 (76).

Paratarbus PETRUNKEVITCH, 1945 [**P. carbonarius*]. Carapace wider than long, subtriangular, with pointed anterior end and convex posterior edge. Pair of oval eyes on low, longitudinally elliptic elevation (38). *Penn.,* N.Am.—FIG. 56,*4.* **P. carbonarius,* Ill.; dorsal side, ×2.1 (76).

Hadrachne MELANDER, 1903 [**H. horribilis*]. Carapace slightly longer than wide, pointed in front, with convex posterior edge. No eyes (38). *Penn.,* N.Am.—FIG. 56,*5.* **H. horribilis,* Ill.; dorsal side, ×1 (76).

Discotarbus PETRUNKEVITCH, 1913 [**D. deplanatus*]. Carapace subtriangular, flat, slightly wider than long, with sides convex. Abdomen flat, disc-shaped, wider than carapace (34, 36). *Penn.,* N. Am.—FIG. 56,*6.* **D. deplanatus,* Ill.; dorsal side, ×2.7 (76).

Phalangiotarbus HAASE, 1890 [**Architarbus subovalis* WOODWARD, 1872]. Carapace fairly semicircular, with straight posterior edge. ?Eyes lacking. *Carb.,* Eu.—FIG. 57,*1.* **P. subovalis* (WOODW.), Eng.; *1a,* dorsal side; *1b,* ventral side, ×9 (76).

Goniotarbus PETRUNKEVITCH, 1945 [**Geraphrynus tuberculatus* POCOCK, 1911]. Carapace with 3 pairs of eyes on flat, trifoliate tubercle; posterior edge convex, slightly sinuous, sides convex (43, 45). *U.Carb.,* Eu.—FIG. 58, *4.* **G. tuberculatus* (POCOCK), Eng.; *4a,* dorsal surface, ×3.6; *4b,* ventral surface, ×4.6 (76).—FIG. 58,*5. G. angulatus* (POCOCK), Eng.; dorsal, ×3.5 (76).

Mesotarbus PETRUNKEVITCH, 1949 [**M. inter-*

medius]. Carapace longer than wide, with 3 pairs of eyes on flat tubercle (43, 45). _U.Carb._, Eu.—Figs. 55,_2_; 59,_2_. *_M. intermedius_, Eng.; 55,_2_, ocular tubercle with eyes, ×27; 59,_2_, dorsal side, ×4.7 (76).—Fig. 58,_2_. _M. angustus_ (Pocock), Eng.; dorsal side, ×5.4 (76).—Fig. 59,_5_. _M. egintoni_ (Pocock), Eng.; dorsal side, ×5.4 (76).—Fig. 58,_3_. _M. hindi_ (Pocock), Eng.; dorsal side, ×5.5 (76).

Leptotarbus Petrunkevitch, 1945 [*_Geraphrynus torpedo_ Pocock, 1911]. Carapace much longer than wide, pointed in front; posterior edge slightly convex. Three pairs of eyes on flat tubercle. Abdomen narrow (38, 43, 45). _U.Carb._, Eu.—Figs. 55,_3_; 59,_3_. *_L. torpedo_ (Pocock), Eng.; 55,_3_, ocular tubercle with eyes, ×29; 59,_3a_, dorsal side, ×7; 59,_3b_, ventral side, ×7 (76).

Orthotarbus Petrunkevitch, 1945 [*_Geratarbus minutus_ Petr., 1913]. Carapace wider than long, with straight posterior edge. Three pairs of eyes on flat tubercle (38, 43, 45). _Carb._, N.Am.-Eu.—Fig. 55,_7_. *_O. minutus_ (Petr.), Ill.; _7a_, dorsal

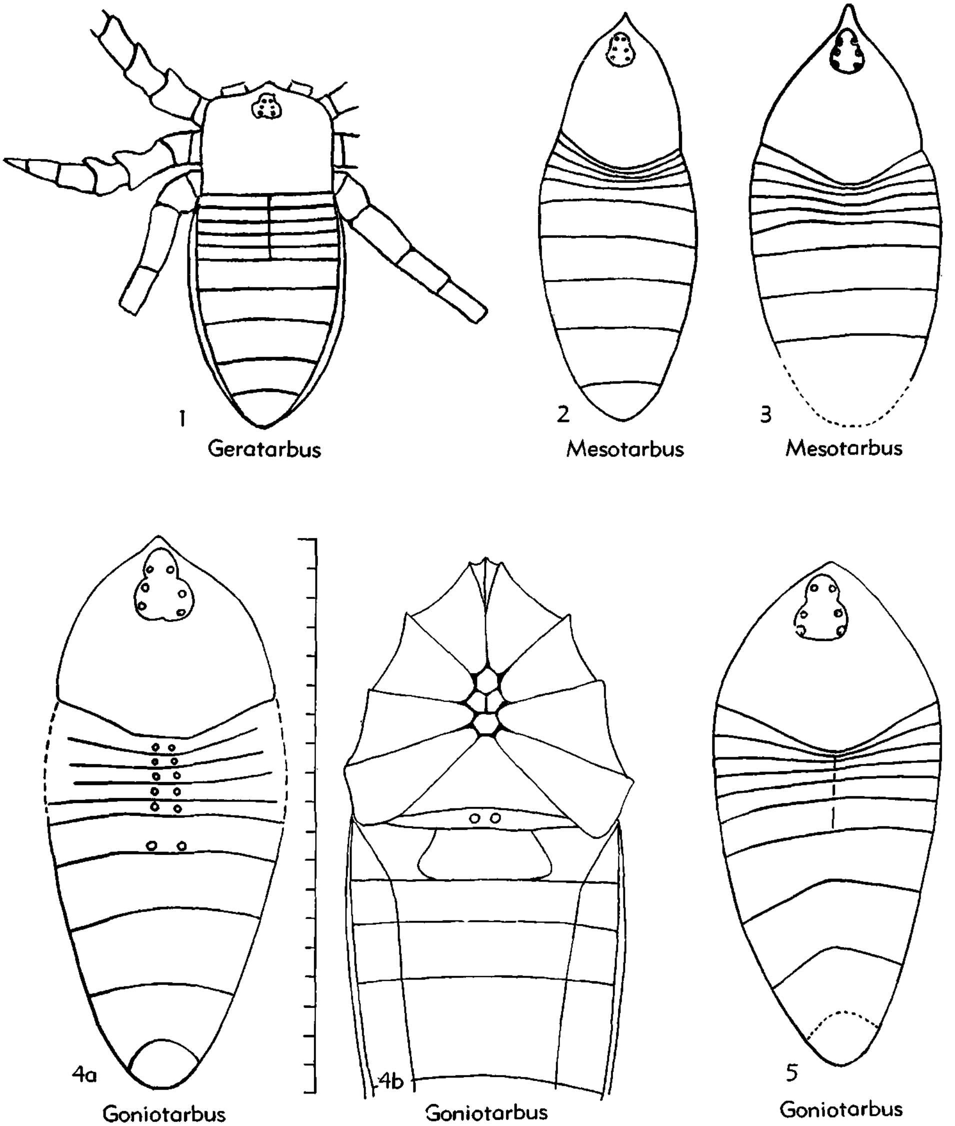


Fig. 58. Architarbida. _1, Geratarbus lacoei,_ Penn., Ill., ×3; _2, Mesotarbus angustus,_ U.Carb., Eng., ×5.4; _3, Mesotarbus hindi,_ U.Carb., Eng., ×5.5; _4, Goniotarbus tuberculatus,_ U.Carb., Eng.; _4a,_ dorsal side, ×3.6; _4b,_ ventral side, ×4.6; _5, Goniotarbus angulatus,_ U.Carb., Eng., ×3.5 (76) (p. P90-P92).

side, ×3.5; *7,* ventral side, ×3.5.—Fig. 55,*1,8. O. robustus* Petr., Ill.; *1a,* ocular tubercle of type, ×27; *1b,* of paratype, ×30; *8,* dorsal side of another paratype, showing heart, ×2.4; 60*A,B,* photographs of holotype showing dorsal and ventral sides, ×4 (76).—Fig. 59,*1. O. nyranensis* Petr., Czech.; ventral side, ×3.7 (76).

Geratarbus Scudder, 1890 [**G. lacoei*]. Carapace rectangular, wider than long, with 3 pairs of eyes on flat tubercle (38, 45). *Carb.,* N.Am.-Eu.—Figs. 55,*4;* 58,*1.* **G. lacoei,* Ill.; 55,*4,* ocular tubercle, ×50 (76); 58,*1,* dorsal side of holotype, ×3 (76).

Ootarbus Petrunkevitch, 1945 [**O. pulcher*]. Carapace almost semicircular with straight posterior edge; 3 pairs of eyes on flat tubercle (38). *Penn.,* N.Am.—Figs. 55,*5;* 59,*4.* **O. pulcher,* Ill.; 55,*5,* ocular tubercle, ×33; 59,*4,* dorsal side, ×3 (76).

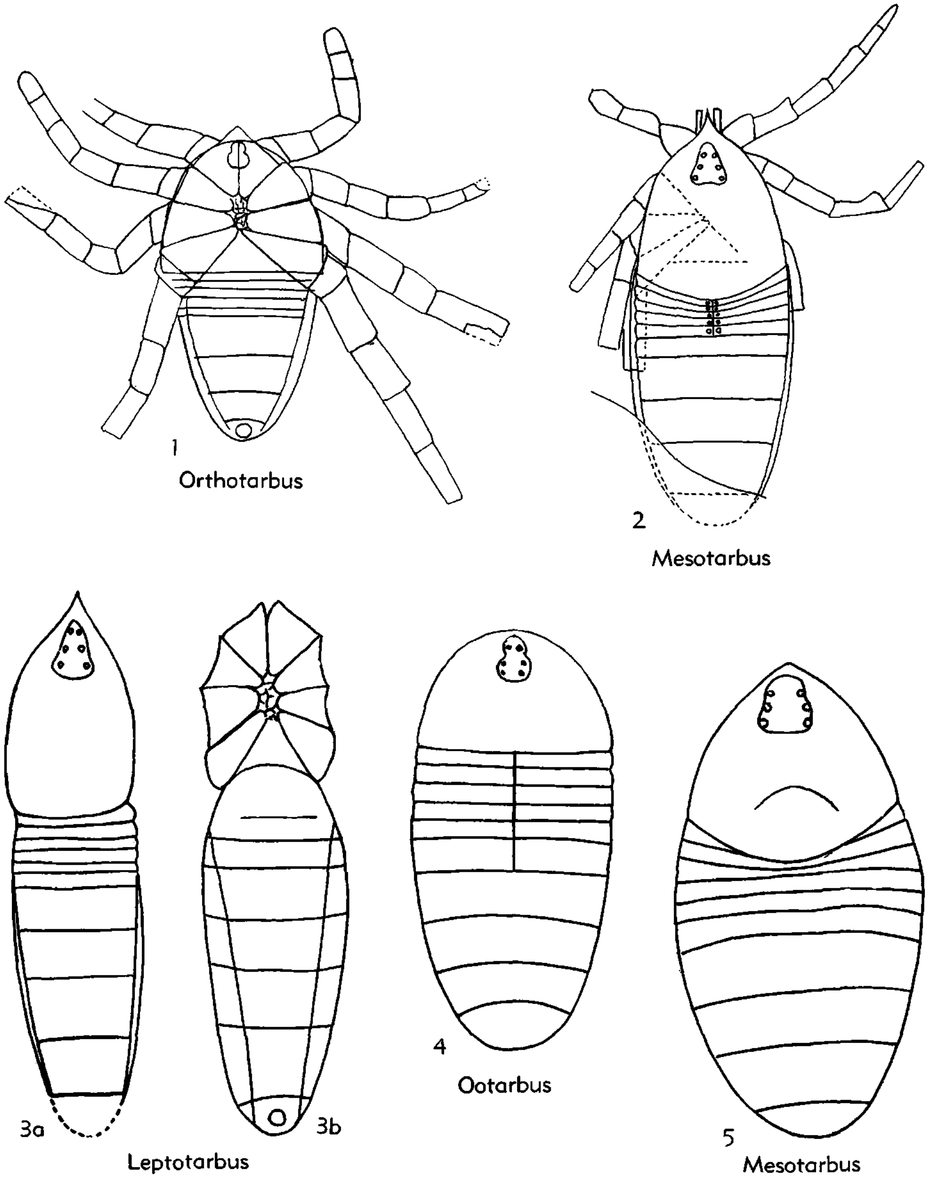


Fig. 59. Architarbida. *1, Orthotarbus nyranensis,* U.Carb., Czech., ×3.7; *2, Mesotarbus intermedius,* U. Carb., Eng., ×4.7; *3, Leptotarbus torpedo,* U.Carb., Eng.; *3a,b,* dorsal and ventral sides, ×7; *4, Ootarbus pulcher,* Penn., Ill., ×3; *5, Mesotarbus eggintoni,* U.Carb., Eng., ×5.4 (76) (p. P91-P92).

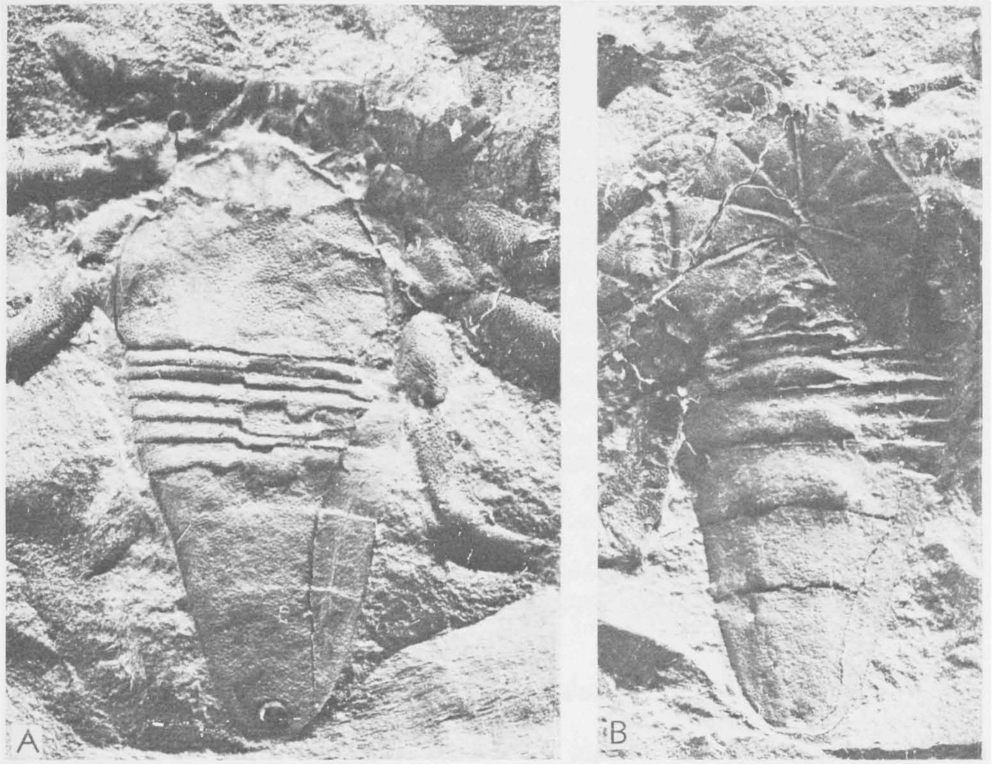


FIG. 60. *Orthotarbus robustus*, Penn., Ill.; *A,B*, photographs of dorsal and ventral sides, ×4 (76).

Metatarbus PETRUNKEVITCH, 1913 [**M. triangularis*]. Carapace subtriangular, wider than long, all sides convex. Ocular tubercle without eyes (34). *Penn.*, N.Am.—FIG. 56,*7*. **M. triangularis*, Ill.; dorsal side, ×2 (76).

Family OPILIOTARBIDAE Petrunkevitch, 1945

Coxae triangular, trochanters of 1st and 2nd pairs of legs single-jointed, those of 3rd and 4th pairs 2-jointed. Abdomen with 11 tergites. *Carb.*

Opiliotarbus POCOCK, 1900 [**Architarbus elongatus* SCUDDER, 1890]. Carapace almost semicircular, with straight posterior edge as in *Ootarbus*, but without ocular tubercle or eyes. Sternum wanting, all coxae meet in median line (38, 45). *Penn.*, N. Am.—FIG. 56,*2*. **O. elongatus* (SCUDDER), Ill.; *2a*, dorsal side, ×2.7; *2b*, ventral side, ×2.7 (76).

Family HETEROTARBIDAE Petrunkevitch, 1913

Coxae of 1st and 2nd pairs of legs small and separated, those of 3rd and 4th pairs much longer, cylindrical, contiguous in median line by their proximal ends. Trochanters single-jointed. First legs very long and slender (34, 45). *Carb.*

Heterotarbus PETRUNKEVITCH, 1913 [**H. ovatus*]. Carapace subtriangular, much wider than long, with convex sides and posterior edge. No eyes (34). *Penn.*, N.Am.—FIG. 56,*1*. **H. ovatus*, Ill.; dorsal side, with chelicerae and coxae superimposed on carapace, ×2.7 (76).

Order ACARIDA Nitzsch, 1818

[*nom. correct.* ENGELMANN, 1860 (*ex* Acari SUNDEVALL,[1] 1833, *ex* Acarina NITZSCH, 1818] [=Monomerostomata LEACH, 1815; Acarides VAN HEYDEN, 1826; Acarenses DUGÈS, 1834; Acari *auctt.*] [Type: *Acarus* LINNÉ, 1758]

Latigastra in which the abdominal segmentation is usually lost, so that the body shows no external segmentation (Figs. 61, 62) or may be divided into a proterosoma and a hysterosoma, with a division line between the 2nd and 3rd pairs of legs, the

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[1] NITZSCH was the first to use the name Acarina as an order. BRÜNNICH used the name Acari in 1772 merely as the plural of the genus *Acarus*, the only genus recognized by him. LATREILLE used the name Acaridiae in 1806 as a family name and included it in only 5 genera. LEACH substituted for his order Monomerostomata the name Acari in 1819, but raised it to the rank of a class.

former usually subdivided into a gnathosoma (formerly called capitulum) and a propodosoma. Gnathosoma bears chelicerae and pedipalpi, both presenting numerous modifications of structure. Chelicerae are of 2 main types which may be found in different representatives of the same suborder or an entire suborder may have the same type of structure. The chelate type occurs in all suborders. It is the only type in Holothyrina, Notostigmatina and Tetrapodilina, in which they are 2-jointed, with movable finger either ventral or lateral in position and used for grasping. Chelicerae of the piercing type are modified as stylets of different structure. Pedipalpi are 6-jointed, but like chelicerae, subject to modifications. Typical number of legs is, of course, 4 pairs, but some have 3 pairs, some, as Tetrapodilina, have 2 pairs, and a few Acarida have even a single pair. Number of leg segments varies from 2 to 7, but usual number is 6. Tarsi end in a pair of claws often accompanied by "caruncle" or arolium. In most Acarida body is soft, some have a dorsal scutum covering hysterosoma. Mouth ventral to chelicerae and protected by a labrum from above and by an extension of the ventral body wall of the gnathosoma from below.

Digestive system presents several variations. Usually a well-developed fore-gut with pharynx and esophagus is followed by a complicated mid-gut with diverticles and ends in a hind-gut which opens to outside by an anus. The latter is ventral in most cases, but dorsal in others, situated near end of abdomen. Excretory system consists of a pair of malpighian tubes and an excretory vesicle. Most species have no heart. When one is present, it is small, almost rudimentary, with a single pair of ostia. Respiration accomplished either by means of tracheal tubes, or is cutaneous when organs of respiration are wanting. Position of tracheal spiracles is of greatest importance in classi-

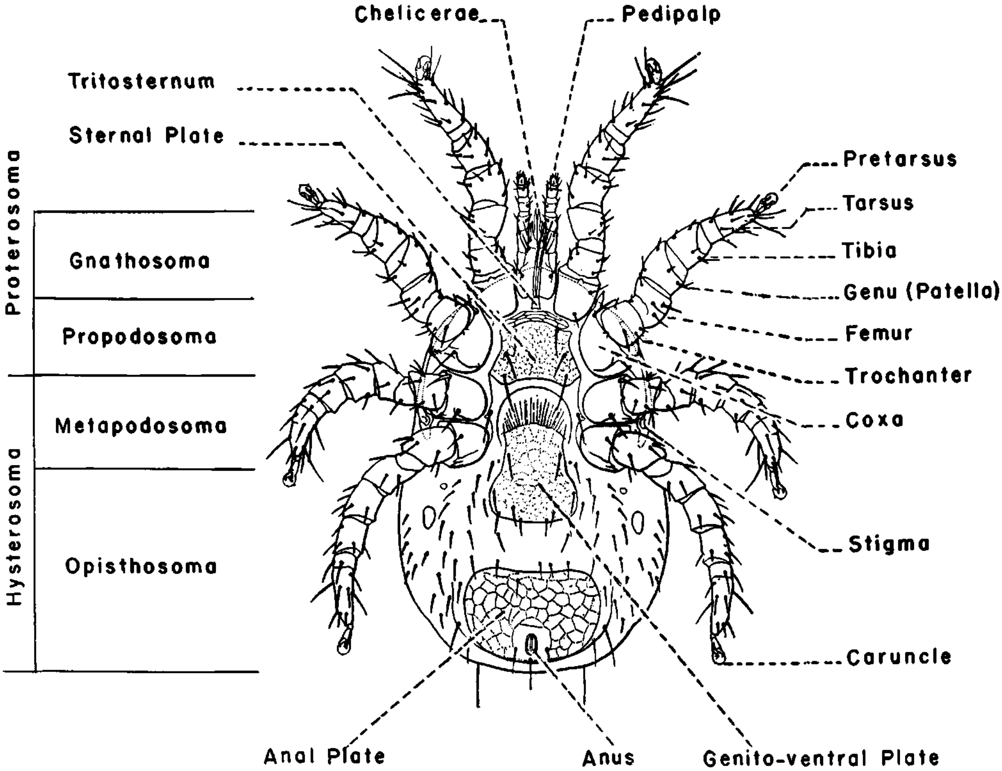


Fig. 61. External morphology of Acarida. *Myonyssus decumani,* a mite parasitic on rats, ventral side (81).

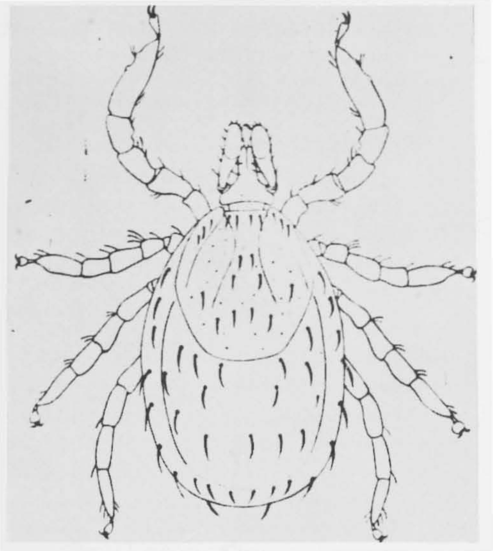


FIG. 62. *Ixodes ricinus,* common European tick, female, ×8 (after Nuttal).

fication. Notostigmatina have 4 pairs of spiracles on dorsal surface of opisthosoma. Parasitoidea (Mesostigmata) have a single pair on metapodosoma. Oribatoidea have *areae porosae* in various regions of their body. Nervous system highly concentrated. Eyes present in some species, but majority are blind. Pair of highly developed salivary glands open into mouth cavity; in some species they are modified as silk glands.

Sexes are separate. Genital openings vary considerably in position. Embryologically these openings belong to the 2nd abdominal sternite in all Arachnida. In some Acarida this position has been secondarily displaced. Males of the parasitic family Demodicidae present an extreme in this respect. In them the genital opening is dorsal in position, situated above either 1st, 2nd or 3rd pair of legs, while in the female it occupies its normal position on the ventral side between the hind coxae. Male copulatory apparatus consists of a penis. Some females have an ovipositor, but eggs are usually laid directly from the genital opening. Development is often complicated. From the egg emerges a 6-legged larva which on molting first turns into a protonymph, then a deutonymph and a tritonymph before reaching adult stage. In some species, as for example in *Pediculoides ventricosus,* all these stages are passed within the egg. The development in some itch mites is so rapid, that a new generation is produced in 10 to 14 days.

Acarida is the 2nd largest order of Arachnida, one of the richest in variations of structure and habit. They are the only order in which plant-eating species are found. Some lead completely parasitic existence on vertebrate and invertebrate hosts. Others are temporary parasites. Several families are strictly aquatic, fresh-water and marine. Some are polymorphic. Many are only a fraction of a millimeter in size, some on the limit of unaided human vision. The largest female ticks gorged with blood reach 25 mm. in size, but their normal, undistended length is no more than 5 or 6 mm. On account of their small size, fossil Acarida are best known from the Baltic amber. The oldest fossil acarid was fairly common in the Devonian. *Dev.-Rec.*

Recent Acarida are divided into 5 suborders, 162 families and nearly 1400 genera.

Suborder NOTOSTIGMATINA With, 1903

[*nom. correct.* Pearse, 1947 (*pro* Notostigmata With, 1903)] [Type: *Opilioacarus* With, 1903]

Four pairs of dorsolateral stigmata. Two pairs of eyes. *Rec.*

Suborder HOLOTHYRINA Reuter, 1909

[*nom. correct.* Petrunkevitch, herein (*pro* Holothyroidea Reuter, 1909)] [Type: *Holothyrus* Gervais, 1842]

Two pairs of lateral stigmata. No eyes. *Rec.*

Suborder TROMBIDIINA Dugès, 1839

[*nom. correct.* Petrunkevitch, herein (*pro* Trombidiei Dugès, 1839)] [=Trombidiformes Reuter, 1909] [Type: *Trombidium* Fabricius, 1775]

A pair of stigmata on or near gnathosoma. *Dev.-Rec.*

Superfamily TROMBIDIOIDEA Leach, 1815

[*nom. transl.* Petrunkevitch, herein (*ex* Trombidides Leach, 1815)] [=Prostigmata Kramer, 1877]

Stigmata at base of chelicerae. *Dev.-Rec.*

Family EUPODIDAE C.L.Koch, 1842

Body soft, with short gnathosoma. Chelae modified. *Dev.-Rec.*

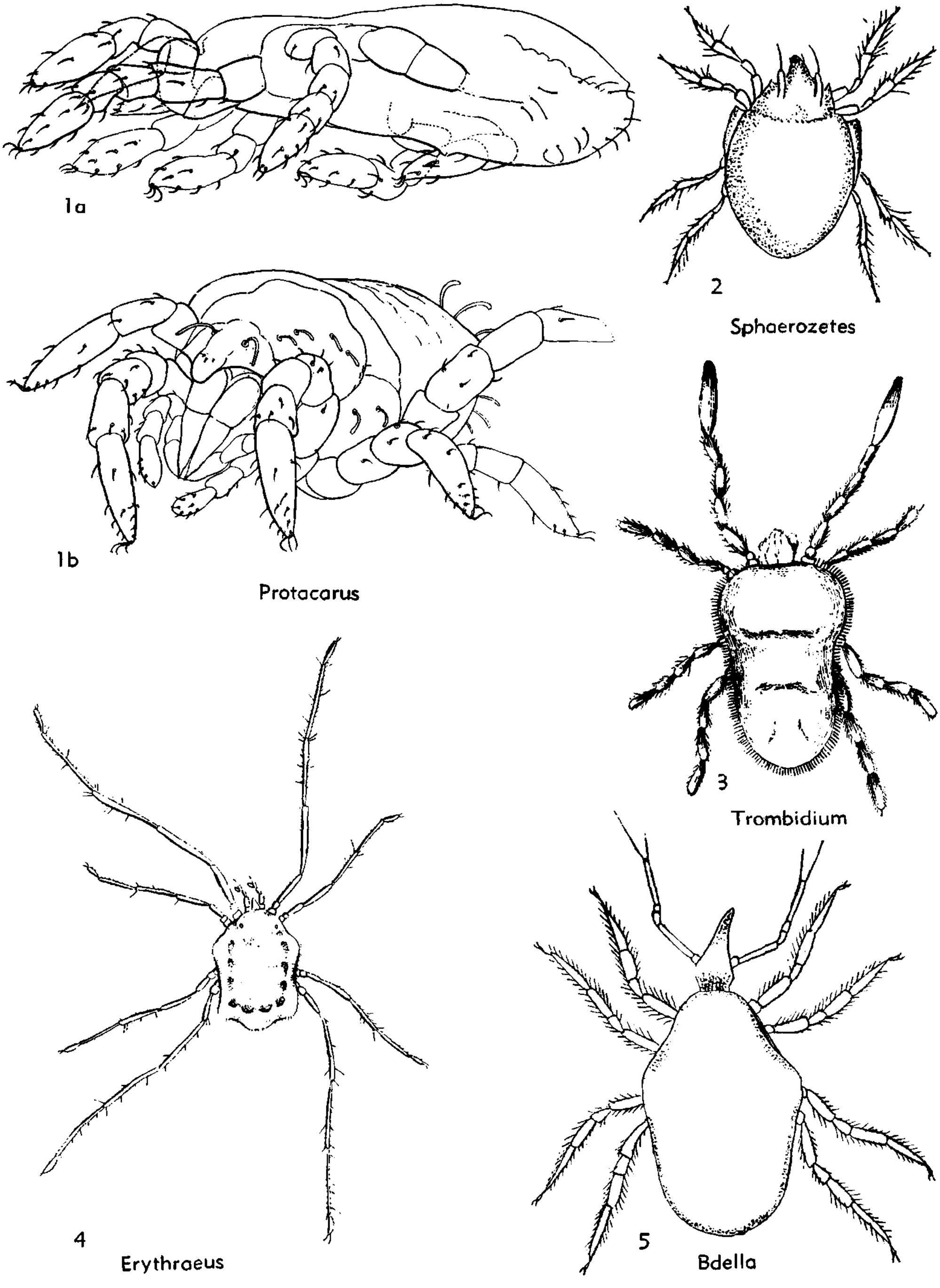


FIG. 63. Acarida. *1, Protacarus crani,* Dev., Old Red Sandstone, Scot.; *1a,b,* ×170 (70). *2-5,* Mites from Oligocene Baltic amber; *2, Sphaerozetes convexulus,* ×20; *3, Trombidium clavipes,* ×30; *4, Erythraeus foveolatus,* ×17; *5, Bdella lata,* ×30 (71) (p. P97-P98).

Protacarus HIRST, 1923 [**P. crani*]. Pedipalpi 7-jointed, with 3 terminal hairs shaped like claws. *Dev.*, Scot.—FIG. 63,*1*. **P. crani; 1a*, side view, ×270; *1b*, holotype, ×170 (70).

Family BDELLIDAE Dugès, 1834

A suture between proterosoma and hysterosoma. Tarsi with pretarsus, 2 claws and pulvillus. Two pairs of eyes. *Oligo.-Rec.*

Bdella LATREILLE, 1795 [**Acarus longicornis* LINNÉ, 1758]. *Oligo.-Rec.*—FIG. 63,*5*. *B. lata* KOCH & BERENDT, Oligo., Balt.; ×30 (71).

Family ERYTHRAEIDAE Oudemans, 1802

Chelicerae stylet-like, single-jointed. Legs long and slender. One or 2 pairs of eyes. *Oligo.-Rec.*

Erythraeus LATREILLE, 1806 [**Acarus phalangioides* DEGEER, 1778] [=*Rhyncholophus* DUGÈS, 1834] *Oligo.-Rec.* [7 species in Baltic amber].—FIG. 63,*4*. *E. foveolatus* (KOCH & BERENDT), Oligo., Balt.; dorsal view, ×17 (71).

Arythaena MENGE, 1854 [**A. troguloides*]. *Oligo.*, Balt.

Family TROMBIDIIDAE Leach, 1815

[*nom. correct.* FLACH, 1864 (*pro* Trombidides LEACH, 1815]

Palpal tibia with apical claw. Chelicerae with bladelike 2nd joint. *Oligo.-Rec.*

Trombidium FABRICIUS, 1775 [**Acarus holosericeus* LINNÉ, 1758]. *Oligo.-Rec.* [6 species in Baltic amber].—FIG. 63,*3*. *T. clavipes* KOCH & BERENDT, Oligo., Balt.; ×30 (71).

Family ANYSTIDAE Oudemans, 1902

Body short and broad. Palpal tibia with 3 claws. Two pairs of eyes. *Oligo.-Rec.*

Anystis VAN HEYDEN, 1826 [**Trombidium cornigerum* HERMANN] [=*Actineda* C.L. KOCH, 1836]. *Oligo.-Rec.* [*A. venustula* (KOCH & BERENDT), Oligo., Balt.].

Family CHEYLETIDAE Leach, 1815

[*nom. correct.* BANKS, 1904 (*pro* Cheyletides LEACH, 1815)]

Body with 1 or 2 dorsal shields. Chelicerae stylet-like. Tarsi with 2 claws and empodium. *Mio.-Rec.*

Cheyletus LATREILLE, 1796 [**Acarus eruditus* SCHRANK, 1781]. *Mio.-Rec.* [*C. burmiticus* COCKERELL, 1917, Mio., Burmese amber].

Family TETRANYCHIDAE Donnadieu, 1875

Plant-feeders with soft skin. Chelicerae fused at base forming a stylophore which is used as a piercing organ. One pair of eyes. *Oligo.-Rec.*

Tetranychus DUFOUR, 1832 [**T. lintearius*]. *Oligo.-Rec.* [*T. gibbus* KOCH & BERENDT, Oligo., Balt.].

Suborder PARASITINA Reuter, 1909

[*nom. correct.* PEARSE, 1936 (*pro* Parasitiformes REUTER, 1909)] [=Mesostigmata + Metastigmata CANESTRINI, 1891] [Type: *Parasitus* LATREILLE, 1795]

One pair of stigmata, lateral or posterior to legs. *Oligo.-Rec.*

Superfamily PARASITOIDEA Oudemans, 1901

[*nom. transl.* BANKS, 1915 (*ex* Parasitidae OUDEMANS, 1901)] [=Mesostigmata CANESTRINI, 1891]

Stigmata lateral to legs. *Oligo.-Rec.*

Family PHYTOSEIIDAE Berlese, 1916

No constriction between podosoma and opisthosoma. Dorsal plate entire. Coxae movable. *Oligo.-Rec.*

Seius C.L. KOCH, 1836 [**S. togatus*]. *Oligo.-Rec.* (*S. bdelloides* KOCH & BERENDT, Oligo., Balt.).

Superfamily IXODOIDEA Leach, 1815

[*nom. transl.* BANKS, 1904 (*ex* Ixodides LEACH, 1815)]

Stigmata behind legs, with stigmal plates. Body sclerotized. *Oligo.-Rec.*

Family IXODIDAE Leach, 1815

[*nom. correct.* MURRAY, 1877 (*pro* Ixodides LEACH, 1815)]

Dorsal scutum present. Hypostome modified as piercing organ. *Oligo.-Rec.*

Ixodes LATREILLE, 1795 [**Acarus ricinus* LINNÉ, 1758]. *Oligo.-Rec.* (*I. tertiarius* SCUDDER, Oligo., Wyo.).—FIG. 62,*1*. *I. ricinus*, Rec., Eu.; female, dorsal side, ×8 (62).

Dermacentor C.L. KOCH, 1844 [**Acarus reticulatus* FABRICIUS]. *Pleisto.-Rec.*, Eu.; *Pleisto.*, Galicia.

Suborder ACARINA Leach, 1815

[*nom. correct.* NITZSCH, 1818 (*pro* Acarides LEACH, 1815] [=Sarcoptiformes REUTER, 1909] [Type: *Acarus* LINNÉ, 1758]

Oligo.-Rec.

Superfamily ACAROIDEA Latreille, 1802

[*nom. transl.* EWING & NESBITT, 1942 (*ex* Acaridiae LATREILLE, 1802)]

Tarsi with caruncles. *Oligo.-Rec.*

Family ACARIDAE Latreille, 1802

[*nom. correct.* EWING & NESBITT, 1942 (*pro* Acaridiae LATREILLE, 1802)] [=Tyroglyphidae DONNADIEU, 1868]

Transverse groove between protero- and hysterosoma. Five pairs of setae on propodosoma. *Oligo.-Rec.*

Acarus LINNÉ, 1758 [**A. siro*]. *Oligo.-Rec.* [*A. rhombeus* KOCH & BERENDT, Oligo., Balt.].

Tyroglyphites Pampaloni, 1902 [**T. miocenicus*]. *M.Mio.*, Sicily.

Superfamily ORIBATOIDEA Dugès, 1834

[*nom. correct.* Banks, 1904 (*pro* Oribatei Dugès, 1834)]

Body wall sclerotized. Tarsi without caruncles. *Oligo.-Rec.*

Family BELBIDAE Willmann, 1931

Genital and anal openings on common ventral plate. Chelicerae chelate. Legs long. *Oligo.-Rec.*

Damaeus C.L. Koch, 1836 [**D. auritus*]. *Oligo.-Rec.* [*D. genadensis* Sellnick, Oligo., Balt.].

Gymnodamaeus Kulczynski, 1902 [**Damaeus bicostatus* C.L. Koch, 1835]. *Oligo.-Rec.* [*G. kulczynskii* Sellnick, Oligo., Balt.].

Belbites Pampaloni, 1902 [**B. disodilia*]. *Mio.*, Sicily.

Family CAMISIIDAE Sellnick, 1928

Genital and anal openings contiguous; anal opening with a pair of opercular plates. *Oligo.-Rec.*

Camisia van Heyden, 1826 [**Notaspis segnis* Hermann, 1804]. *Oligo.-Rec.* [*C. horrida fossilis* Sellnick, Oligo., Balt.].

Nothrus C.L. Koch, 1836 [**N. palustris*]. *Oligo.-Rec.* [*N. illantus* Sellnick, Oligo., Balt.].

Family CARABODIDAE Willmann, 1931

Dorsum sculptured or punctate. Propodosoma with leaflike protuberances. *Oligo-Rec.*

Carabodes C.L. Koch, 1836 [**C. coriaceus*]. *Oligo.-Rec.* [*C. gerberi* Sellnick, Oligo., Balt.].

Otocepheus Berlese, 1904 [**O. longior*]. *Oligo.-Rec.* [*O. niger* Sellnick, Oligo., Balt.].

Tectocepheus Berlese, 1913 [**Tegeocranus velatus* Michael, 1888]. *Oligo.-Rec.* [*T. similis* Sellnick, Oligo., Balt.].

Cepheus C.L. Koch, 1836 [**C. latus*]. *Oligo.-Rec.* [*C. implicatus* (Sellnick), Oligo., Balt.].

Xenillus Robineau-Desvoidy, 1839 [**Notaspis tegeocranus* Hermann, 1804]. *Oligo.-Rec.* [*X. tegeocraniformis* (Sellnick), Oligo., Balt.].

Carabodites Pampaloni, 1902 [**C. pavesii*]. *M.Mio.*, Sicily.

Plateocranus Sellnick, 1919 [**Nothrus sulcatus* Karsch]. *Oligo.* [*P. sulcatus* (Karsch), Oligo., Balt.].

Scutoribates Sellnick, 1919 [**S. perornatus*]. *Oligo.*, Balt.

Family CERATOZETIDAE Jacot, 1925

With pteromorphs attached to hysterosoma and curving ventrally. *Oligo.-Rec.*

Chamobates Hull, 1916 [**Oribata cuspidata* Michael, 1884]. *Oligo.-Rec.* [*C. difficilis* Sellnick, Oligo., Balt.].

Melanozetes Hull, 1916 [**Oribates mollicomus* C.L. Koch, 1840]. *Oligo.-Rec.* [*M. foderatus* Sellnick, Oligo., Balt.].

Sphaerozetes Berlese, 1885 [**Oribates orbicularis* C.L. Koch, 1835]. *Oligo.-Rec.*—Fig. 63,2. *S. convexulus* (Koch & Berendt), Oligo., Balt., ×20 (71).

Family CYMBAEREMEIDAE Willmann, 1931

Pteromorphs wanting. Dorsal shield turned under ventrally. *Oligo.-Rec.*

Cymbaeremaeus Berlese, 1896 [**Eremaeus cymba* Nicolet, 1855]. *Oligo.-Rec.* [*C. acuminatus* (Sellnick), Oligo., Balt.].

Tectocymba Sellnick, 1919 [**T. rara*]. *Oligo.*, Balt.

Family ORIBATIDAE Kramer, 1877

[Type: *Oribata* Latreille, 1802] [=Eremaeidae Willman, 1931 (type: *Eremaeus* C.L. Koch, 1836)]

Dorsal shield not turned under. Hysterosoma without pteromorphs. *Oligo.-Rec.*

Caleremaeus Berlese, 1910 [**Notaspis monilipes* Michael, 1882]. *Oligo.-Rec.* [*C. gleso* Sellnick, Oligo., Balt.].

Ceratoppia Berlese, 1908 [**Notaspis bipilis* Hermann, 1804]. *Oligo.-Rec.* [*C. bipilis fossilis* Sellnick, Oligo., Balt.].

Lucoppia Berlese, 1908 [**Zetes lucorum* C.L. Koch, 1840]. *Oligo.-Rec.* [*L. simplex* Sellnick, Oligo., Balt.].

Oppia C.L. Koch, 1836 [**O. nitens*]. *Oligo.-Rec.* [*O. curvicornum* (Sellnick), Oligo., Balt.].

Eremaeus C.L. Koch, 1836 [**E. hepaticus*]. *Oligo.-Rec.* [*E. oblongus fossilis* Sellnick, Oligo., Balt.].

Licneremaeus Paoli, 1908 [**Notaspis lichnophorus* Michael, 1882]. *Oligo.-Rec.* [*L. fritschi* Sellnick, Oligo., Balt.].

Suctobelba Paoli, 1908 [**Notaspis trigona* Michael, 1888]. *Oligo.-Rec.* [*S. subtrigonus fossilis* Sellnick, Oligo., Balt.].

Gradidorsum Sellnick, 1919 [**G. asper*]. *Oligo.*, Balt.

Strieremaeus Sellnick, 1919 [**S. illibatus*]. *Oligo.*, Balt.

Oppites Pampaloni, 1902 [**O. melilli*]. *M.Mio.*, Sicily.

Family GALUMNIDAE Grandjean, 1936

Hysterosoma with movably hinged pteromorphs, their ends projecting far beyond line of attachment to body. *Oligo.-Rec.*

Galumna van Heyden, 1826 [**Notaspis alata* Hermann, 1804]. *Oligo.-Rec.* [*G. clavata* Sellnick, Oligo., Balt.].

Family HAPLOZETIDAE Grandjean, 1936

With movable pteromorphs. Tectopedium IV with leaflike extension. *Oligo.-Rec.*

Protoribates BERLESE, 1908 [**Oribata monodactyla* HALLER, 1884]. *Oligo.-Rec.* [*P. longipilis* SELLNICK, Oligo., Balt.].

Family HYPOCHTHONIIDAE Berlese, 1910

Genital and anal openings on common, narrow plate. Hysterosoma flat below, weakly arched above. *Oligo.-Rec.*

Trhypochthonius BERLESE, 1904 [**Hypochthonius tectorum* BERLESE, 1896]. *Oligo.-Rec.* [*T. badiformis* SELLNICK, Oligo., Balt.].

Family HERMANNIELLIDAE Grandjean, 1934

Pair of lateral tubes on hysterosoma, with openings of oil glands. *Oligo.-Rec.*

Hermanniella BERLESE, 1908 [**Hermannia granulata* NICOLET, 1855]. *Oligo.-Rec.* [*H. concamerata* SELLNICK, Oligo., Balt.].

Family LIACARIDAE Willmann, 1931

Hysterosoma without pteromorphs. Dorsal shield not bent under. Coxae 3 and 4 ventral, far from sides. *Oligo.-Rec.*

Cultroribula BERLESE, 1908 [**Notaspis juncta* MICHAEL, 1885]. *Oligo.-Rec.* [*C. lauta* SELLNICK, Oligo., Balt.].

Family NEOLIODIDAE Willmann, 1931

Dorsal shield not bent under. Adults carry exuviae of preceding instars on back. *Oligo.-Rec.*

Neoliodes BERLESE, 1888 [**Notaspis theleproctus* HERMANN, 1804]. *Oligo.-Rec.* [*N. quadriscutatus* SELLNICK, Oligo., Balt.].

Platyliodes BERLESE, 1916 [**Nothrus doderleinii* BERLESE, 1883]. *Oligo.-Rec.* [*P. ensigerus* SELLNICK, Oligo., Balt.].

Embolocarus SELLNICK, 1919 [**E. pergratus*]. *Oligo.*, Balt.

Family ORIBATELLIDAE Jacot, 1925

Pteromorphs not extending anteriorly beyond opisthosoma. Lamellae cover most of propodosoma. *Oligo.-Rec.*

Oribatella BANKS, 1895 [**O. quadridentata*]. *Oligo.-Rec.* [*O. mirabilis* SELLNICK, Oligo., Balt.].

Tectoribates BERLESE, 1910 [**Oribata tecta* MICHAEL, 1883]. *Oligo.-Rec.* [*T. parvus* SELLNICK, Oligo., Balt.].

Family ORIBATULIDAE Jacot, 1929

Pteromorphs do not bend under. Four pairs of genital setae. *Oligo.-Rec.*

Eporibatula SELLNICK, 1928 [**Eremaeus rauschensis* SELLNICK, 1928]. *Oligo.-Rec.* [*E. pellucida* SELLNICK, Oligo., Balt.].

Liebstadia OUDEMANS, 1906 [**Notaspis similis* MICHAEL, 1888]. *Oligo.-Rec.* [*L. similiformis* SELLNICK, Oligo., Balt.].

Scheloribates BERLESE, 1908 [**Zetes latipes* C.L. KOCH, 1844]. *Oligo.-Rec.* [*S. areatus* SELLNICK, Oligo., Balt.].

Family ORIPODIDAE Jacot, 1925

Pteromorphs coalesced along anterior edge of opisthosoma, forming bridge over propodosoma. *Oligo.-Rec.*

Oripoda BANKS, 1904 [**O. elongata*]. *Oligo.-Rec.* [*O. baltica* SELLNICK, Oligo., Balt.].

Family PARAKALUMMIDAE Grandjean, 1936

Pteromorphs large, hinged. A suture between propodo- and hysterosoma. *Oligo.-Rec.*

Neoribates BERLESE, 1914 [**Oribates roubali* BERLESE, 1900]. *Oligo.-Rec.* [*N. borussicus* SELLNICK, Oligo., Balt.].

Family PHENOPELOPIDAE Petrunkevitch, nov.

[*nom. subst.* PETR., herein (*pro* Pelopidae EWING, 1917, *ex Pelops* C.L. KOCH, 1836, *non Pelops* GISTL, 1834)]

Pteromorphs large, hinged, posteriorly not extending beyond line of attachment. Chelicerae long, with minute shears. *Oligo.-Rec.*

Phenopelops PETRUNKEVITCH, 1955 [*nom. subst.* PETR., herein (*pro Pelops* C.L. KOCH, 1836, *non* GISTL, 1834)] [**Notaspis hirsutus* C.L. KOCH, 1836]. *Oligo.-Rec.* [*P. punctulatus* (SELLNICK), Oligo., Balt.].

Family PHTHIRACARIDAE Perty, 1841

Cephalothorax withdrawable into notogaster; opening of latter closed by cephalic shield (aspis). *Oligo.-Rec.*

Hoploderma MICHAEL, 1898 [**Hoplophora laevigata* C.L. KOCH, 1844]. *Oligo.-Rec.* [*H. multipunctata* SELLNICK, Oligo., Balt.].

Oribotritia JACOT, 1924 [**Hoplophora decumana* C.L. KOCH, 1836]. *Oligo.-Rec.* [*O. translucida* SELLNICK, Oligo., Balt.].

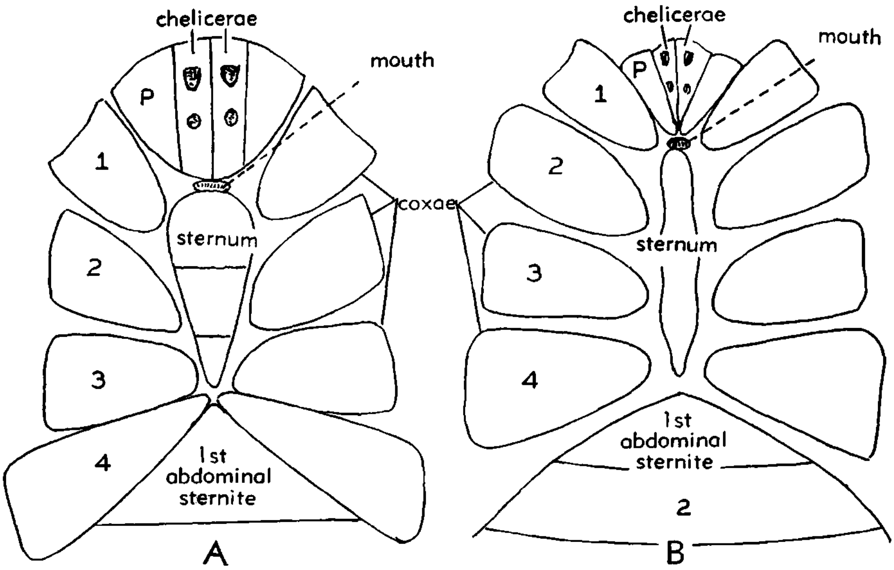


FIG. 64. Coxosternal region of Stethostomata; *A, Plesiosiro madeleyi,* U.Carb., Eng., ×20; *B, Cryptomartus priesti,* U. Carb., Eng., ×14 (76).

Suborder TETRAPODILINA Bremi, 1872

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Tetrapodili BREMI, 1872)] [=Eriophyiformes REUTER, 1909] [Type: *Eriophyes* VON SIEBOLD, 1850]

Body annulate, with only 2 pairs of legs. No respiratory system. Chelicerae stylet-like. Plant-eaters. No fossil representatives of this suborder are known. *Rec.*

Subclass STETHOSTOMATA Petrunkevitch, 1949

Arachnida with broad juncture between cephalothorax and abdomen as in Latigastra, but with configuration of coxosternal region differing from that of other subclasses in having basal joints of chelicerae wedged in between pedipalpal coxae and placed on one level with all other coxae (Fig. 64). Mouth between 1st pedal coxae, immediately in front of sternum. Carapace entire. Abdomen segmented, with fixed number of segments, 11 in one order, 10 in the other. Respiration by means of book lungs. *Carb.*

Order HAPTOPODIDA Pocock, 1911

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Haptopoda POCOCK, 1911)] [Type: *Plesiosiro* POCOCK, 1911]

Carapace with a pair of eyes (Fig. 65, *2,4*). Abdomen composed of 11 segments. Tergites entire, 1st tergite abbreviated. Sternites 3 to 10 bisected by a median longitudinal line; 2nd sternite by far the largest, with strongly convex posterior edge and a pair of round genital openings. Two pairs of book lungs, 1st pair on second sternite, 2nd pair on 3rd sternite, both pairs close to lateral edges (Fig. 65,*1,3*). Lateral pleura unsegmented, soft. Chelicerae 3-jointed, chelate (Fig. 65,*7*). All tarsi subsegmented (Fig. 65,*5,6*). *Carb.*

Family PLESIOSIRONIDAE Pocock, 1911

First tarsus 6-jointed, 2nd to 4th tarsi 4-jointed. Sternum wedge-shaped, pointed behind. *Carb.*

***Plesiosiro** POCOCK, 1911 [**P. madeleyi*]. Carapace longer than wide, with sides converging to a point, straight posterior edge, median longitudinal ridge and pair of lateral ridges. Pair of round eyes

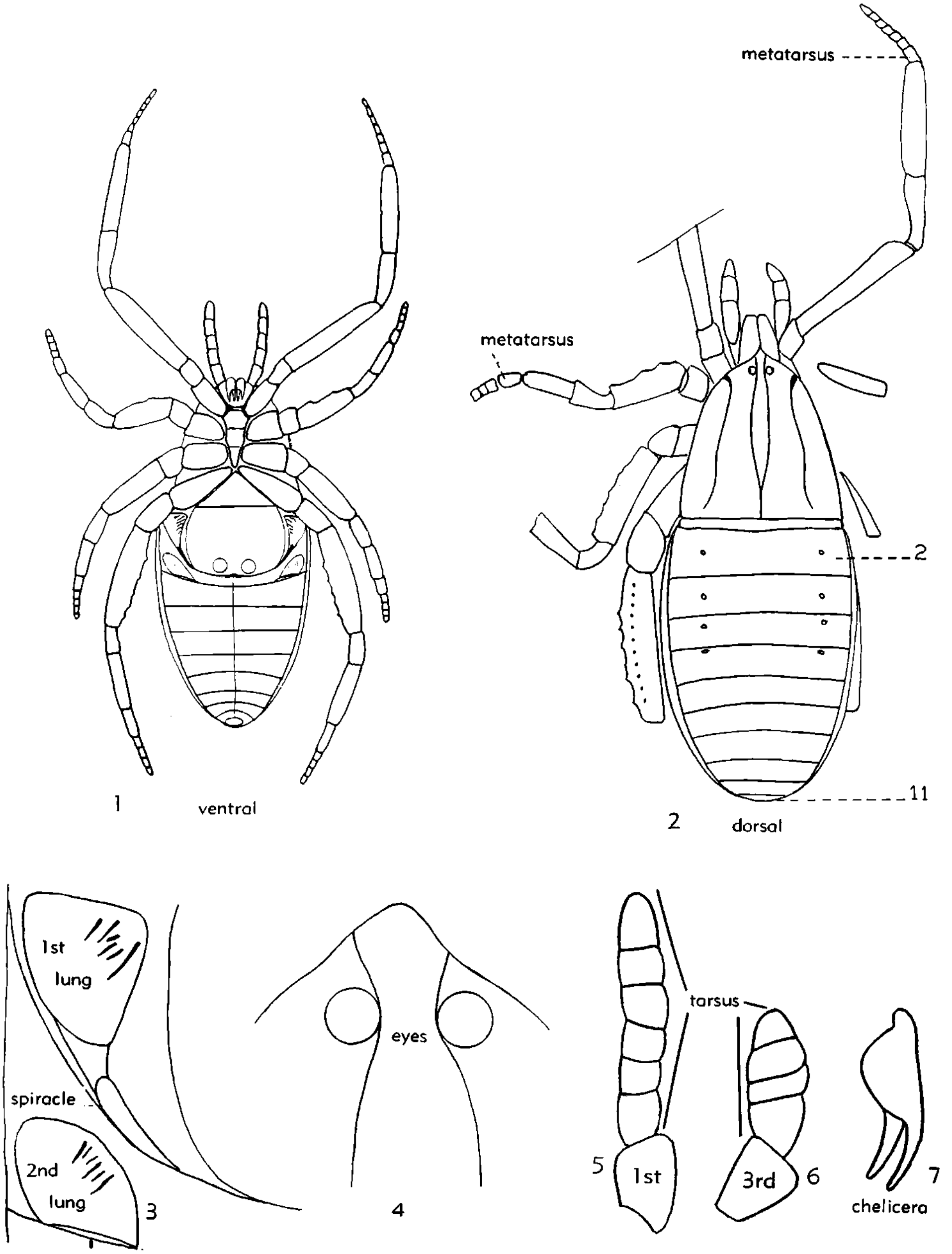


Fig. 65. External morphology of Haptopodida; *Plesiosiro madeleyi,* U. Carb., Eng.; *1,* Ventral side, completely restored, ×4.7. *2,* Dorsal side, ×4.7. *3,* Book lungs and spiracles of right side of abdomen, ×17. *4,* Anterior end of carapace with eyes and median ridge, ×45. *5,6,* First and 3rd tarsus, ×45. *7,* Chelicerae, ×21 (76).

close to anterior edge (Fig. 65,*2,4*). *Carb.*, Eng.—FIG. 64*A*, 65,*1,2*. **P. madeleyi*; 64*A*, coxosternal region, ×20; 65,*1*, ventral side, ×4.7; 65,2, dorsal side, ×4.7 (76).

Order ANTHRACOMARTIDA Karsch, 1882

[*nom. correct.* PEARSE, 1936 (*pro* Anthracomarti KARSCH, 1882), emend. PETRUNKEVITCH, 1949] [Type: *Anthracomartus* KARSCH, 1882]

Carapace entire, without eyes. Abdomen composed of 10 segments; 2nd and 3rd tergites fused without trace of division line, forming a common tergite for both segments; 1st and 10th tergites entire, 2nd to 9th divided by 2 pairs of longitudinal lines into a median, a pair of submarginal and a pair of marginal plates (Fig. 66,*2a*); 10th tergite bent under ventrally, its ventral portion wedged in between marginal plates of 9th sternite (Fig. 66,*2b*). All 10 sternites present, clearly separated by intersegmental lines; 1st sternite triangular, entire; 3rd to 9th sternites divided by a pair of longitudinal lines into a median and a pair of lateral (marginal) plates (Fig. 66,*2b*); 10th sternite completely enclosed between strongly curved median 9th plate and ventral portion of 10th tergite. Genital openings on 2nd sternite (Fig. 66,*1c,3c*), a single opening in male, a genital opening followed by a pair of openings leading into seminal receptacles in female. Anus on 10th sternite, disc-shaped, closed by an operculum consisting of a large anterior and a small posterior valve (Fig. 66,*2b,3b*). Chelicerae 3-jointed, their 3rd joint not known, but its existence indicated by articulations at end of 2nd joint (Fig. 66,*1d*). Basal joint wedged in between pedipalpal coxae and these between 1st pedal coxae (Figs. 64*B*, 66,*1a*). Pedipalpi 6-jointed, considerably shorter and more slender than legs (Fig. 68,*5*). Legs 7-jointed, stout and shorter than total length of body. Tarsi with a pair of claws on onychium (Fig. 66,*3a*). Three pairs of book lungs with openings on 2nd, 3rd and 4th sternites (Fig. 66,*1b*), with apodemes for attachment of pulmonary muscles. Sexes separate, recognizable by secondary sexual characters of the 2nd, 3rd and 4th sternites (Fig. 66, *2c,2d,3c*) and by proportions of carapace and legs. Males with narrow depression "*A*" on 2nd sternite and forked depression "*B*" on 3rd sternite. Females with broadly triangular depression "*A*" and semilunar depression "*B*."

The classification of Anthracomartida is based on the shape of the carapace and of the abdomen, on the structure of the 9th tergite and the proportions of the central area formed by the median plates of tergites 4 to 8. The scalloping of the abdominal edge, once stressed by POCOCK as an important character, is of very minor value. *Carb.*

DISCUSSION

For some unaccountable reason Anthracomartida were often considered to be primitive Arachnida. This is decidedly wrong and the reverse is true. The configuration of their coxosternal region, similar to that in Haptopodida and comparable only with that of Xiphosura, represents an extreme stage of the trend consisting in a backward displacement of the mouth. The dorsoventrally flattened body, combined with a sclerotization of the body wall, must have required for proper functioning of the processes of nourishment, respiration and reproduction, the retention of abdominal segmentation, and subdivision of hard tergites and sternites into transverse rows of smaller, hinged plates held together by soft membranes, thus permitting expansion of the body cavity. Even so, hampered by the clumsy shape of their body (Fig. 69) and the awkward position of the mouth, requiring some peculiar way of eating and presumably special type of food; confronted with changing environment and new exigencies of meeting them, yet unable to do so because of the law of irreversibility of evolution which in their case reached its end, these contemporaries of other Carboniferous animals succeeded only in producing minor, generic changes insufficient to prevent early extinction. This becomes strikingly clear when one compares Anthracomartida with scorpions which, having exhausted all macroevolutionary possibilities during the same geological period, managed to survive and to produce new families from one of the intermediate macroevolutionary stages of a trend which in its further stages also proved to be lethal, but which did not involve a conflict between progressive adaptation and irreversibility of evolution.

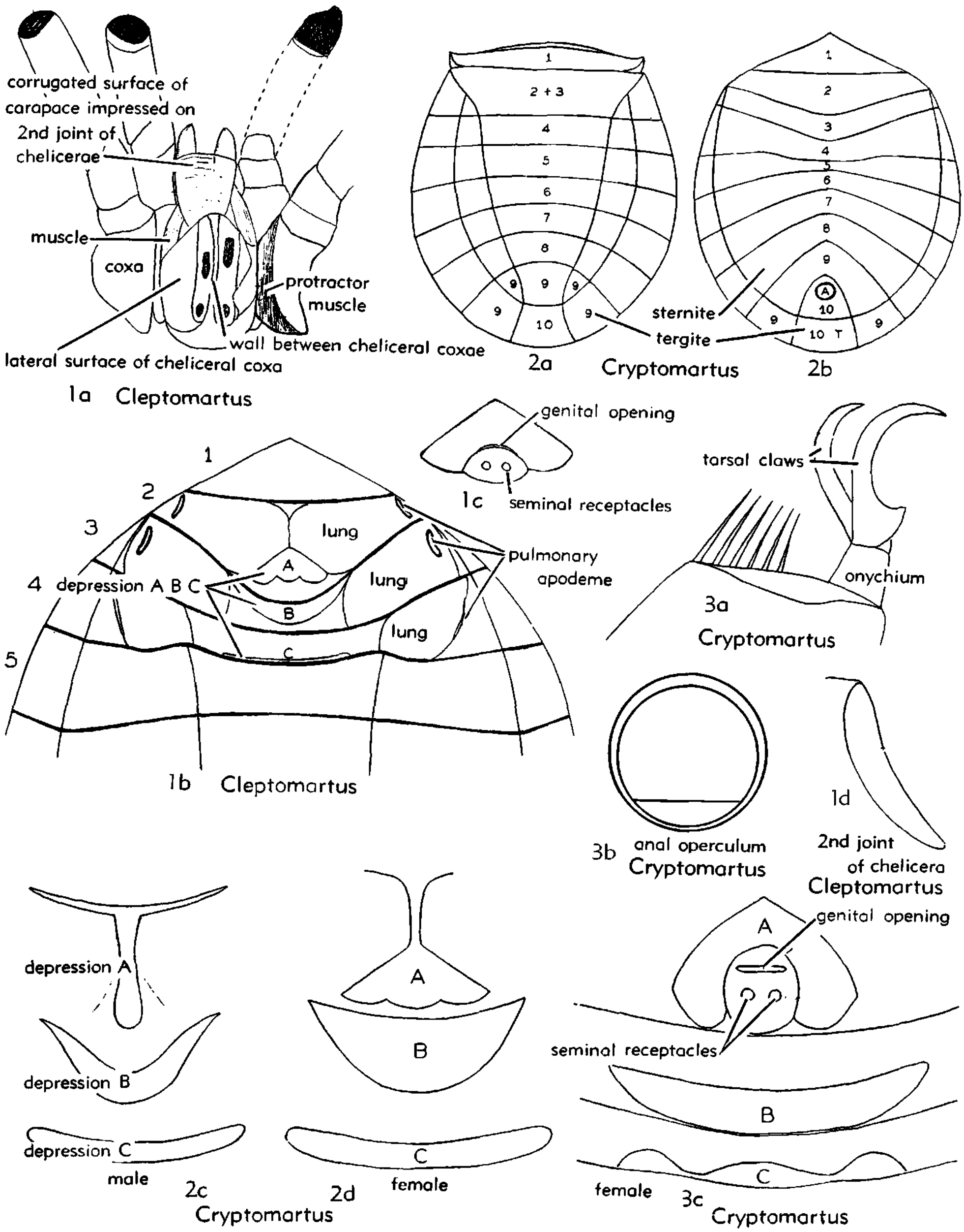


Fig. 66. External morphology of Anthracomartida. *1, Cleptomartus plautus,* U.Carb., Eng.; *1a,* anterior end of coxosternal region, ×8.5; *1b,* genital region, ×12; *1c,* genital opening and seminal receptacles of female, enlarged; *1d,* 2nd joint of chelicerae, enlarged. *2, Cryptomartus priesti,* U.Carb., Eng.; *2a,* segmentation of dorsal side of abdomen; *2b,* ventral side; *2c,d,* ventral abdominal depressions of male and female, ×15.5. *3, Cryptomartus hindi,* U.Carb., Eng.; *3a,* claws; *3b,* anal operculum; *3c,* genital region with ventral depressions of female, ×13 (76) (p. P105).

Family ANTHRACOMARTIDAE Haase, 1890

[=Anthracomartidae + Brachypygidae Pocock, 1911 + Pleomartidae + Coryphomartidae Petrunkevitch, 1945; emend. Petr., 1953]

Characters of the order. *Carb.*

Brachypyge Woodward, 1878 [**B. carbonis*]. Median plate of 9th tergite hexagonal, formed by complete fusion with submarginal plates. Carapace subtriangular, with rounded anterior end. Abdomen distinctly longer than wide, with edge escalloped in posterior half (45). *Carb.*—Fig. 67, *6*. **B. carbonis,* Belg.; dorsal side, ×1.5 (76).

Coryphomartus Petrunkevitch, 1945 [**Anthracomartus triangularis* Petr., 1913]. Ninth tergite as in *Brachypyge*. Carapace triangular with concave sides. Abdomen with smooth edge (38, 45). *U. Carb.,* N.Am.—Fig. 67,*7*. **C. triangularis* (Petr.), N.Scot.; dorsal side, ×3.6 (76).

Maiocercus Pocock, 1911 [**Eophrynus carbonis* Howard & Thomas, 1896]. Carapace subtriangular, sculptured, 9th tergite with submarginal plates. Abdomen orbicular, wider than long, with escalloped edge (45). *Carb.*—Fig. 68,*6*. **M. carbonis* (Howard & Thomas), Eng.; dorsal side, ×1.6 (76).

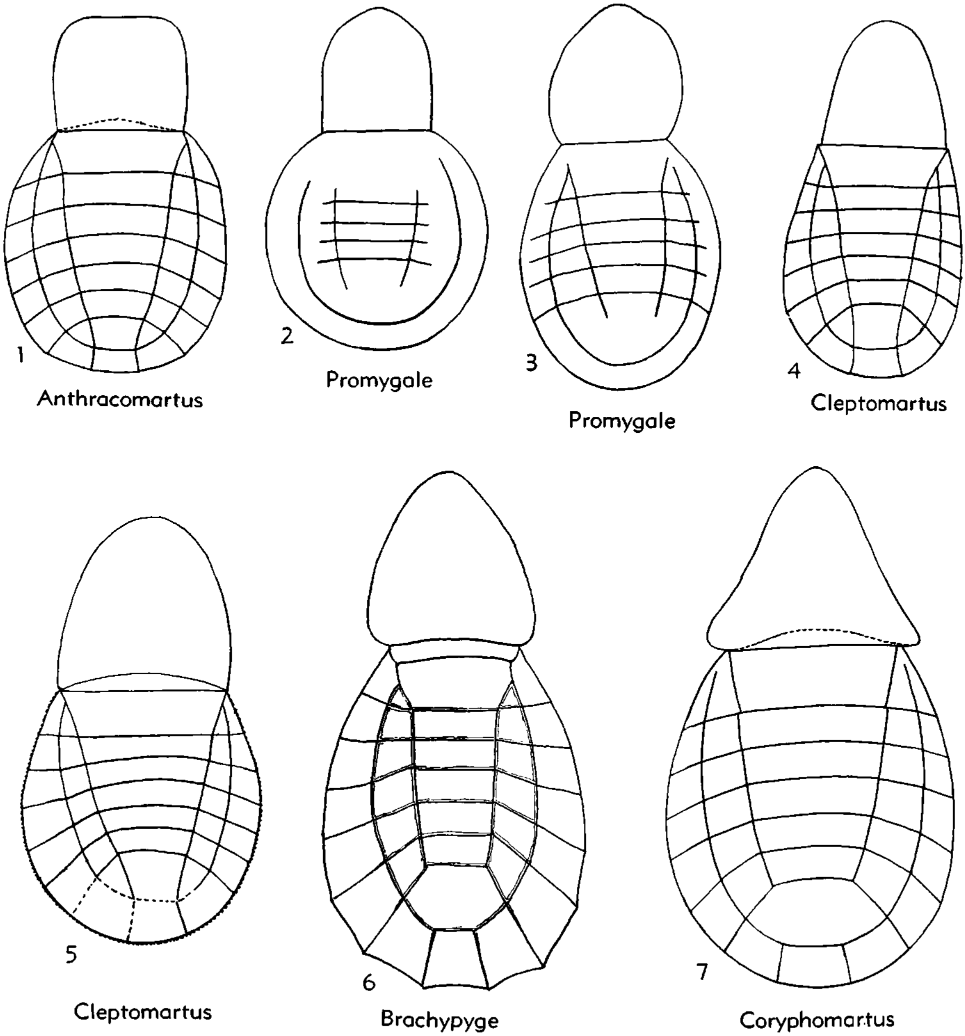


Fig. 67. Anthracomartidae. *1, Anthracomartus völkelianus,* U.Carb., Ger., ×2.5; *2, Promygale bohemica,* U.Carb., Czech., ×3.2; *3, Promygale elegans,* U.Carb., Czech., ×4.4; *4, Cleptomartus planus,* U.Carb., Eng., ×4.7; *5, Cleptomartus denuiti,* Carb., Belg., ×3.4; *6, Brachypyge carbonis,* U.Carb., Belg., ×1.5; *7, Coryphomartus triangularis,* U.Carb., Nova Scotia, ×3.6 (76) (p. P104-P107).

Cryptomartus Petrunkevitch, 1949 [**Anthracomartus hindi* Pocock, 1911]. Carapace with almost vertical sides converging anteriorly, with median crest on cephalic portion (Fig. 68,*3*). Ninth tergite as in *Maiocercus* (45). *Carb.*—Figs. 66,*3;* 68,*3*. **C. hindi* (Pocock), Eng.; 66,*3c*, genital openings and depressions of female, ×13 (76); 68,*3*, dorsal side of female, ×2.7 (76).—Figs. 64*B;* 66,*2c,2d;* 68,*5*. *C. priesti* (Pocock), Eng.; 64*B*, coxosternal region, ×14; 66,*2c,d*, median depressions on 2nd to 4th sternites of male and female, ×15.5; 68,*5*, ventral side, ×2.9 (76).

Cleptomartus Petrunkevitch, 1949 [**C. plautus*]. Carapace flat, as wide as long, evenly rounded in front. Ninth tergite as in *Maiocercus* (43, 45). *Carb.*—Figs. 66,*1;* 68,*2;* 69. **C. plautus*, Eng.;

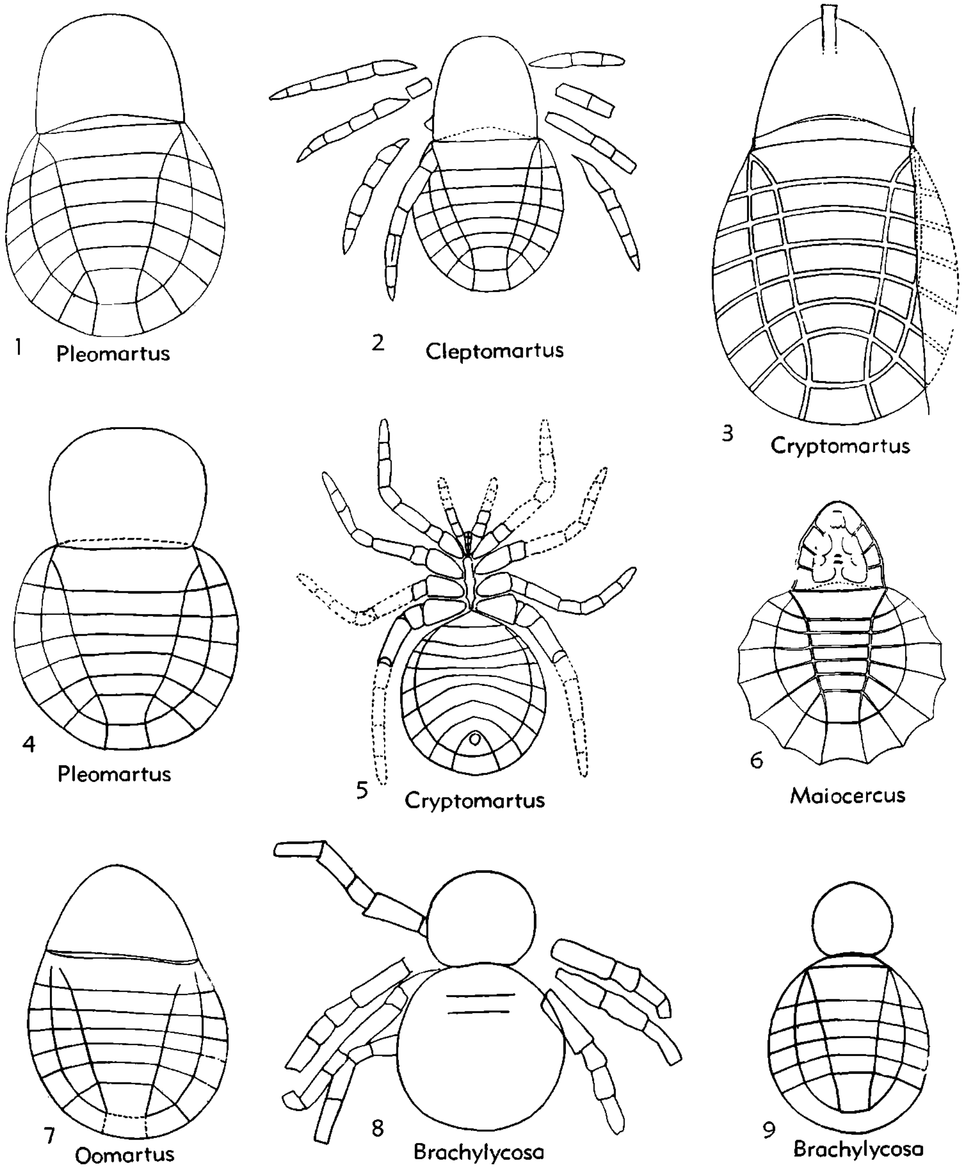


Fig. 68. Anthracomartidae. *1, Pleomartus trilobitus,* Penn., Ark., ×3.1; *2, Cleptomartus plautus,* U.Carb., Eng., female, ×3; *3, Cryptomartus hindi,* U.Carb., Eng., female, ×2.7; *4, Pleomartus palatinus,* U.Carb., Ger., ×2.3; *5, Cryptomartus priesti,* U.Carb., Eng., ventral side, ×2.9; *6, Maiocercus carbonis,* U.Carb., Eng., ×1.6; *7, Oomartus nyranensis,* U.Carb., Czech., ×1; *8, Brachylycosa carcinoides,* U.Carb., Czech., ×1.3; *9, Brachylycosa kustae,* U.Carb., Czech., ×1.3 (76) (p. P104-P107).

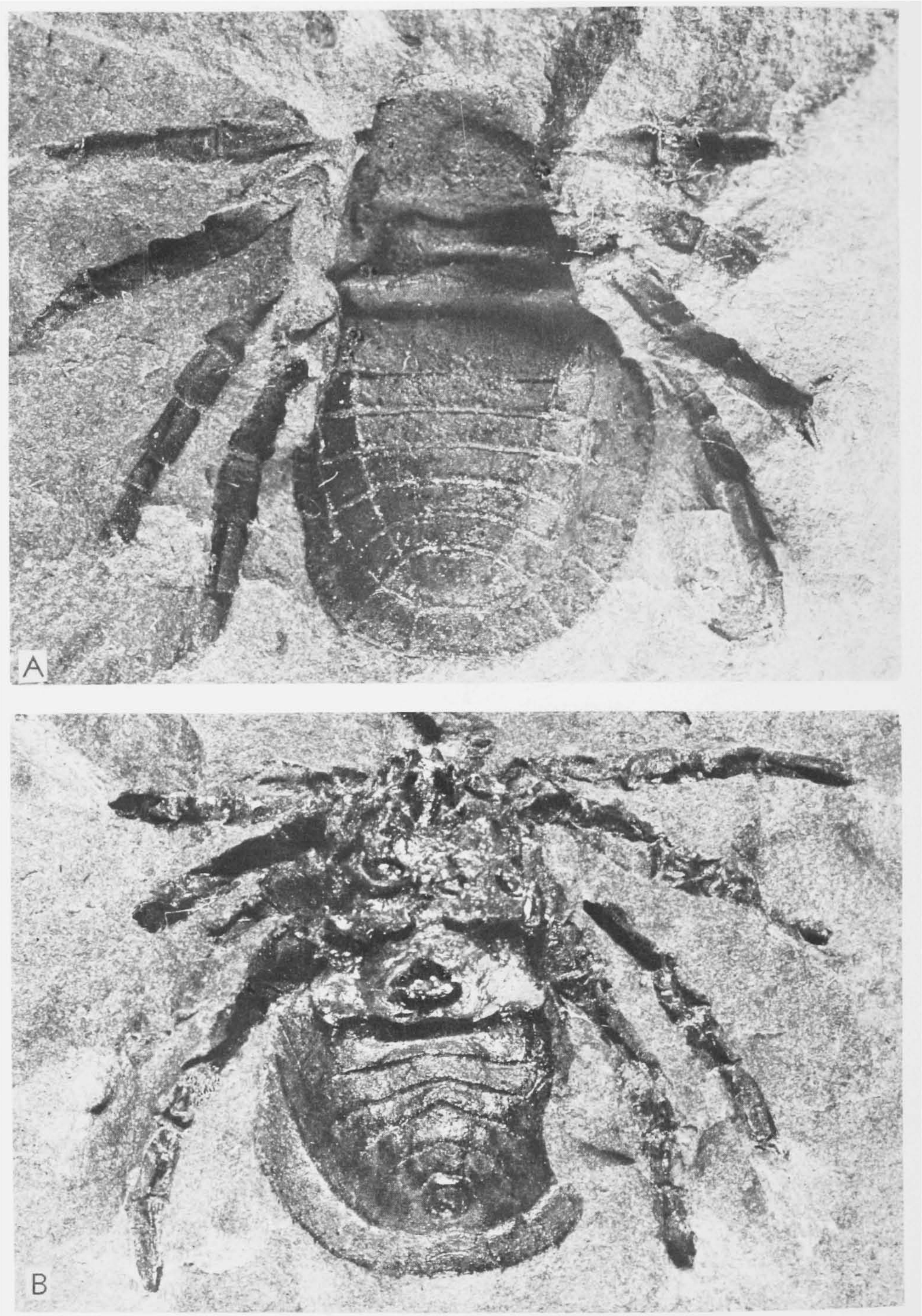


FIG. 69. Anthracomartidae. *Cleptomartus plautus*, U.Carb., Eng.; *A,B,* Photographs of dorsal and ventral sides, ×7.5 (76) (p. P105).

66,*1a,* coxae of chelicerae wedged in between pedipalpal coxae, ×8.5; 66,*1b,* external morphology of anterior 5 sternites of female, ×12 (76); 68,*2,* female, ×3; 69, dorsal and ventral sides of holotype, ×7.5 (76).—FIG. 67,*4*. *C. planus* PETR., Eng.; ×4.7 (76).—FIG. 67,*5*. *C. denuiti* (PRUVOST), Belg.; ×3.4 (76).

Anthracomartus KARSCH, 1882 [**A. völkelianus*]. Carapace as wide as long, with parallel sides and almost truncated front. Ninth tergite as in *Maiocercus* (34, 38, 45). *Carb.,* Eu.—FIG. 67,*1*. **A. völkelianus,* Ger.; ×2.5 (76).

Pleomartus PETRUNKEVITCH, 1945 [**Anthracomartus trilobitus* SCUDDER, 1884]. Carapace transversely rectangular, much wider than long. Ninth tergite as in *Maiocercus* (38, 45). *U.Carb.,* N.Am.-Eu.—FIG. 68,*1*. **P. trilobitus* (SCUDDER), Penn. (Pottsville), Ark.; ×3.1 (76).—FIG. 68,*4*. *P. palatinus* (AMMON), Ger.; ×2.3 (76).

Promygale FRITSCH, 1899 [**Kreischeria bohemica* FRITSCH, 1899]. Carapace considerably longer than wide, narrowed anteriorly. Ninth tergite as in *Maiocercus* (9, 45). *Carb.,* Eu.—FIG. 67,*2*. **P. bohemica* (FRITSCH), Czech.; ×3.2;—FIG. 67,*3*. *P. elegans* (FRITSCH), Czech.; ×4.4 (76).

Brachylycosa FRITSCH, 1904 [**Arthrolycosa carcinoides* FRITSCH, 1899]. Carapace more or less disclike. Ninth tergite as in *Maiocercus* (9, 45). *Carb.,* Eu.—FIG. 68,*8*. **B. carcinoides* (FRITSCH), Czech.; ×1.3 (76).—FIG. 68,*9*. *B. kustae* PETRUNKEVITCH, Czech.; ×1.3 (76).

Oomartus PETRUNKEVITCH, 1953 [**O. nyranensis*]. Carapace parabolic, body oval. Ninth tergite as in *Maiocercus* (45). *Carb.,* Eu.—FIG. 68,*7*. **O. nyranensis,* Czech.; ×1 (76).

Anthracophrynus ANDRÉE, 1913 [**A. tuberculatus*]. Abdomen with pair of tubercles on all median plates. Ninth tergite as in *Maiocercus*. *Carb.,* Ger.

Subclass SOLUTA Petrunkevitch, 1949

Arachnida with 2 types of juncture between cephalothorax and abdomen: broad juncture in some and juncture restricted to middle third in others while width of abdomen remains same as that of carapace. Abdomen segmented, composed of 8 to 11 segments. Tergites divided by 2 longitudinal lines into median and a pair of marginal plates. Sternites entire. Coxosternal region of same type as in Recent spiders, i.e., consisting of sternum with lower lip and 5 pairs of coxae in same ventral plane. Chelicerae 2-jointed, retrovert, 2nd joint developed as fang. Pedipalpi 6-jointed, their coxa without maxillary lobe. Legs 7-jointed, with a pair of claws. Respiration by means of book lungs (45). *Dev.-Rec.*

DISCUSSION

All Soluta have the same configuration of the coxosternal region, almost identical with that of Araneida. The question may be raised, *why* are they not placed as an order in the same class with the Araneida? There are several different configurations of the coxosternal region in Caulogastra, just as there are several in Latigastra. The reason for the segregation of Soluta in a subclass of their own is the still labile status of other important characters by which they differ from all Caulogastra and which are not present in any other fossil or living Arachnida. It is the combination of their characters, rather than any particular character, that makes the Soluta different from the other 3 subclasses. As long as no fossil Soluta are found with a different configuration of the coxosternal region, the class may be considered as being represented by a single order, the Trigonotarbida. In accordance with our present knowledge we may assume that the subclass Soluta became extinct in the Late Carboniferous, but left sufficient evidence to show the main trends of its evolution since its appearance in the Devonian; these are the loss of posterior segments in a progressive series until only 8 segments were left and an arrested loss of the 1st anterior segment.

When imperfectly preserved, Soluta may be confused with spiders and (in case of only 4 genera) with Anthracomartida. They can be always distinguished from the latter by the absence of marginal plates in abdominal sternites, and from spiders by the presence of marginal plates in abdominal tergites.

Order TRIGONOTARBIDA Petrunkevitch, 1949

[*nom. correct.* PETR., herein (*pro* Trigonotarbi PETR., 1949)]
[Type: *Trigonotarbus* POCOCK, 1911]

Configuration of coxosternal region as in Araneida. *Dev.-Carb.*

Family PALAEOCHARINIDAE Hirst, 1923

Abdomen composed of 11 segments, the last 2 of which are reduced, forming a pygidium (Fig. 70, *1a,2c*). Carapace with pair of median eyes and pair of lateral organs (interpreted by Hirst as compound eyes, 17) (Fig. 70,*2a*). *Dev.*

Palaeocharinoides Hirst, 1923 [**P. hornei*]. Sternum pointed in front, angular behind (17, 45). *Dev.*, Eu.—Fig. 70,*1*. **P. hornei*, Old Red Sandstone, Scot.; *1a*, ventral side with dorsal segmentation shown by dotted lines, ×30; *1b*, carapace in side view, showing crest, ×40; *1c*, sternum, ×60; *1d*, chelicera, ×50 (70).

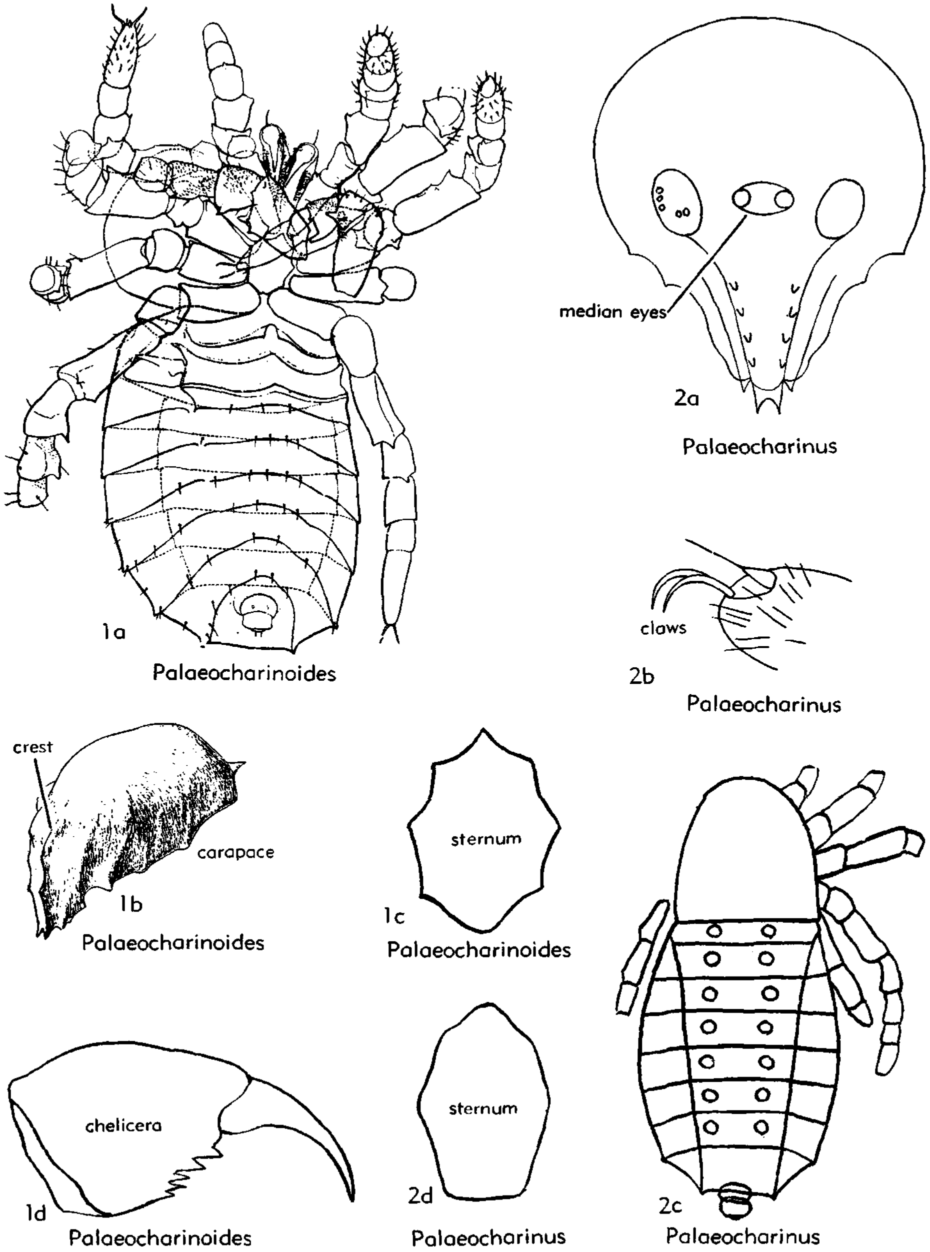


Fig. 70. Order Trigonotarbida; Paleocharinidae. *1, Paleocharinoides hornei*, Dev., Old Red Sandstone, Scot.; *1a*, ventral side of a complete specimen, ×30; *1b*, side view of carapace, ×40; *1c*, sternum, ×60; *1d*, chelicera, ×50. *2, Palaeocharinus* sp., Dev., Old Red Sandstone, Scot.; *2a*, front view of carapace, ×25; *2b*, claws, ×50; *2c*, dorsal side of specimen, ×18; *2d*, sternum, ×60 (70, 76) (p. P108-P109).

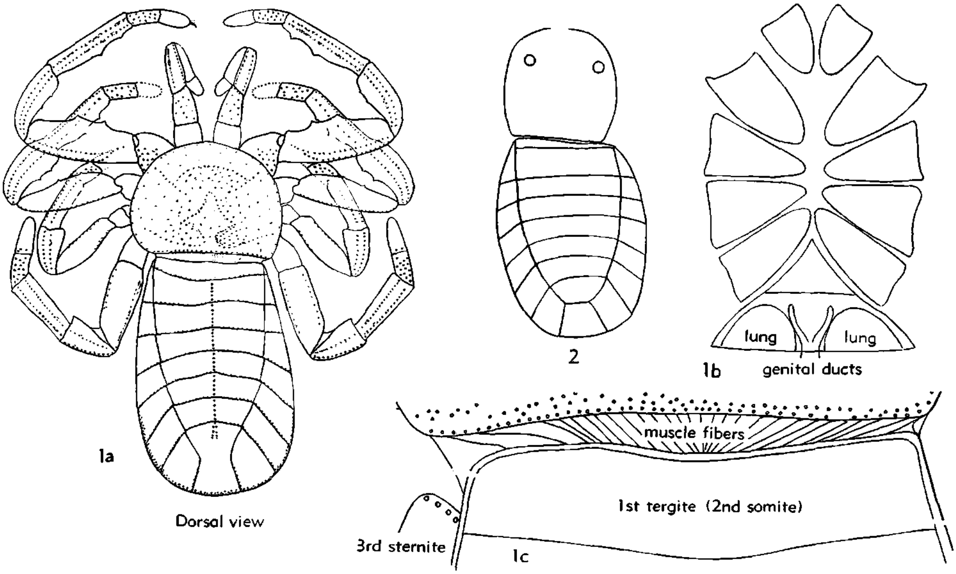


FIG. 71. Anthracosironidae. *1, Anthracosiro woodwardi,* U.Carb., Eng.; *1a,* female, ×2.7; *1b,* coxosternal region, ×6; *1c,* junction between cephalothorax and abdomen showing muscles, ×12. *2, Anthracosiro fritschi,* U.Carb., Eng.; dorsal side, showing eyes, ×6 (76) (p. P109).

Palaeocharinus HIRST, 1923 [**P. rhyniensis*]. Sternum bluntly pointed in front, truncated behind (17, 45) (Fig. 70,*2d*). *Dev.,* Eu.—FIG. 70,*2d.* **P. rhyniensis,* Old Red Sandstone, Scot.; sternum, ×60.—FIG. 70,*2a-c. P.* sp.; *2a,* front view of carapace showing crest, ocular tubercle and pair of special organs (HIRST's "compound eyes"), ×25; *2b,* claws, ×50; *2c,* dorsal side, ×18 (70).

Family ANTHRACOSIRONIDAE Pocock, 1903

Abdomen broadly joined to cephalothorax; 10 abdominal segments, but tergite of 1st segment reduced to a muscular membrane, sclerotized 1st visible tergite in reality belongs to 2nd segment. Single pair of book lungs on 2nd sternite. All 10 sternites present. Anus with round operculum on 10th sternite (45). *Carb.*

Anthracosiro POCOCK, 1903 [**A. woodwardi*]. Carapace flat, rounded in front, with straight posterior edge. Legs stout, granular (45). *U.Carb.,* Eu.—FIGS. 71, 72. **A. woodwardi,* Eng.; 71,*1a,* dorsal side, ×2.7 (legs partly reconstructed); *1b,* sternocoxal region, ×6; *1c,* juncture of abdomen with carapace, ×12; 72, photo of dorsal side, ×5.5.—FIG. 71,*2. A. fritschi* POCOCK, Eng.; dorsal side, showing eyes characteristic of the species, ×6 (76).

Family EOPHRYNIDAE Karsch, 1882

[emend. PETRUNKEVITCH, 1949]

Abdomen composed of 9 segments; anterior tergite as wide as carapace; but juncture reduced to middle third. Ninth tergite entire, enclosed between median and lateral plates of 8th tergite and often fused with median plate of the latter, forming with it a single, hourglass-shaped plate. Carapace usually sculptured and with an anterior, pointed, often spikelike process. Abdomen usually tubercular, often with a pair of posterior thorns. Four pairs of book lungs with openings on 2nd to 5th sternites (45). *Carb.*

Subfamily AREOMARTINAE Petrunkevitch, nov.

Abdominal tergites smooth or granular, but not with regularly arranged rows of large tubercles. *Carb.*

Areomartus PETRUNKEVITCH, 1913 [**A. ovatus*]. Tergites smooth. Carapace triangular, with shallow, hexagonal depressions. No eyes (34, 45). *Penn.,* N.Am.—FIG. 73,*2.* **A. ovatus,* W.Va.; ×5 (76).

Vratislavia FRITSCH, 1904 [**Architarbus silesiacus* RÖMER, 1876]. Carapace transversely rectangular, presumably without eyes. Four slender spurs at posterior end of abdomen. *Carb.,* Eu.—FIG. 74,*3.* **V. silesiaca* (RÖMER), Ger.; ventral side, ×4 (66a).

Anzinia PETRUNKEVITCH, 1953 [**Kreischeria theveenini* PRUVOST, 1919]. Carapace triangular, finely granular in front, ornamented at base, presumably without eyes. Abdomen with 4 short, pointed projections at posterior end (45). *Carb.*, Eu.—FIG. 73,*3*. **A. thevenini* (PRUVOST), Fr.; ×4.7 (76).

Hemiphrynus FRITSCH, 1899 [**H. longipes*]. Carapace with anterior, spikelike projection. Abdomen with 4 short, pointed thorns at posterior end (9, 45). *Carb.*, Eu.—FIGS. 73,*6*; 77,*4*. **H. longipes*, Czech.; 73,*6*, ventral side, ×1.35; 77,*4*, photo of holotype, ×0.9 (76).—FIG. 74,*1*. *H. hofmanni* FRITSCH, Czech.; ventral side, ×1.35 (76).

Pseudokreischeria PETRUNKEVITCH, 1953 [**Eophrynus pococki* GILL, 1924]. Carapace ornamented, with short anterior spike. Abdomen with 4 posterior projections (45). *U.Carb.*, Eu.—FIG. 75,*1*. **P. pococki* (GILL), Eng.; carapace and front part of abdomen, ×2.5—FIG. 75,*2*. *P. varia* (PETR.), Eng.; dorsal side of posterior portion of abdomen, ×2.5 (76).

Subfamily EOPHRYNINAE Karsch, 1882

[*nom. transl.* PETRUNKEVITCH, herein (*ex* Eophrynidae KARSCH, 1882)]

Abdominal tergites with rows of conspicuous, large tubercles. *Carb.*

Cyclotrogulus FRITSCH, 1904 [**Eophrynus sturii* HAASE, 1890]. Carapace triangular, without eyes. Abdomen rounded behind, with 6 rows of dorsal abdominal tubercles and a pair of spurious divi-

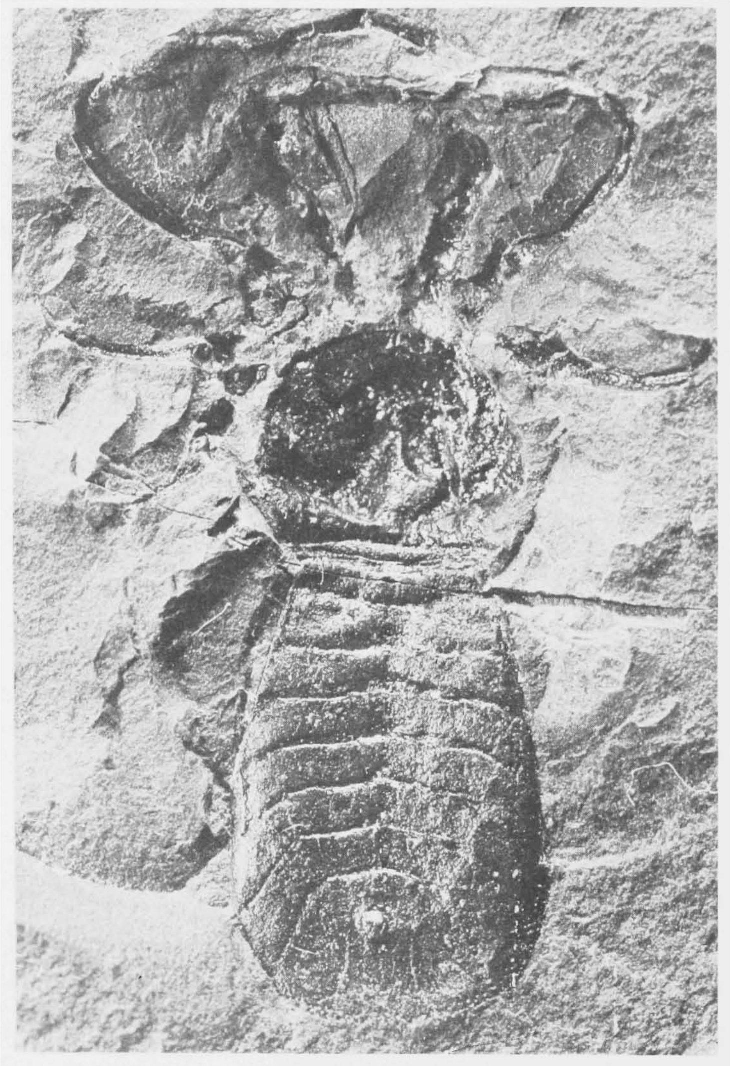


FIG. 72. *Anthracosiro woodwardi*, U.Carb., Eng.; photograph of dorsal side, ×5.5 (76) (p. P109).

sion lines (9, 14, 45). *Carb.,* Eu.—FIG. 75,*3*. **C. sturii* (HAASE), Ger.; ×2.4 (76).

Poconoia PETRUNKEVITCH, 1953 [**Trigonomartus whitei* EWING, 1930]. Carapace rounded in front, ornamented, with pair of eyes. Abdomen rounded behind, with 6 rows of tubercles and pair of spurious division lines. Median 2 rows of tubercles largest. *Penn.,* N.Am.—FIG. 76,*1*. **P. whitei* (EWING), ×6.6 (76).

Kreischeria GEINITZ, 1882 [**K. wiedei*]. Carapace ornamented, subtriangular, presumably with rounded anterior end, longer than wide, with pair of eyes. Abdomen with 4 rows of tubercles and 4 posterior spurs (45). *Carb.,* Eu.—FIG. 76,*3*. **K. wiedei,* Ger.; ×1 (76).

Petrovicia FRITSCH, 1904 [**P. proditoria*]. Carapace with pointed anterior spike. Abdomen with 4 rows of tubercles and 4 posterior spurs which form a

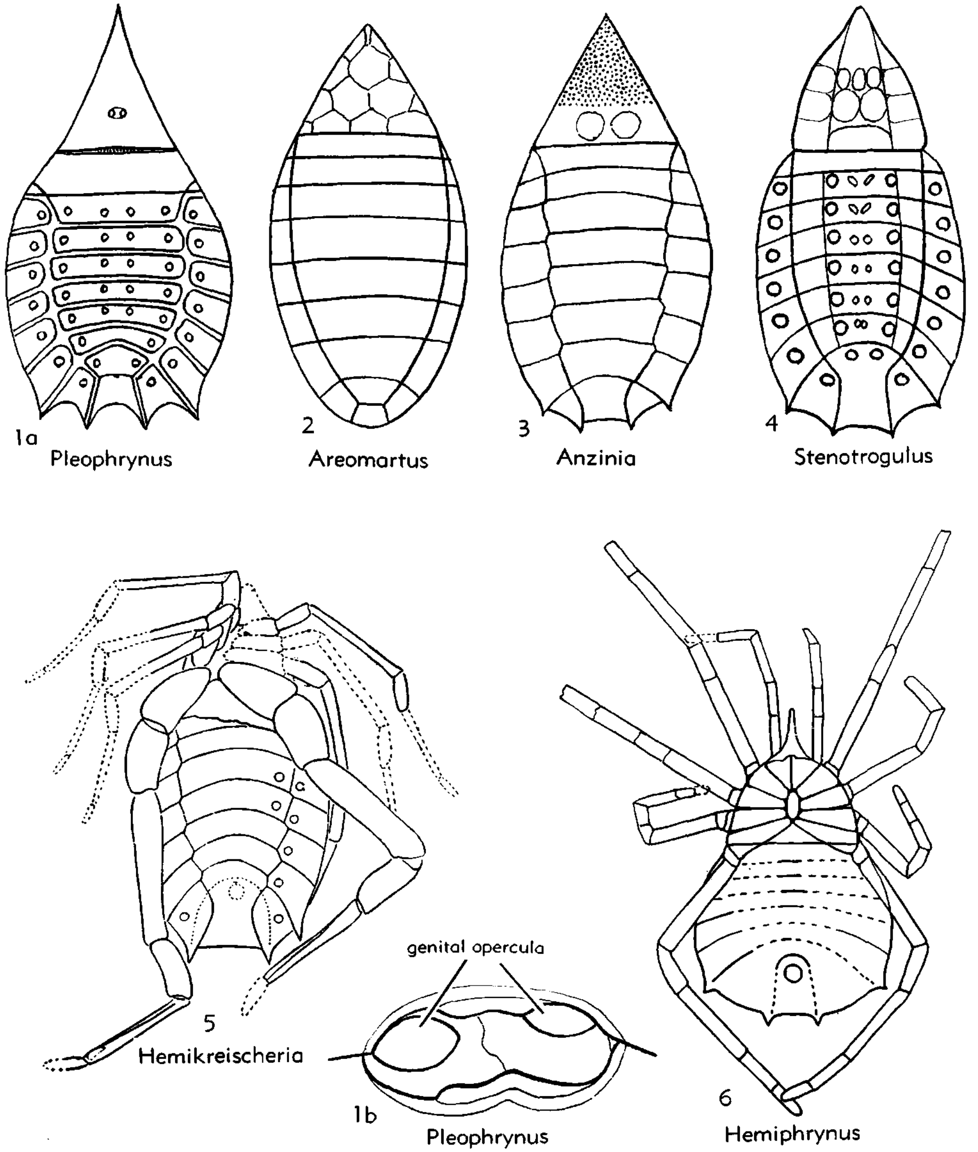


FIG. 73. Eophrynidae. *1, Pleophrynus ensifer,* Penn., Ill.; *1a,* dorsal side, ×1.35; *1b,* genital opercula, ×15. *2, Areomartus ovatus,* Penn., Ill., ×5. *3, Anzinia thevenini,* U.Carb., Fr., ×4.7. *4. Stenotrogulus salmii,* U. Carb., Czech., ×1.9. *5, Hemikreischeria geinitzi,* U.Carb., Fr., ×1.8. *6, Hemiphrynus longipes,* U. Carb., Czech., ×1.35 (76) (p. P109-P112).

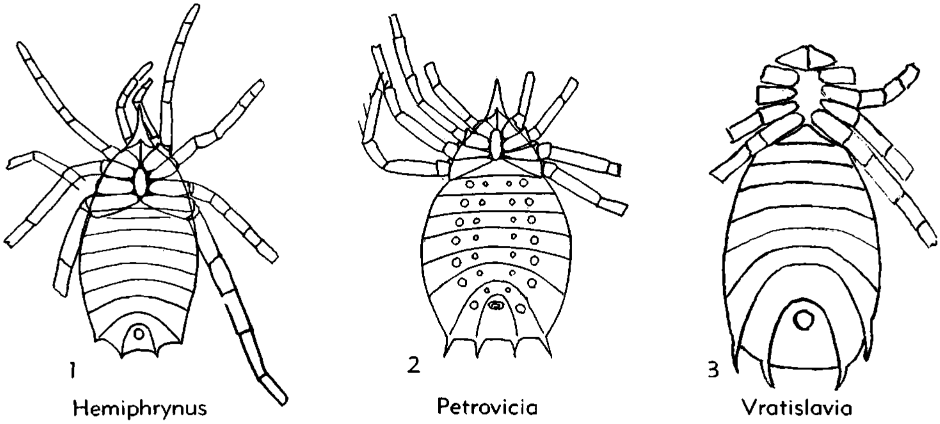


FIG. 74. Eophrynidae. _1, Hemiphrynus hofmanni,_ U.Carb., Czech., ×1.35. _2, Petrovicia proditoria,_ U.Carb., Czech., ×1.35. _3, Vratislavia silesiaca,_ U.Carb., Pol. (Silesia), ×4 (76) (p. P109-P111).

transverse row. Tibiae with ventral spines (9, 45). _Carb.,_ Eu.—FIGS. 74,_2_; 77,_1_. _*P. proditoria,_ Czech.; 74,_2_, ventral side, ×1.35; 77,_1_, photo of holotype, ×1.3 (76).

Hemikreischeria FRITSCH, 1904 [_*Kreischeria geinitzi_ THEVENIN, 1902]. Shape of carapace not known. Abdomen with 4 rows of tubercles and 4 posterior spurs. Fourth legs much stouter and longer than the others. _Carb.,_ Eu.—FIG. 73,_5_. _*H. geinitzi_ (THEVENIN), Fr.; ×1.8 (79).

Stenotrogulus FRITSCH, 1904 [_*Eophrynus salmii_ STUR, 1877]. Carapace subtriangular, ornamented, longer than wide, without eyes. Six rows of tubercles, medial row composed of smaller and elongated, not round, tubercles. Abdomen with a pair of spurious division lines and 4 posterior spurs (9, 45). _Carb.,_ Eu.—FIG. 73,_4_. _*S. salmii_ (STUR), Ger.; ×1.9 (76).

Acrokreischeria PETRUNKEVITCH, 1953 [_*Kreischeria verrucosa_ POCOCK, 1911]. Carapace acutely drawn out in front, with concave sides and rounded corners, ornamented, without eyes. Abdomen with 6 rows of tubercles, a pair of spurious division lines and 4 short projections behind (45). _U.Carb.,_ Eu.—FIG. 76,_2_. _*A. verrucosa_ (POCOCK), Wales, ×1.8 (76).

Pleophrynus PETRUNKEVITCH, 1945 [_*P. ensifer_]. Carapace triangular, longer than wide, acutely pointed in front, ornamented, with pair of eyes on tubercle situated behind middle. Abdomen with 6 rows of tubercles and 4 posterior spurs (38, 45). _Penn.,_ N.Am.—FIG. 73,_1_. _*P. ensifer,_ Ill.; _1a,_ dorsal side, ×1.35; _1b,_ genital atrium with a pair of opercula, ×15 (76).

Eophrynus WOODWARD, 1871 [_*Curculioides prestvici_ BUCKLAND, 1837]. Carapace subtriangular, with pointed spike in front, ornamented, as long as wide, with pair of eyes on tubercle slightly behind middle. Abdomen with 6 rows of tubercles and 4 spurs at end (12, 45). _U.Carb.,_ Eu.—FIGS. 32; 78. _*E. prestvici_ (BUCKLAND), Eng.; 32; photo, dorsal and ventral sides of lectotype, ×3; 78, drawing of same, showing details of structure, ×1.5 (76).

Family TRIGONOTARBIDAE Petrunkevitch, 1949

Abdomen composed of 8 segments and broadly joined to cephalothorax. Eighth tergite entire, enclosed between median and marginal plates of strongly curved 7th tergite and turned under ventrally, where it occupies the space between the ends of the strongly curved 7th sternite, behind the 8th sternite (Fig. 79,_1_). Posterior edge of abdomen evenly rounded. Carapace subtriangular, with a pair of eyes. Two pairs of book lungs with openings on 2nd and 3rd sternites (43, 45). _Carb._

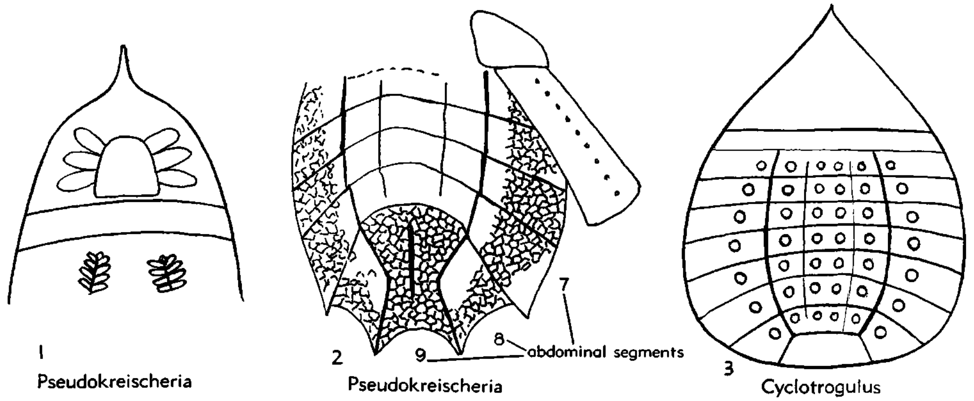
Trigonotarbus POCOCK, 1911 [_*T. johnsoni_]. Carapace as long as wide, with convex sides and pair of eyes on tubercle in middle (45). _U.Carb.,_ Eu.—FIGS. 77,_2_; 79. _*T. johnsoni,_ Eng.; 77,_2_, photo of holotype, ×6; 79,_1_, ventral side, ×6.8; 79,_2_, dorsal side, ×9 (76).

Family TRIGONOMARTIDAE Petrunkevitch, 1949

Abdomen composed of 8 segments, and broadly joined to cephalothorax. Eighth tergite with marginal plates and limited to dorsal surface, lacking ventrally folded part. _Carb._

Trigonomartus PETRUNKEVITCH, 1913 [_*Anthracomartus pustulatus_ SCUDDER, 1884]. Carapace triangular, high, with median crest and pustulose

FIG. 75. Eophrynidae. *1, Pseudokreischeria pococki,* U.Carb., Eng.; anterior part of dorsal side, ×2.5. *2, Pseudokreischeria varia,* U.Carb., Eng.; posterior dorsal side of abdomen, ×2.5. *3, Cyclotrogulus sturii,* U.Carb., Czech., ×2.4 (76) (p. P110-P111).



surface, without eyes. Abdomen with pustulose surface (34, 45). *U.Carb.,* Eu.-N.Am.—FIGS. 80,*1;* 81,*1.* **T. pustulatus* (SCUDDER), Ill.-Ger.; 80,*1,* dorsal side, ×2.8; 81,*1,* ventral side, ×2.9 (76).

Aphantomartus POCOCK, 1911 [**A. areolatus*]. Carapace ornamented, subtriangular, with pair of eyes ⅓ its length from anterior end. Dorsal lines dividing abdomen strongly converging, straight. Surface of abdomen with flattened tubercles (45). *Carb.,* Eu.—FIG. 80,*3.* **A. areolatus,* Wales; ×3 (76).

Lissomartus PETRUNKEVITCH, 1949 [**Trigonomartus schucherti* PETR., 1913]. Carapace and abdomen smooth, not ornamented (43, 45). *Penn.,* N. Am.—FIG. 80,*2.* **L. schucherti* (PETR.), Ill.; *2a,* dorsal side, ×2.4; *2b,* ventral side, ×2 (76).

Phrynomartus PETRUNKEVITCH, 1945 [**Eophrynus waechteri* GUTHÖRL, 1938]. Carapace ornamented, abdomen with 4 rows of tubercles and 4 posterior spurs. *Carb.,* Eu.—FIG. 80,*4.* **P. waechteri* (GUTHÖRL), Saar; ×3.3 (76).

Elaverimartus PETRUNKEVITCH, 1953 [**E. pococki*]. Carapace semicircular, without eyes, granular. Second and 3rd coxae rectangular (cylindrical), 4th coxae triangular (45). *U.Carb.,* Eu.—FIGS. 80,*6;* 81,*2.* **E. pococki,* Scot.; 80,*6,* dorsal side, ×7.5; 81,*2,* ventral side, ×6 (76).

Planomartus PETRUNKEVITCH, 1953 [**Anthraco-*

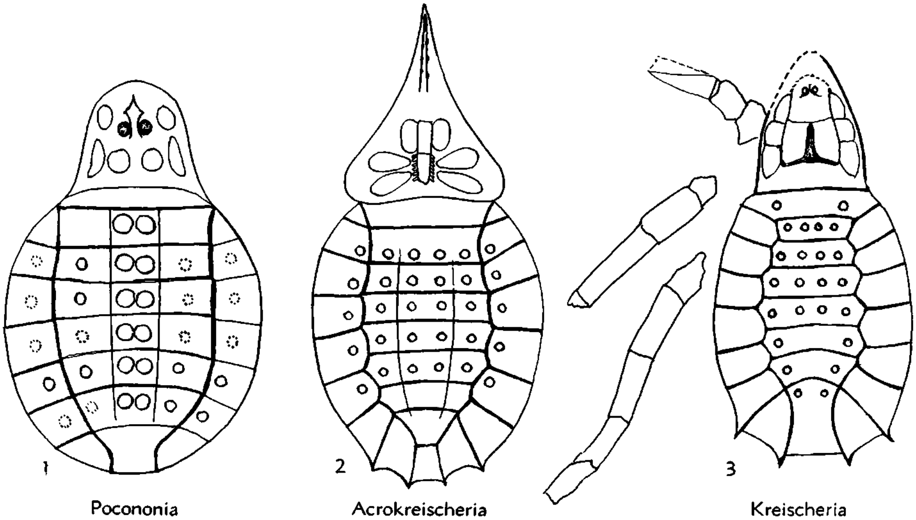


FIG. 76. Eophrynidae. *1, Pocononia whitei,* Penn., Va., ×6.6. *2, Acrokreischeria verrucosa,* U.Carb., Wales, ×1.8. *3, Kreischeria wiedei,* U.Carb., Ger., ×1 (76) (p. P111-P112).

martus krejcii KUŠTA, 1883]. Carapace subtriangular, rounded in front. Eighth tergite entire, more or less hexagonal (45). *Carb.*, Eu.—FIG. 80,*5*. **P. krejcii* (KUŠTA), Czech.; dorsal side (dotted lines indicate original derivation of 8th tergite from a median and a pair of marginal plates fused into a single plate), ×3 (76).

Subclass CAULOGASTRA Pocock, 1893

[Type: *Araneus* CLERCK, 1757]

Arachnida with a constriction between cephalothorax and abdomen, due to a modification of the 1st abdominal segment (or

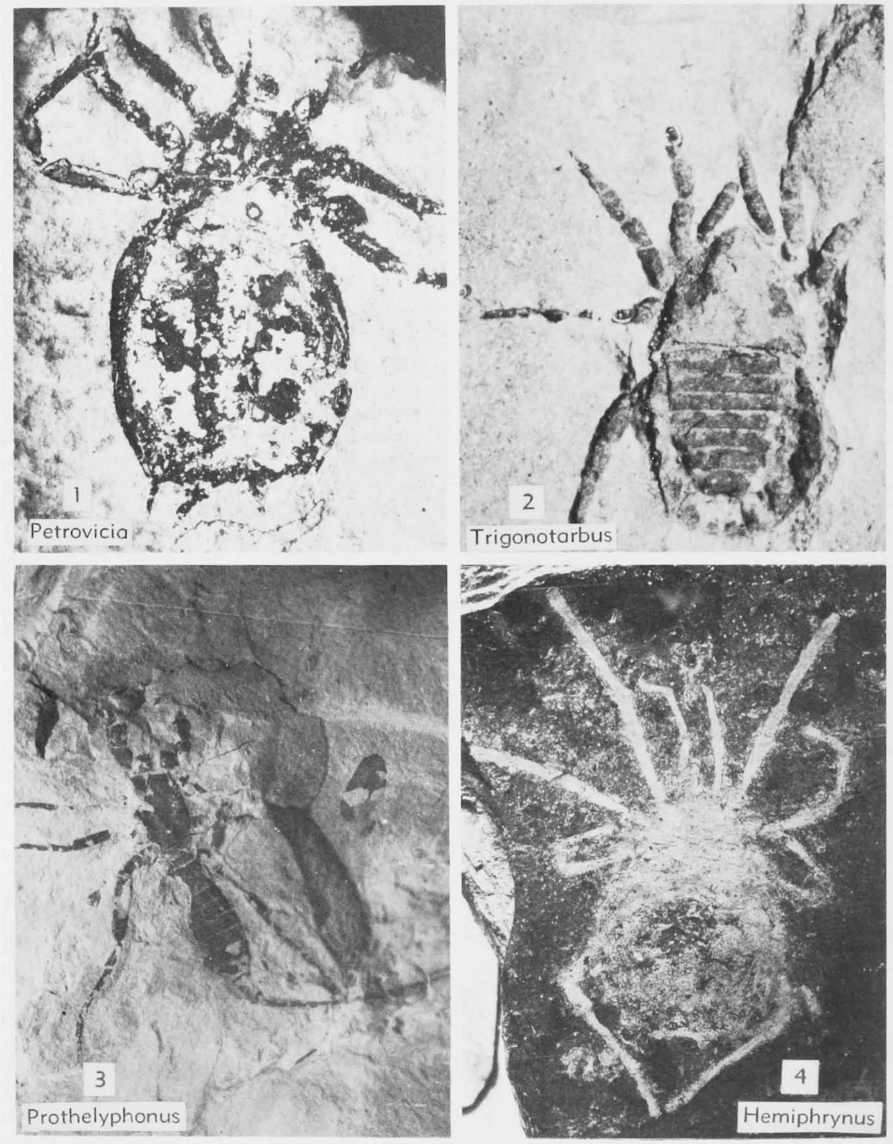


FIG. 77. Trigonotarbida *(1,2,4)*; Thelyphonida *(3)*. *1, Petrovicia proditoria,* U.Carb., Czech.; photograph of holotype, ×1.3. *2, Trigonotarbus johnsoni,* U.Carb., Eng.; photograph of holotype, ×6. *3, Prothelyphonus bohemicus,* U.Carb., Czech.; photograph of holotype, ×0.65. *4, Hemiphrynus longipes,* U.Carb., Czech.; photograph of holotype, ×0.9 (76) (p. P110-P120).

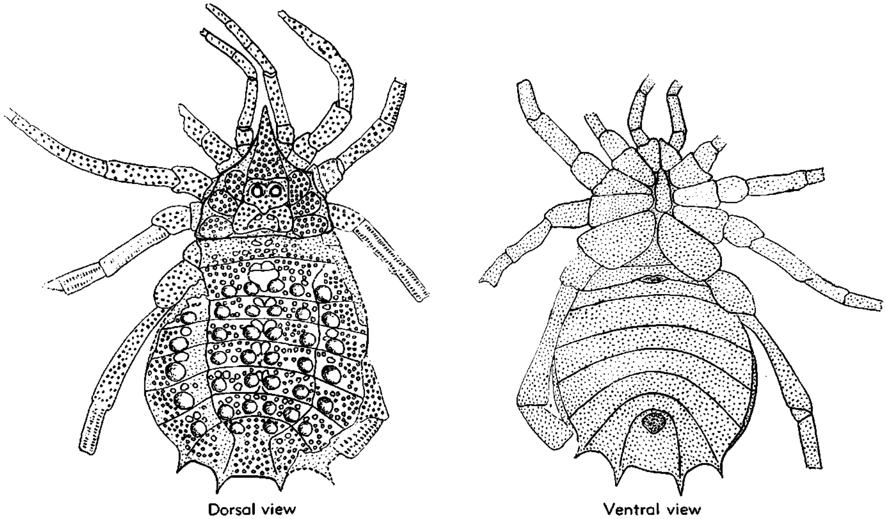


Fig. 78. *Eophrynus prestvici,* U.Carb., Eng.; dorsal and ventral sides of lectotype, ×1.5 (76) (p. P112).

2nd, when the 1st is lost) into a pedicel permitting greater independent motion of the abdomen as a unit. Existence of a pedicel not always apparent when the latter is concealed under the posterior edge of the carapace or under the projecting anterior edge of the tergite of the abdominal segment following upon the pedicel (45). *?Dev., Carb.-Rec.*

Superorder LATISTERNA Petrunkevitch, 1949

[Type: *Eukoenenia* Börner, 1901]

Caulogastra with pedipalpal coxae widely separated by anterior sternal plate and devoid of maxillary lobes (Fig. 82,*2b*). *Jur.-Rec.*

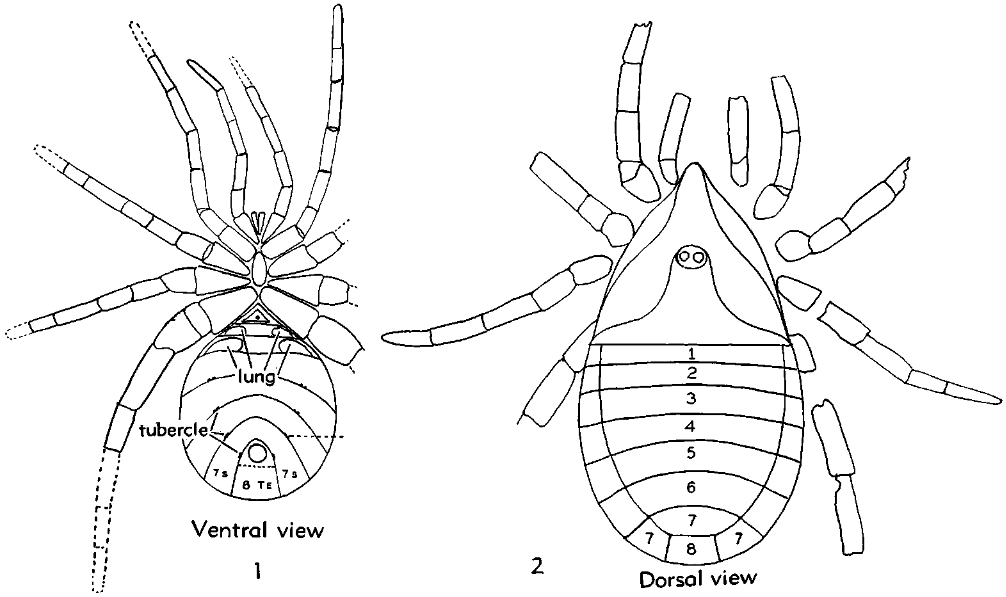


Fig. 79. *Trigonotarbus johnsoni,* U.Carb., Eng.; *1,* ventral side, ×6.8; *2,* dorsal side showing details of external morphology, ×9 (76) (p. P112).

Order PALPIGRADIDA Thorell, 1888

[*nom. correct.* Pearse, 1936 (*pro* Palpigradi Thorell, 1888)] [=Microthelyphonida[1] Grassi & Calandruccio, 1885] [Type: *Eukoenenia* Börner, 1901 (=*Koenenia* Grassi-C., 1885, *non* Beushausen, 1884)]

Carapace segmented, composed of 4 sclerites: large propeltidium extending just beyond 2nd pair of legs; pair of very small, triangular mesopeltidia belonging to the segment bearing 3rd pair of legs; and metapeltidium belonging to last thoracic segment, bearing 4th pair of legs (Fig. 82, *2a,b*). Abdomen composed of 11 segments; 12th segment lost, 9th to 11th segments reduced to a pygidium bearing at its end a dorsal, multijointed whip or flagellum which gives the creature the appearance of a minute whip scorpion (Fig. 82,*1a*). Mouth anteroventral, provided with anterior and posterior lip, the latter hinged to 1st sternal plate which is in reality sternite 2+3 separating widely the pedipalpal and 1st pedal coxae. This is followed by 2 independent mesosternites and a metasternite (Fig. 82,*2b*). All coxae movable, none with maxillary lobes. Chelicerae 3-jointed, chelate (Fig. 82,*2c*),

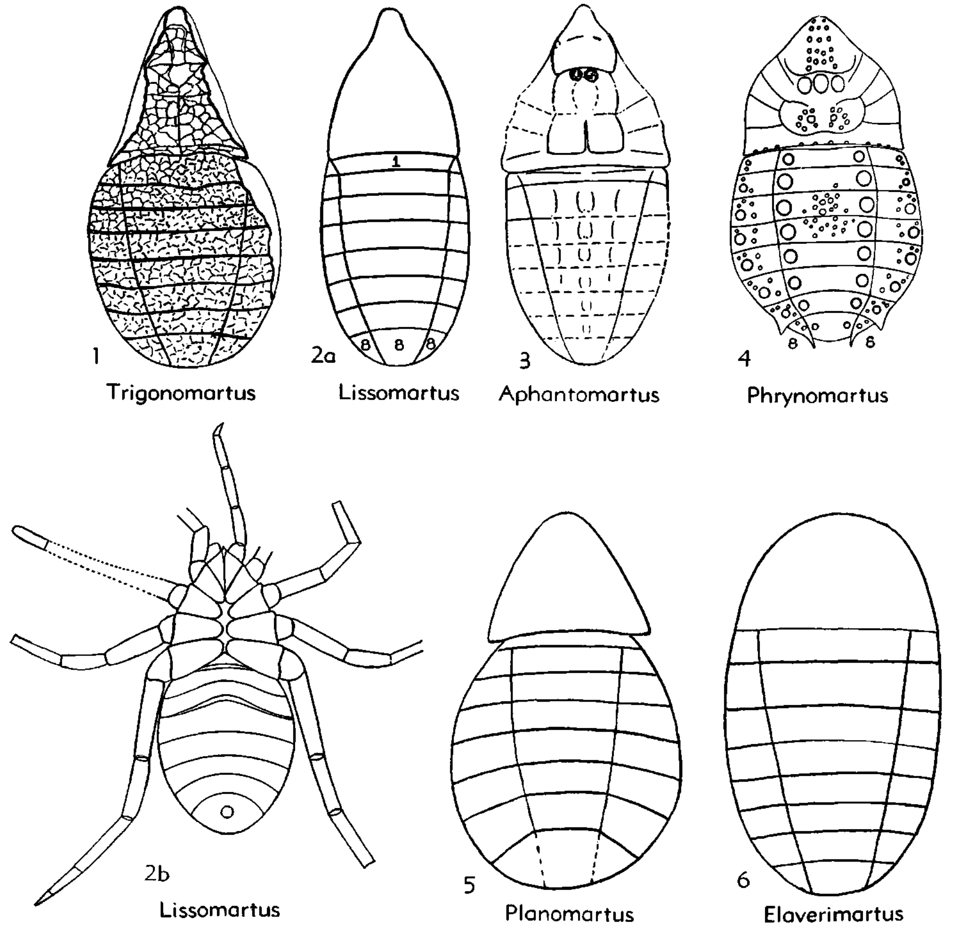


Fig. 80. Trigonomartidae. *1, Trigonomartus pustulatus,* Penn., Ill., ×2.8; *2, Lissomartus schucherti,* Penn., Ill.; *2a,b,* dorsal and ventral sides, ×2.4; *3, Apantomartus araeolatus,* U.Carb., Eng., ×3; *4, Phrynomartus waechteri,* U.Carb., Saar, ×3.3; *5, Planomartus krejcii,* U.Carb., Czech., ×3; *6, Elaverimartus pococki,* U.Carb., Eng.; dorsal side of body, ×7.5 (76) (p. P113).

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[1] The name Microthelyphonida has priority over Palpigradi, but after the publication of Thorell's paper, in which the latter name was proposed, has not been used nor is generally known at present. Since there is no International Rule prohibiting the use of a later name in the case of an order, it is not reasonable to replace a generally accepted name by an obsolete one.

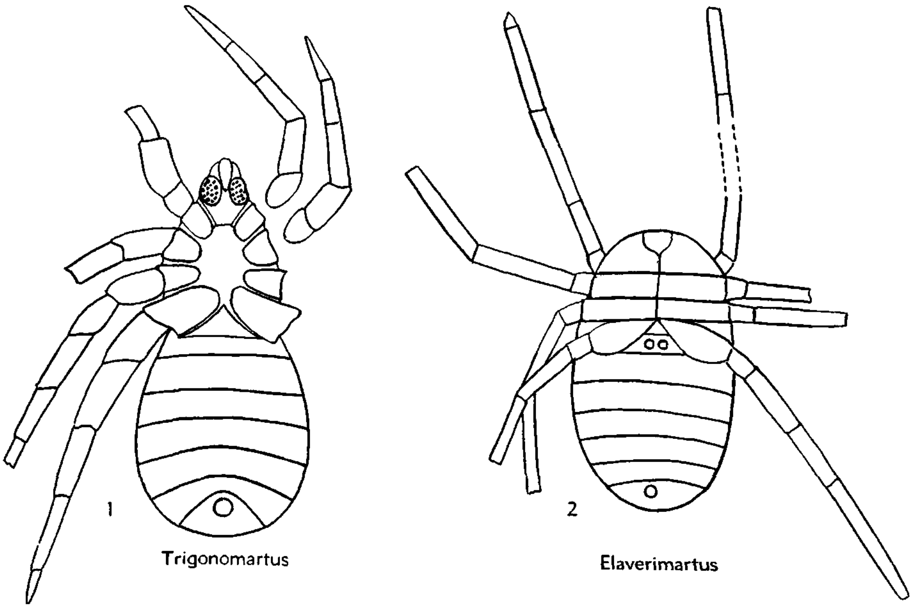

Fig. 81. Trigonomartidae. *1, Trigonomartus pustulatus,* Penn., Ill., ventral side, ×2.9; *2, Elaverimartus pococki,* U.Carb., Eng., ventral side, ×6 (76) (p. P113).

their movable finger lateral in position. Pedipalpi pediform, used for walking (hence the name Palpigradi), 6-jointed, but without patella, with metatarsus subdivided into 2 segments and tarsus into 3 segments and with a pair of claws on a pseudonychium (Fig. 82,*2d*). First legs tactile, longer and stouter than pedipalpi, 7-jointed, with a patella, but metatarsus subdivided into 4 segments and tarsus into 3; 2nd and 3rd legs 7-jointed, without subsegmentation; 4th legs also 7-jointed, but with tarsus subdivided into 2 segments. All pedal tarsi end in 2 claws on a pseudonychium.

Fore-gut without a gizzard, esophagus opening directly into mid-gut, while the pharynx serves as a filter. Thoracenteron with single pair of pouchlike diverticles; chylenteron in the shape of a lobed sac. Stercoral pouch wanting; hind-gut short; anus terminal, without operculum. Heart restricted to abdomen, with 4 pairs of ostia. Book lungs and tracheal tubes wanting, respiration taken care of by 3 pairs of ventral evertible sacs situated on 4th to 6th segments. Nervous system concentrated in the cephalothorax, but with 3 neuromeres in 2nd abdominal segment. Sexes separate. Oviparous. *Jur.-Rec.*

DISCUSSION

The Palpigradida are soft-bodied arachnids of very small size, varying from 0.65 to 2.8 mm., and represented by a single Recent family with 4 genera and 21 species. Most of these species are found in southern Europe, southern United States of America and south to Paraguay and Chile, one in Asia and 2 in Africa. A single fossil species was found in the Solnhofen lithographic shale of Germany (Jur.), mistaken for an insect by its discoverer, later correctly referred by Haase to the order Palpigradida and considered by him to be sufficiently different from its Recent relative *Eukoenenia* to require the erection of a special family. The difference between the Recent family Eukoeneniidae and the fossil family Sternarthronidae is in the presence of separate sternites in the latter, corresponding to the single, large sternite 2+3 of *Eukoenenia.*

Family EUKOENENIIDAE Petrunkevitch, 1955, nov.

[*nom. nov.* Petr., *pro* Koeneniadae Grassi & Calandruccio, 1885] [Type: *Eukoenenia* Börner, 1901, proposed as subgenus of *Koenenia* Grassi-C. without knowledge that *Koenenia* was preoccupied]

First sternite large, resulting from complete fusion of sternites 2 and 3. *Rec.*

Eukoenenia BÖRNER, 1901 [**Koenenia mirabilis* GRASSI & CALANDRUCCIO, 1885] [=*Koenenia* GRASSI-C., 1885 (*non* BEUSHAUSEN, 1884)]. *Rec.*—FIG. 82,*1*. **E. mirabilis* (GRASSI-C.); *1a,* dorsal side, ×17 (68); *1b,* side view of cephalothorax, ×17 (64).

Family STERNARTHRONIDAE
Haase, 1890

Thoracic sternites 2 and 3 separated from each other by intersegmental membrane. *Jur.,* Eu.

Sternarthron HAASE, 1890 [**S. zitteli*]. Ger.,—FIG. 83. **S. zitteli; 1,* dorsal side, ×1; *2,* same, ventral side showing sternites, ×3 (67).

Superorder CAMAROSTOMATA
Petrunkevitch, 1949

[Type: *Thelyphonus* LATREILLE, 1802]

Caulogastra with pedipalpal coxae permanently fused along line of contact, their common dorsal wall forming a camarostome in the shape of an elongated depression semicircular in cross section into which the upper lip fits snugly, leaving a slitlike cavity (Fig. 84,*2*). The periphery of this cavity opens to the outside and serves for admission of food, while the mouth opens into it at its posterior end. The camarostome serves not only for admission of food to the mouth, but also as a filter, for which pur-

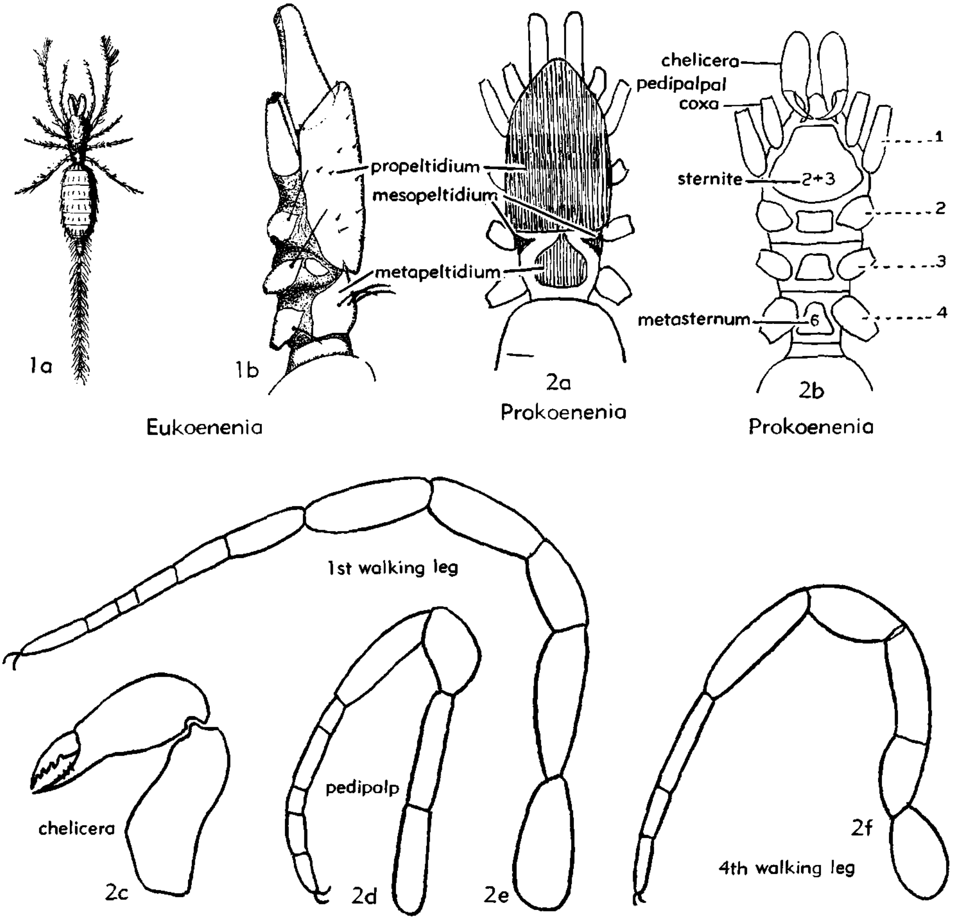

FIG. 82. External morphology of Palpigradida. *1, Eukoenenia mirabilis,* Rec., Italy; *1a,* ×17 (68); *1b,* side view of its cephalothorax, enlarged (64). *2, Prokoenenia wheeleri,* Rec., Calif.; *2a,* dorsal side of cephalothorax, showing segmented carapace, enlarged; *2b,* ventral side showing coxosternal region; *2c,* chelicera; *2d,* pedipalp; *2e,* 1st leg; *2f,* 4th leg (76) (p. P116-P118).

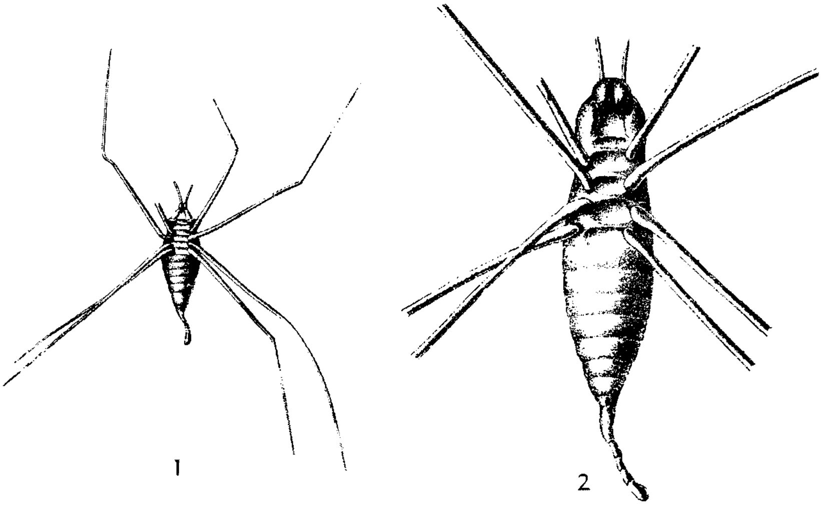

FIG. 83. *Sternarthron zitteli,* only known fossil palpigrade, U.Jur., Ger.; *1,* complete specimen, ×1; *2,* ventral side of body, ×3 (67) (p. P118).

pose its wall, as well as the wall of the upper lip, is covered with fine bristles. Neither pedipalpal nor pedal coxae have any maxillary lobes or maxillary glands, but in some males the pedipalpal coxae are produced into long processes with only ornamental use (Fig. 84,*1*).

Camarostomata breathe by means of book lungs, wherein they differ from Ricinuleida which also possess a camarostome, but breathe by means of tracheal tubes. *Carb.-Rec.*

Order THELYPHONIDA Latreille, 1804

[*nom. transl.* CAMBRIDGE, 1872 (*ex et correct. pro* Thelyphoni LATREILLE, 1804)] [=Uropygi THORELL, 1882 (*partim*); Holopeltidia BÖRNER, 1904] [Type: *Thelyphonus* LATREILLE, 1802]

Carapace entire, with doublure in front and slight infolding on sides, usually longer than wide, with or without eyes. Abdomen composed of 12 segments, 1st segment greatly shortened, 10th to 12th segments reduced to a pygidium ending in a dorsal, multijointed whip or flagellum (Fig. 33). Chelicerae 2-jointed, retrovert. Pedipalpi 6-jointed, stout, raptorial, with terminal joint pointed for piercing and holding by flexion against preceding joint which sometimes has a short projection at its anteroventral end, serving to hold an object stronger and making the palp subchelate. Pedipalpal coxae fused permanently along line of contact, which remains visible, while both contact walls disappear and leave a common cavity within the fused coxae. First pedal coxae slender and small, far apart and like all other coxae devoid of maxillary lobes. First legs tactile, without patella, with tarsus subdivided into 9 segments; 2nd to 4th legs, with patella, their tarsi always subdivided into 3 segments and bearing 2 claws. Sternum composed of 3 or 4 successive sternites; 1st large, triangular, with apex directed backward, 2nd and 3rd minute; 4th (called metasternite) situated between 4th coxae and easily mistaken for 1st abdominal sternite which is usually concealed in a fold of intersegmental membrane (Fig. 84,*1*). Lower lip lacking; mouth opens directly into camarostome. Fore-gut with pharynx, esophagus and gizzard, which is poorly developed, so that pharynx is main pumping organ. Thoracenteron with 4 pairs of diverticles; chylenteron with 7 or 8 pairs, its median tube enlarged posteriorly and serving in place of a stercoral pouch which is lacking. Hind-gut short. Anus terminal, without operculum. Heart with 9 pairs of ostia, 1st and 2nd pairs in cephalothorax. Two pairs of book lungs in 2nd and 3rd abdominal segments. Seven abdominal neuromeres incorporated in thoracic ganglionic mass, last 5 (8th to 12th) neuromeres forming an abdominal ganglionic mass in

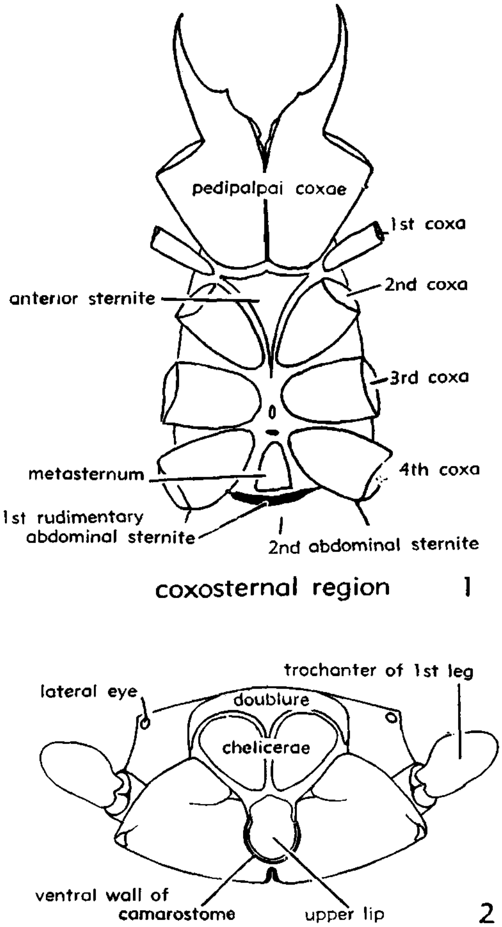

FIG. 84. Morphology of Thelyphonida. *1*, Coxosternal region of male *Labochirus proboscideus*, a whip scorpion from Ceylon, enlarged. *2*, Transverse section through the head of *Mastigoproctus giganteus*, a whip scorpion from Arizona, showing camarostome formed by a dorsal depression of the fused pedipalpal coxae and upper lip fitting the depression (76).

8th and 9th segments. Pair of median and 3 pairs of lateral eyes on carapace usually present in Recent species and some fossil ones. Pair of excretory coxal glands in the cephalothorax with openings at base of 1st coxae. Poison glands lacking, but so-called anal glands, situated in abdomen, with a pair of openings each closed by an operculum on 12th segment, produce a volatile and highly irritating fluid that turns immediately into gas used for protection. Sexes separate, recognizable by secondary sexual characters. Males with accessory sexual glands of fenestrated type, situated dorsally to pair of tubular testes. Females with pair of tubular ovaries. Oviparous. *Carb.-Rec.*

DISCUSSION

Thelyphonida, commonly called whip scorpions, are tropical and subtropical arachnids varying in size from 18 to 65 mm. They represent one of the most stable orders among all arthropods, having retained their fundamental structure from the Carboniferous to the present, the Carboniferous genera belonging to the same family with the Recent ones. Nevertheless, the number of genera increased from 2 in the Carboniferous to 10 in the present fauna with 70 living species, distributed over Asia, Oceania and America; not found in Europe, Africa and Australia.—FIG. 33,*2*. *Mastigoproctus giganteus* (LUCAS), Rec., Mex.; ×1.5.

Family THELYPHONIDAE Lucas, 1835

Characters of order. *Carb.-Rec.*

Geralinura SCUDDER, 1884 [**G. carbonaria*]. Carapace oval, without eyes. *Penn.*, N.Am.—FIG. 85,*1*. **G. carbonaria*, Ill.; *1a*, dorsal side, ×4; *1b*, sternum, ×8.2 (76).—FIG. 85,*3*. *G. similis* PETRUNKEVITCH, Ill.; *3a*, ventral side showing coxosternal region, appendages and flagellum, ×2.6; *3b*, dorsal side of same, ×2.6 (76).

Prothelyphonus FRITSCH, 1904 [**Thelyphonus bohemicus* KUŠTA, 1884]. Carapace an elongated hexagon with eyes. *Carb.*, Eu.-N.Am.—FIGS. 77,*3*; 85,*4*. **P. bohemicus* (KUŠTA), Czech.; 77,*3*, holotype, photo, ×0.67; 85,*4*, dorsal side with missing portions of appendages restored, ×1.9 (76).—FIG. 85,*5*. *P. britannicus* (POCOCK), Eng.; ventral side, ×5.5 (76).—FIG. 85,*2*. *P. giganteus* (PETR.), Ill.; *2a*, dorsal side, ×3; *2b*, ventral side with appendages, ×3 (76).

Thelyphonus LATREILLE, 1802 [**Phalangium caudatum* LINNÉ, 1758]. Carapace with eyes. Pair of anal gland openings (formerly called "ommatidia") on last pygidial segment. *Mio.-Rec.* [*T. hadleyi* PIERCE, Mio., Calif.].

FIG. 85. Thelyphonida. *1*, *Geralinura carbonana*, Penn., Ill.; *1a*, ×4; *1b*, sternum, ×8.2. *2*, *Prothelyphonus giganteus*, Penn., Ill.; *2a,b*, dorsal and ventral, ×3. *3*, *Geralinura similis*; *3a,b*, Penn., Ill., ventral and dorsal, ×2.6. *4*, *Prothelyphonus bohemicus*, U.Carb., Czech., ×1.9. *5*, *Prothelyphonus britannicus*, U.Carb., Eng., ×5.5 (76) (p. P120).

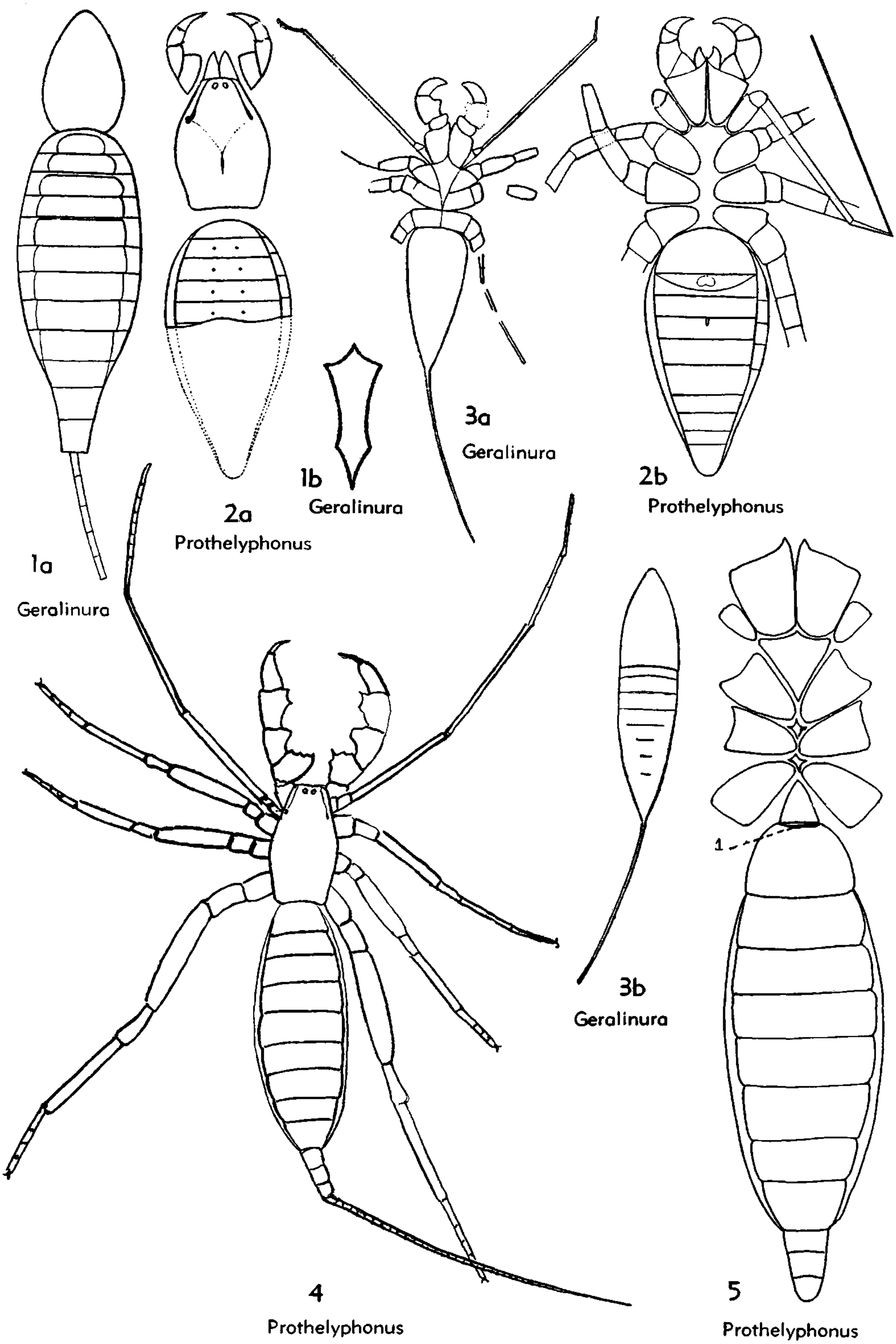

Fig. 85. *(See facing page.)*

Order SCHIZOMIDA Petrunkevitch, 1945

[=Tartarides CAMBRIDGE, 1872; Colopyga COOK, 1899; Schizopeltidia BÖRNER, 1904] [Type: *Schizomus* COOK, 1899 (*nom. subst. pro Schizonotus* THORELL, 1897, *nom. subst. pro Nyctalops* CAMBRIDGE, 1872 (*non Nyctalops* WAGLER, 1832)]

Carapace segmented (Fig. 86,*1*), without doublure and without eyes. Abdomen composed of 12 segments, the 1st considerably abbreviated, the 9th to 12 reduced to a pygidium. Telson short, with 1 to 7 segments. Pedipalpal coxae fused and forming a camarostome as in Thelyphonida. First pedal coxae wide apart, 2nd coxae separated by triangular sternite whose apex is directed backwards, 3rd coxae contiguous in middle line, 4th coxae separated by metasternite (Fig. 86,*2*). Chelicerae 2-jointed, chelate. Pedipalpi raptorial, their terminal joint pointed. First pair of legs tactile, without patella, tarsus subdivided into 3 to 8 segments. Second to 4th legs with patella, tarsus 2- to 5-jointed, ending with onychium bearing 3 claws. Pair of book lungs in 2nd abdominal segment. Heart restricted to abdomen with 5 pairs of ostia. Anterior 4 abdominal neuromeres incorporated in the thoracic ganglionic mass, 5th to 12th neuromeres forming an abdominal ganglionic mass in the 2nd abdominal segment. Thor-

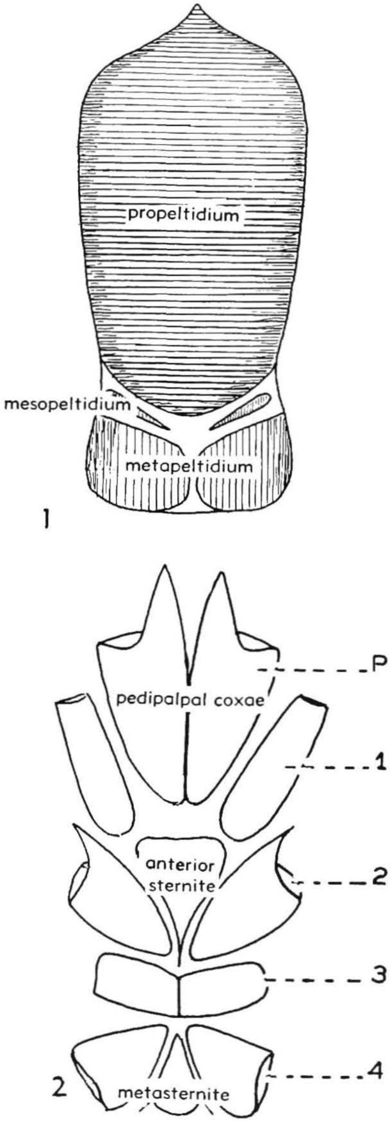

FIG. 86. External morphology of Schizomida. *1*, Segmented carapace of *Schizomus crassicaudatus*, from Ceylon. *2*, Coxosternal region of *Trithyreus pentapeltis*, from California (76).

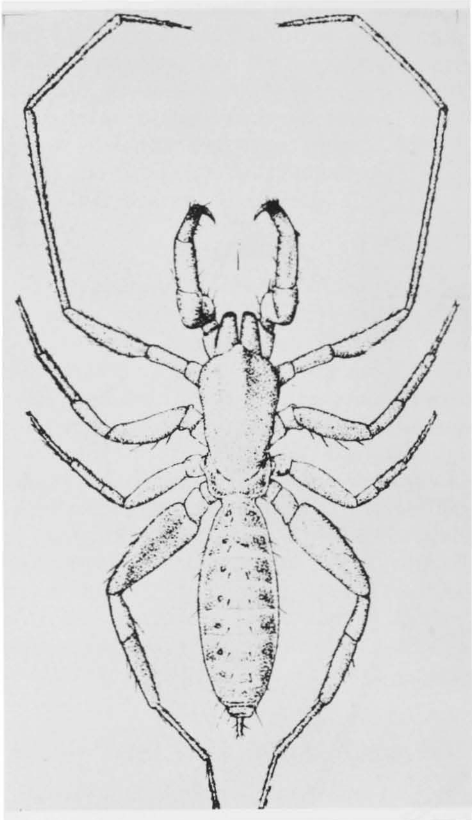

FIG. 87. *Schizomus peradeniyensis*, Rec., from Ceylon; female, ×17 (by permission from *Traité de Zoologie*, tome 6, sous la direction du PR. GRASSÉ, Masson & Cie., Editeurs, Paris) (p. P123).

acenteron with 1 pair of diverticles, chylenteron with 7 pairs. Anal glands lacking. Sexes separate, outwardly distinguished by structure of telson (flagellum). *U.Tert. (?Plio.)-Rec.*

Schizomida are soft-bodied, small arachnids from 2 to 7 mm. in length. They are found in the tropical and subtropical regions of the world. Recent Schizomida represent a single, very uniform family with only 28 species and 3 closely related genera. Fossil Schizomida are known only from the Upper Tertiary.

Family SCHIZOMIDAE Chamberlin, 1922

[=Schizonotidae THORELL, 1888; Hubbardiidae[1] COOK, 1899]

First tarsus 8-jointed, others 3-jointed. Telson 1- to 4-jointed (39). *?Plio., Rec.*

Calcoschizomus PIERCE, 1950 [**C. latisternum*]. Telson rodlike, unsegmented (46). *?Plio.,* N.Am. —FIG. 90,*2*. **C. latisternum,* Ariz.; ×4 (77).

Schizomus COOK, 1899 [*pro Schizonotus* THORELL, 1888 (*non* RATZEBURG, 1852); *etiam Nyctalops* CAMBRIDGE, 1872 (*non* WAGLER, 1832)] [**Nyctalops crassicaudatus* CAMBRIDGE, 1872]. *Rec.*—FIG. 86,*1*. *S. crassicaudatus* (CAMBRIDGE), Ceylon; carapace, ×30 (76).—FIG. 87. *S. peradeniyensis* GRAVELY, Ceylon; female, ×17 (75).

Family CALCITRONIDAE Petrunkevitch, 1945

First tarsus 7-jointed, 2nd 5-jointed, 3rd and 4th 4-jointed. Telson 3- to 7-jointed (39). *?Plio.*

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[1] The name Hubbardiidae was proposed by COOK for his genus *Hubbardia,* which was later proved to be a synonym of *Nyctalops* CAMBRIDGE, a preoccupied name changed by THORELL to *Schizonotus.* This name also proved to be preoccupied and was changed to *Schizomus.* Still later, CHAMBERLIN quite correctly changed the family name Schizonotidae to Schizomidae.

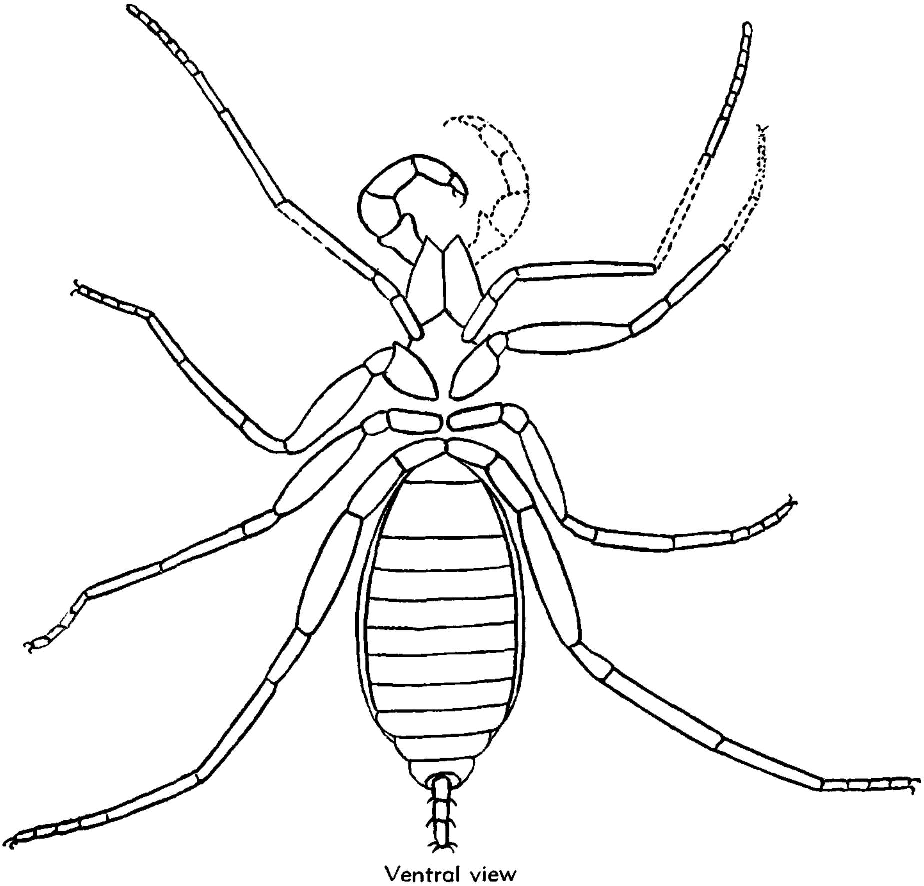

FIG. 88. *Calcitro fisheri,* ?Plio., Ariz.; ventral side, ×21 (76) (p. P124).

Calcitro Petrunkevitch, 1945 [**C. fisheri*]. Telson 3-jointed. Order of legs 1432. *?Plio.*, N.Am.—Figs. 88, 89. **C. fisheri*, Ariz.; 88, ventral side, ×15; 89, photo of holotype, ×21 (76).

Onychothelyphonus Pierce, 1950 [**O. bonneri*]. Telson 7-jointed. Order of legs 4132 (46, 47). *?Plio.*, N.Am.—Fig. 90. **O. bonneri*, Ariz.; *1a*, ventral side, ×10; *1b*, telson, ×50 (77).

Order KUSTARACHNIDA
Petrunkevitch, 1913

[*nom. correct.* Petr., herein (*pro* Kustarachnae Petr., 1913)]
[Type: *Kustarachne* Scudder, 1890]

Presumptive Camarostomata with pedipalpal coxae completely fused along the line of contact, leaving no trace of their paired origin. All coxae triangular, contiguous, radiating fanlike from a minute sternum. Abdomen segmented, ending in a small pygidium, without telson. Carapace entire. Pedipalpi chelate. Trochanters of legs 2-jointed, distal joint conical. Legs slender and long. Chelicerae not known (34, 45). *Penn.*

Family KUSTARACHNIDAE
Petrunkevitch, 1913

Characters of order. *Penn.*, N.Am.

Kustarachne Scudder, 1890 [**K. tenuipes*]. Carapace evenly rounded, with pair of eyes on transversely ellipsoidal tubercle. *Penn.*, N.Am.—Fig. 91,*1*. **K. tenuipes*, Ill.; *1a*, ventral side, ×4; *1b*, carapace, ×4 (76).—Fig. 91,*2*. *K. conica* Petrunkevitch, Ill.; ventral side, ×4 (76).—Fig. 91,*3*. *K. extincta* (Melander), Ill.; *3a*, ventral side, ×4; *3b*, carapace, ×4 (76).

Superorder LABELLATA
Petrunkevitch, 1949

[Type: *Araneus* Clerck, 1757]

Caulogastra with mouth anteroventral between 2 lips, with pedipalpal coxae contiguous, but free (43). *?Dev., Carb.-Rec.*

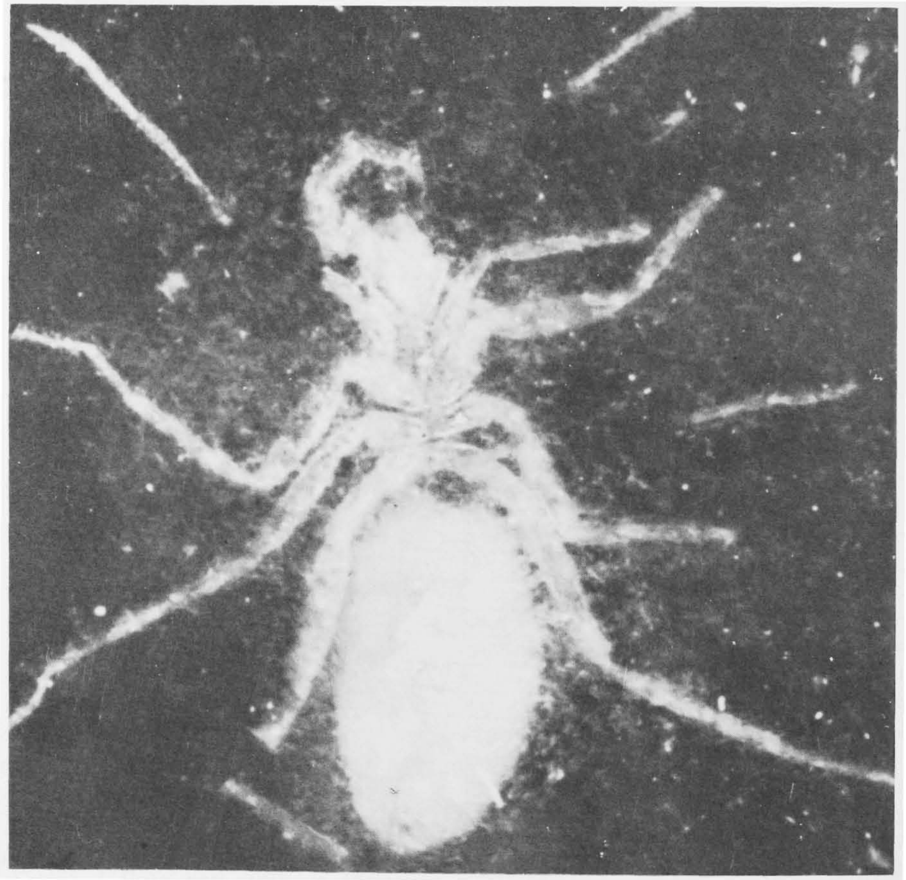

Fig. 89. *Calcitro fisheri*, ?Plio., Ariz.; photo of holotype, ×21 (76) (p. P124).

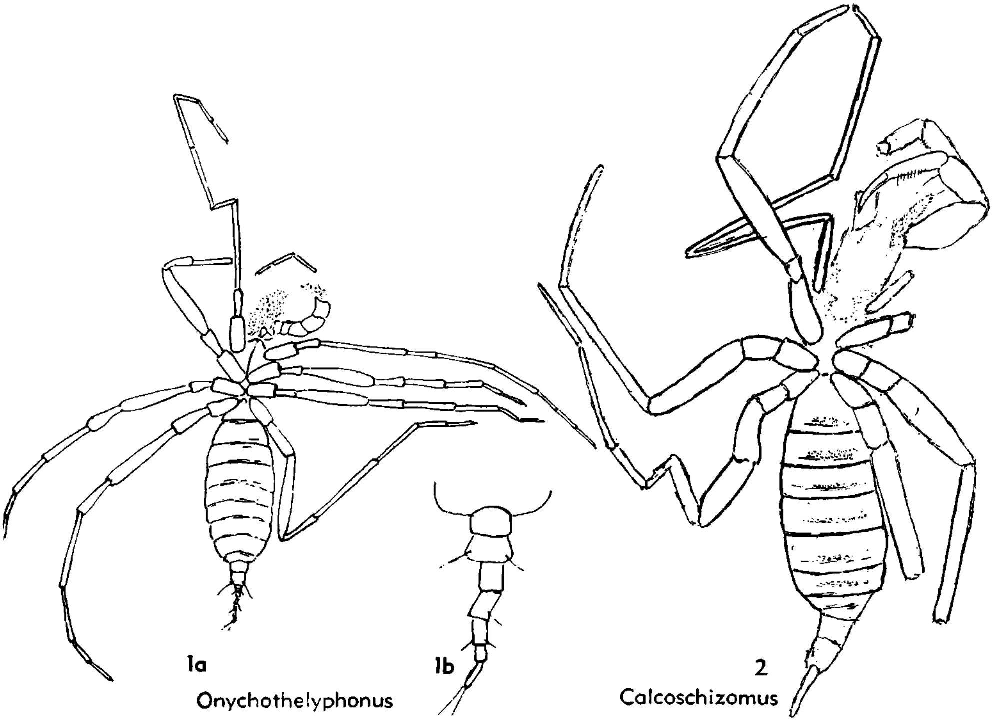

FIG. 90. Schizomida. *1, Onychothelyphonus bonneri,* ?Plio., Ariz., *1a,* ×10; *1b,* flagellum, ×50. *2, Calcoschizomus latisternum,* ?Plio., Ariz., ×4 (p. P123-P124).

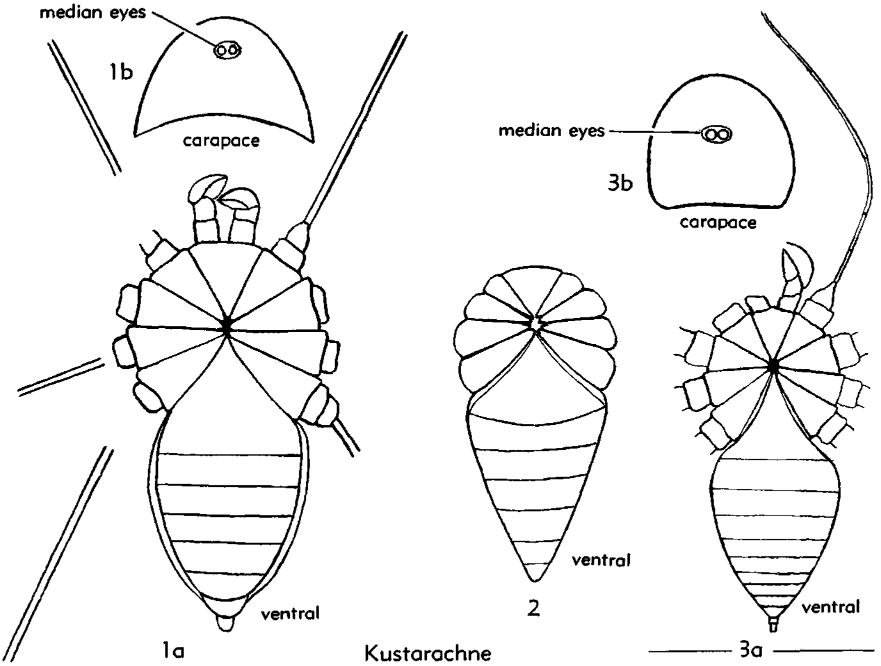

FIG. 91. Kustarachnida. *1, Kustarachne tenuipes,* Penn., Ill., *1a,* ×4; *1b,* carapace, ×4. *2, Kustarachne conica,* Penn., Ill., ×4. *3, Kustarachne extincta,* Penn., Ill.; *3a,* ×4; *3b,* carapace, ×4 (76) (p. P124).

Order PHRYNICHIDA Petrunkevitch, 1945

[=Phryneides[1] GERVAIS, 1844; Amblypygi THORELL, 1883] [Type: *Phrynichus* KARSCH, 1879 (=*Phrynus* LAMARCK, 1801; =*Phrynus* OLIVIER, 1793, *secundum* GERVAIS, 1844, p. 2, footnote; source not mentioned and not known)]

Labellata with raptorial pedipalpi, modified 1st legs and segmented abdomen ending in a pygidium.

Carapace entire, flat, usually wider than long, with pair of median eyes and 3 pairs of lateral eyes. Chelicerae 2-jointed, retrovert. Pedipalpi raptorial, powerful, long, 6-jointed, with terminal joint pointed. Pedipalpal coxae free, movable, without maxillary lobes or glands. All pedal coxae movable, 1st pair small, widely separated and wedged in between pedipalpal and 2nd coxae (Fig. 92). Sternal plate single, with 3 or 4 separate sclerites arising from it in a median row and representing trito-, tetra-, penta-, and when present, hexasternite, usually called metasternite. Tritosternite long and narrow, extending forward between pedipalpal coxae. First legs slender, with very long, multijointed, flexible, antenna-like tarsi, held away from the ground and used as organs of touch; 2nd, 3rd and 4th tarsi 4- or 5-jointed, ending in a pair of claws which are in some genera accompanied by a pulvillus. Abdomen composed of 12 segments, the 12th reduced to a pygidium, without a telson.

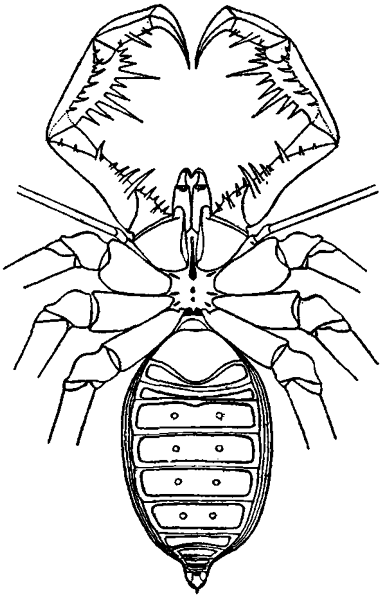

FIG. 92. *Tarantula fuscimana*, Rec., from Panama, showing ventral side of body and raptorial pedipalpi, ×2 (76).

Fore-gut with pumping pharynx, short esophagus and pumping gizzard. No pharyngeal filter, but a rough preoral brush serving as filter. Thoracenteron with 4 pairs of diverticles, chylenteron highly branched. Anus terminal, without operculum. Two pairs of book lungs with openings on 2nd and 3rd sternites. Pair of ventral, evertible sacs present in some Recent species. Heart limited to abdomen, with 6 pairs of ostia. Sexes separate. Oviparous. Female carries eggs attached to venter of abdomen. *Carb.-Rec.*

Phrynichida are harmless creatures possessing neither offensive nor defensive poison glands of any kind. Denizens of tropical countries, varying in size of body from 8 to 37 mm.; 60 living and 4 fossil species. Two families: Tarantulidae, strictly Recent, and Phrynichidae.

Family PHRYNICHIDAE Pocock, 1900

[=Phrynidae SUNDEVALL, 1833]

Tarsi without pulvillus. *Carb.-Rec.*

Phrynichus KARSCH, 1879 [**Phalangium reniforme* LINNÉ, 1758]. Fourth tibia not subsegmented. *Rec.*—FIG. 36. *P. reniformis* (LINNÉ), Asia; dorsal view (Cuvier).

Graeophonus SCUDDER, 1890 [**G. carbonarius*]. Carapace with rounded median projection bearing tubercle with pair of eyes and with longitudinal groove in posterior half (45). *Carb.*, Eu.-N.Am.—FIG. 93,*1*. **G. carbonarius*, Ill.; *1a,c*, dorsal and ventral sides, ×3; *1b*, dorsal side of abdomen of another specimen, showing muscular attachments, ×3 (76).—FIG. 93,*2*. *G. anglicus* POCOCK, Eng.; *2a*, carapace (eyes not preserved) and appendages, ×4 (76); *2b,c*, holotype, dorsal side showing eyes and ventral side showing all but 1st legs, ×2.5 (78).

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[1] GERVAIS' name Phryneides, used by him as the name of an order, was based on the generic name *Phrynus* LAMARCK, 1801 (=*Phrynus* OLIVIER, 1793). It had for its type *Phalangium reniforme* LINNÉ and it has been shown later that *Phalangium lunatum* PALLAS, 1772, placed by FABRICIUS in his genus *Tarantula*, 1793, is a synonym of *P. reniforme*, but that the specimen of *P. reniforme* used by FABRICIUS as type of his genus *Tarantula* was in reality a *Phalangium palmatum* HERBST. So *palmatum* is now the type of *Tarantula* FABRICIUS and *reniforme* the type of *Phrynichus*, *nom. nov.* proposed by KARSCH because the 2 species, *reniforme* and *lunatum*, are not co-generic. Phryneides of GERVAIS has not only priority over Amblypygi THORELL, but is derived from the name of the genus in which LINNÉ's species was correctly placed. The name Phrynichida is simply a substitute for Phryneides in accordance with rule 54(b) of the Copenhagen Decisions.

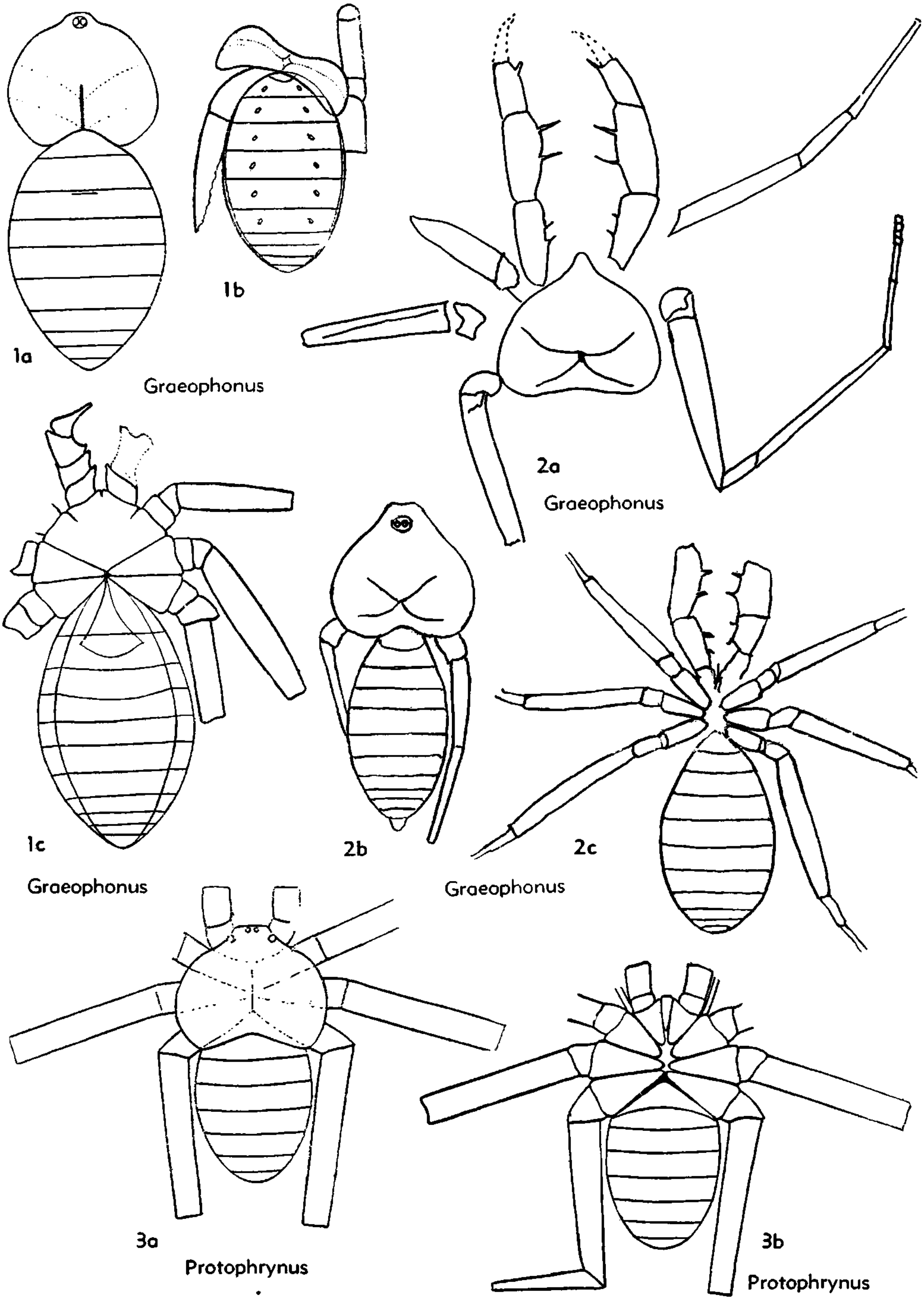


FIG. 93. Phrynichida. *1, Graeophonus carbonarius,* Penn., Ill.; *1a,c,* dorsal and ventral sides of holotype, ×3; *1b,* dorsal side of another specimen showing paired attachments of dorsoventral muscles, ×3. *2, Graeophonus anglicus,* U.Carb., Eng.; *2a,* carapace and appendages, ×4; *2b,* dorsal side showing eyes, ×2.5; *2c,* ventral side of holotype, ×2.5. *3, Protophrynus carbonarius,* Penn., Ill.; *3a,b,* dorsal and ventral, ×3 (76) (p. P126-P128).

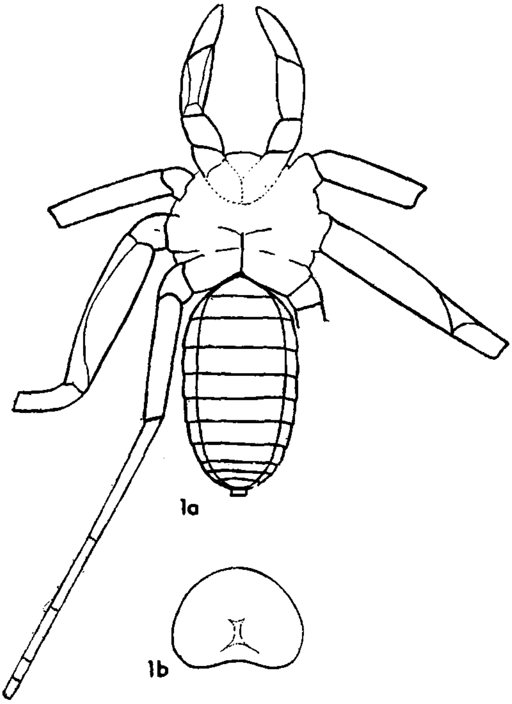


FIG. 94. *Thelyphrynus elongatus,* Penn., Ill.; *1a,* ×3; *1b,* carapace, ×3 (76) (p. P128).

Protophrynus PETRUNKEVITCH, 1913 [**P. carbonarius*]. Anterior projection of carapace truncated, bearing pair of sessile eyes; 3 pairs of lateral eyes (34). *Penn.,* N.Am.—FIG. 93,*3*. **P. carbonarius,* Ill.; *3a,b,* dorsal and ventral sides, ×3 (76).

Thelyphrynus PETRUNKEVITCH, 1913 [**T. elongatus* (misspelled *Telyphrynus* on p. 60, correctly spelled on p. 66)]. Carapace evenly rounded in front, without eyes. *Penn.,* N.Am.—FIG. 94. **T. elongatus,* Ill.; *1a,b,* ventral side and carapace, ×3 (76).

Order ARANEIDA Clerck, 1757

[*nom. correct.* DALLAS, 1864 (*pro* Araneidea BLACKWALL, 1861; *pro* Araneides LATREILLE, 1801; *pro* Aranei CLERCK, 1757)] [=Araneae *auctt.* (CLERCK's name validated by action of Intern. Zool. Congress, Paris, 1948)] [Type: *Araneus* CLERCK, 1757]

Labellata with maxillary lobes and glands, 1st pair of legs similar to others and abdomen with spinnerets, without pygidium.

Carapace entire, with up to 4 pairs of eyes. Abdomen in primitive families segmented, composed of 12 distinct segments; in all other families reduced to 5 or 6 segments completely fused in the adult, without trace of external segmentation. First abdominal segment always reduced to slender pedicel usually with only dorsal tergite (*lorum pediculi*), but in some genera with ventral sternite (*plagula sternalis*). Anus at end of abdomen, without operculum. Coxosternal region (Fig. 97*B*) similar to that in Trigonotarbida, with lip and sternum. All coxae movable. Pedipalpal coxae with maxillary glands and either rudimentary or more commonly well-developed maxillary lobes. Chelicerae 2-jointed, retrovert (Fig. 97*F*), 2nd joint developed as fang, with opening of poison gland below tip. Pedipalpi 6-jointed, terminal joint, with or without claw in females and immature specimens; with more or less complicated copulatory organ in mature males (Fig. 106,*1b*). Legs 7-jointed, either with 3 claws or with 2 claws and claw tufts serving as organ of adhesion. Abdominal appendages modified as spinnerets on 4th and 5th segments (Fig. 97*B,C*) with spinning tubes of various kinds for passage of silk from silk glands situated in abdomen. Maximum number of spinnerets 4 pairs, in segmented spiders, 3 pairs in most spiders, 2 pairs in majority of Theraphosina, 1 pair in few genera scattered over several families. In so-called cribellated spiders a perforated plate called cribellum and corresponding to 1st pair of spinnerets of segmented spiders, is situated in front of the 3 pairs of normal spinnerets and serves for passage of special silk. Presence of cribellum (Fig. 103,*5b*) is always correlated with presence of a so-called calamistrum or brush of specialized hairs on 4th metatarsi (Fig. 103, *1b,2c*). The calamistrum is used to brush the silk out of the cribellum (Figs. 95, 96).

Mouth anteroventral, between rostrum (upper lip) and labium. Fore-gut with pharynx, esophagus and gizzard. Pharynx composed of 2 plates and serves as pumping organ and filter. Gizzard has 3 plates and acts as main pumping organ. Its dorsal dilator muscles are attached to apodeme visible on outside of carapace and called thoracic groove (Fig. 97*A*). Mid-gut with several diverticles in cephalothorax, forming thoracenteron, and several greatly ramified diverticles in abdomen, forming chylenteron, often called liver. Mid-gut ends in a stercoral pouch in which excrements are stored. Hind-gut short, opening at true end of abdomen, which often is far in front of actual end when abdomen is dorsally prolongated far beyond anus. Pair of poison glands in cephalothorax, with ducts opening just below tip of fangs. Malpighian tubes in abdomen, opening into digestive tube at end of mid-gut. Coxal glands in cephalothorax, with pair of openings at base of 1st coxae and another pair at base of 3rd coxae. Respiration either by means of 2 pairs of book lungs situated in 2nd and 3rd abdominal segments, or 1 pair of book lungs and 1 pair of branched tracheal tubes in place of 2nd pair of book lungs, or 2 pairs of branched tracheal tubes in place of book lungs.

Circulatory system highly complex, of open type, but with strictly morphologically predetermined veinous channels for return of blood to the heart. Heart limited to abdomen, with 2 to 5 pairs of ostia, complicated cephalothoracic arterial system and 3 posterior, abdominal arteries. Blood pumped forward and backward. Nervous system highly concentrated, with all abdominal neuromeres incorporated in thoracic ganglionic mass, from which nerves pass through petiolus into abdomen. Known sense organs

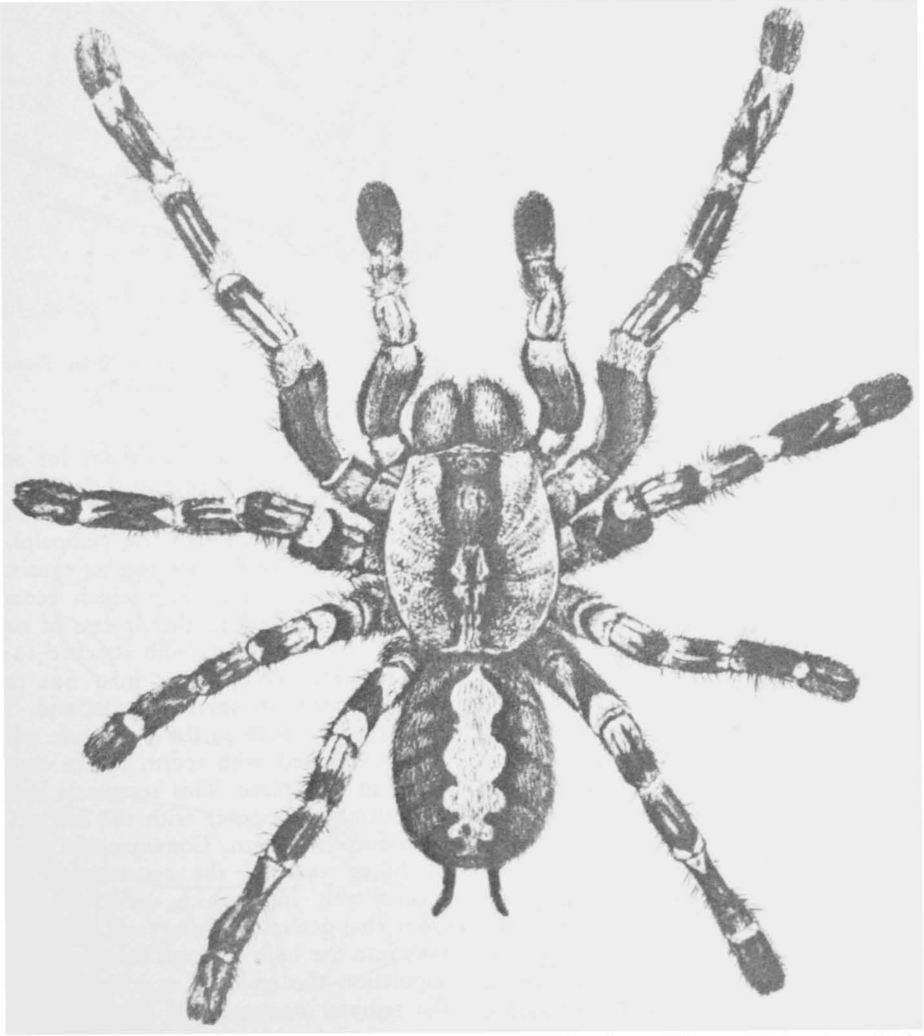


FIG. 95. *Poecilotheria regalis*, a theraphosid spider from India, female, ×1 (by permission from *Traité de Zoologie*, tome 6, sous la direction du PR. GRASSÉ, Masson & Cie., Editeurs, Paris).

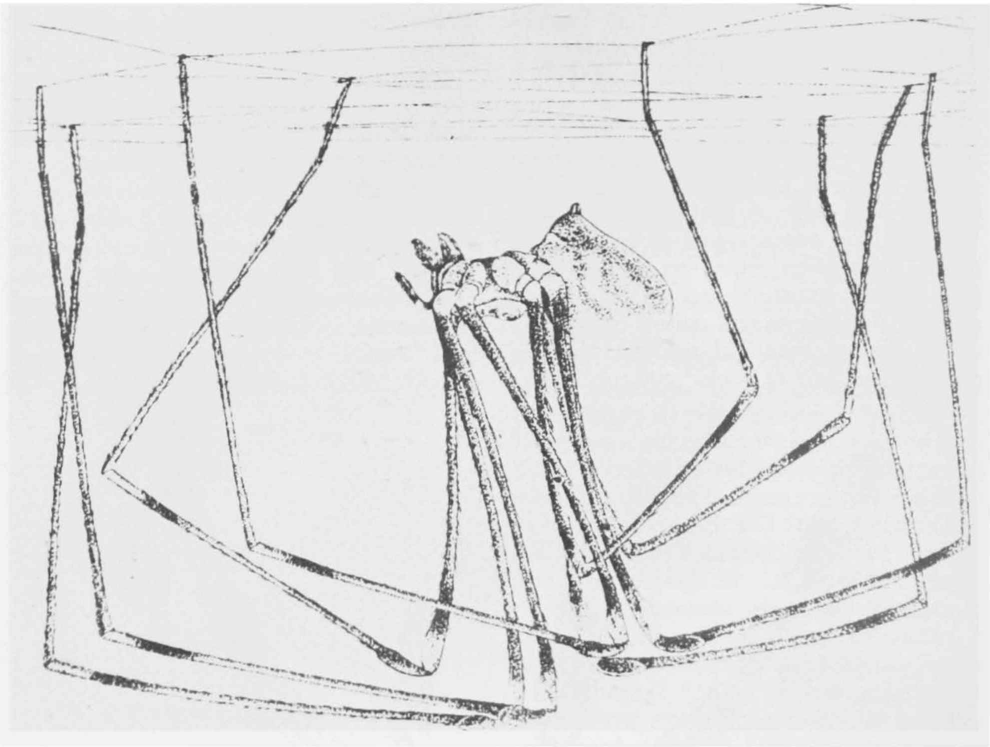


FIG. 96. *Artema mauricia,* a pholcid spider from tropical Africa, ×2 (by permission from *Traité de Zoologie,* tome 6, sous la direction du PR. GRASSÉ, Masson & Cie., Editeurs, Paris).

comprise eyes, organs of touch and lyriform organs. Eyes are of 2 types: pair of median eyes with direct retina, rods facing refractive apparatus, and 3 pairs of lateral eyes with inverted retina, rods facing away from lens. Configuration of eye group and their number of great systematic value. Organs of touch consist of various hairs; type called trichobothria, sensitive to gentle touch and especially to currents of air, have different distribution in different families. Sound-producing organs of stridulating type are common, but auditory organs remain unknown. Lyriform or slit organs and tarsal organs called by me "drums" are presumably olfactory in function.

Reproductive organs with openings on 2nd abdominal segment. In females the genital opening, through which eggs are laid, is usually accompanied by a pair of openings leading into seminal receptacles, and by an external chitinous organ, epigynum. Sperm introduced by the male into the receptacles remains in them for some time and is added to eggs as they are being laid. Males have their organs of copulation on the terminal joint of the pedipalpi. In their simplest form these organs consist of a soft sac (hematodocha) which becomes distended by blood in the process of copulation, and a chitinous bulb attached to the hematodocha, and ending in a fine tube, embolus, with an opening at its end. The cavity of the bulb is the receptacle which has to be filled with sperm before copulation can take place. This receptacle has no connection whatsoever with the rest of the reproductive system. Consequently the act of filling requires the construction of a special web, into which sperm is ejected from the genital opening and allowed to pass into the bulb through the embolus. In copulation the embolus is introduced into the seminal receptacle of the female, the sperm is injected and the process repeated with the other palp.

All spiders are oviparous. Embryonic development leads, with very few exceptions, to the formation of a spiderling having all essential characteristics of a spider, but differing in many respects from the adult, especially by the fact that their mid-gut is still a closed sac, isolated by its wall from both fore-gut and hind-gut and filled with embryonic yolk. During the 1st instar, spiderlings live either in a common web made by their mother before her death, or are carried on her back, as in Lycosidae, or

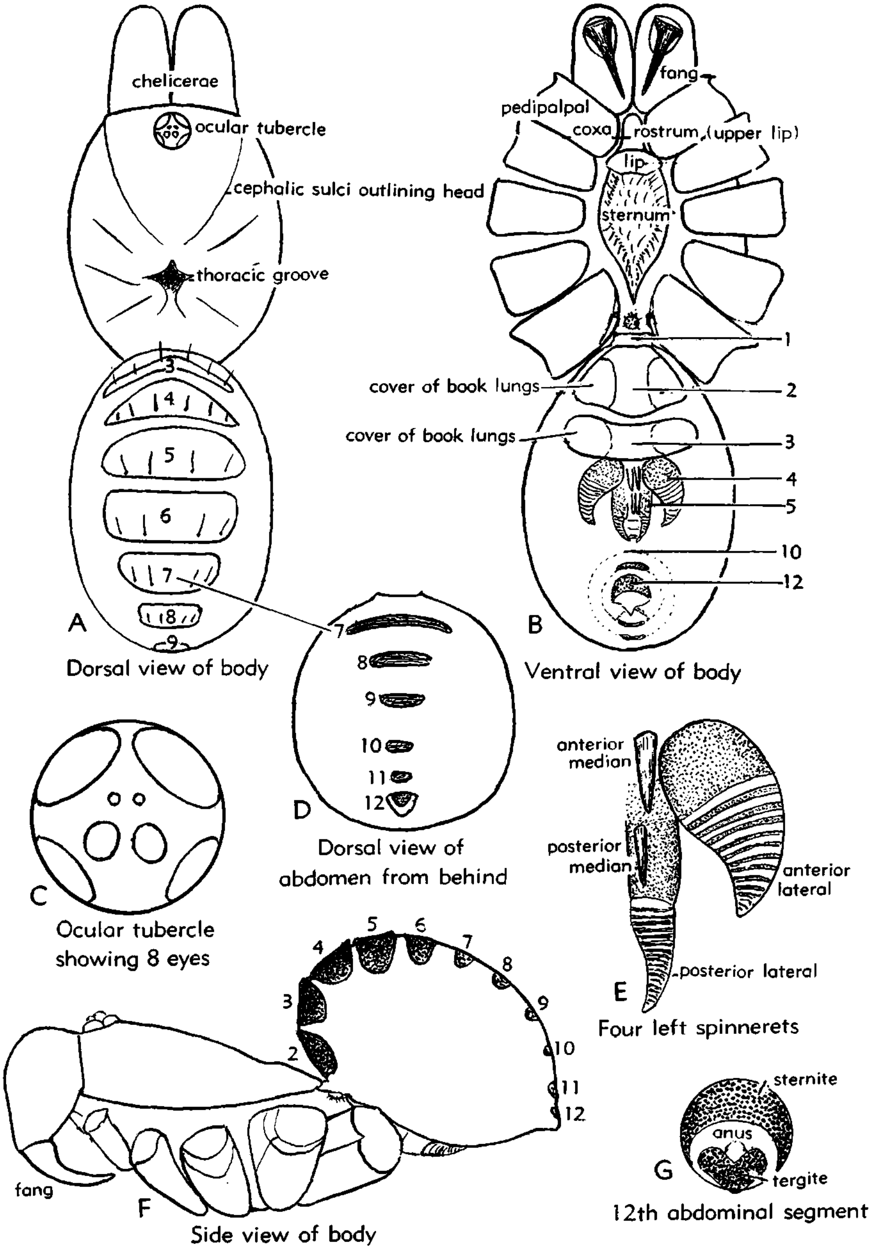


Fig. 97. External morphology of segmented spiders of the suborder Liphistiina. *Liphistius malayanus,* Rec., from the Malay Peninsula, female (76).

simply stay together when the egg cocoon is attached to the underside of a rock or bark and left to itself. The proportions of body and legs of 1st-instar spiderlings differ greatly from those of the adult, and the embryonic yolk is their only food. The advent of the 2nd instar induces hunger, independent feeding and dispersal as a natural preventive of extermination of the species through cannibalism. Maturity is normally attained after about 7 molts, but this number varies even within the same species. *?Dev., Carb.-Rec.*

DISCUSSION

The natural classification of spiders, proposed by me in 1933, is based on correlation of external characters with internal anatomy, supplemented by evaluation of evolutionary trends common to all Arachnida. Five suborders are recognized, 2 of which have no fossil representatives. The classification of fossil spiders is far from simple. Characters, easily visible in living spiders and imperative for correct identification even of suborders, are often missing. This applies especially to Paleozoic and such Tertiary spiders as are preserved in sedimentary rocks and not in amber. The structure of their internal organs is quite unknown and consequently their placement even in a suborder is not always certain. The total number of living genera is 2,735 and of fossil genera 84, or a total of 2,819 genera. Practically all Tertiary spiders belong to the suborder Dipneumonina (91 genera), the suborder Theraphosina being represented by only 3 genera. The Paleozoic spiders naturally belong to extinct genera. Two of the Paleozoic families are placed here in the suborder Liphistiina on account of their clearly segmented abdomen and general appearance. Their spinnerets are not preserved. The number of abdominal segments cannot be ascertained even in living specimens of *Liphistius* without rotating them, because only some of the segments can be seen in any one position (Fig. 97*A,D,F*). Two other Paleozoic families are tentatively placed here in the suborder Dipneumonina. Their representatives show abdominal segmentation, but their general appearance is that of dipneumone spiders, but not all important characters are preserved.

At present 81 families of spiders are recognized, 10 of them extinct. Of the 5 suborders, the Dipneumonina is by far the richest in genera and species (59 families, 2,401 genera). Theraphosina come second with 8 families and 370 genera. Apneumonina come third with 7 families and 27 genera. Liphistiina come fourth with 4 families and 14 genera. Hypochilina come last with 1 family and 2 genera. *Incertae sedis genera* are not included in this count.

Above figures are interesting inasmuch as they shed additional light on the evolution of spiders. Loss of abdominal segmentation, reduction in the number of cardiac ostia through loss of posterior cardiomeres, replacement of book lungs by tracheal tubes and the extension of the latter into the cephalothorax, and the loss of spinnerets are the important changes in the evolution of spiders. Liphistiina must be regarded as the most primitive spiders because they still have the maximum number of abdominal segments, of cardiac ostia, of book lungs and of spinnerets. At present they are represented by only 3 living genera with a few species. Their nearest relatives are undoubtedly the Theraphosina whose abdominal segments 6 to 12 are lost, segments 2 to 5 are fused without trace of external segmentation, cardiac ostia reduced to 4 or 3 pairs, spinnerets reduced to 3, or more commonly 2 pairs, while the book lungs are as in Liphistiina.

If the Paleozoic families referred tentatively to Dipneumonina have chelicerae of the diaxial type, which remains unknown because their chelicerae are not preserved, the change of chelicerae from their normal paraxial position, characteristic of Liphistiina and Theraphosina, to a diaxial one of all common spiders, must have taken place already in the Paleozoic. In Dipneumonina the 2nd pair of book lungs become replaced by tracheal tubes and the heart was reduced to 3 pairs of ostia in Trionychi and Dionychi, and even to 2 pairs in Quadrostiati, in the latter coupled with an extension of tracheae into the cephalothorax. In Apneumonina book lungs disappeared completely, tracheal tubes took their place and the heart became reduced to 2 pairs of ostia. It seems probable that Apneumonina evolved from Quadrostiati and are the youngest evolutionary group.

Suborder LIPHISTIINA Pocock, 1892

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Liphistiomorphae POCOCK, 1892)] [Type: *Liphistius* SCHIÖDTE, 1849]

Chelicerae paraxial. Abdomen segmented. Four pairs of spinnerets. Two pairs of book lungs. Five or 4 pairs of cardiac ostia. *?Dev., Carb.-Rec.*

Family ARTHROLYCOSIDAE Fritsch, 1904

[*emend.* PETRUNKEVITCH, 1923]

Eyes on distinct tubercle. *Carb.*

Arthrolycosa HARGER, 1874 [**A. antiqua*]. Carapace with convex sides. Two pairs of eyes (45). *Penn.,* N.Am.—FIG. 98,*1*. **A. antiqua,* Ill.; ×1.3 (76).—FIG. 98,*3*. *A. danielsi* PETRUNKEVITCH, Ill.; *3a,b,* ventral and dorsal sides, ×2.3; *3c,* tubercle with 4 eyes, ×16 (76).

Eocteniza POCOCK, 1911 [**E. silvicola*]. Head clearly outlined, sides forming a concave line with anterior end of thorax. Sides of thorax convex. Single pair of eyes (45). *Carb.,* Eu.—FIG. 98,*2*. **E. silvicola,* Eng.; ×3.5 (76).

Family ARTHROMYGALIDAE Petrunkevitch, 1923

Eye tubercle wanting, presence of eyes doubtful. *?Dev., Carb.*

Protolycosa ROEMER, 1866 [**P. anthracophila*]. Abdominal tergites with transverse rows of tubercles (45). *Carb.,* Eu.—FIG. 99,*1*. **P. anthracophila,* Ger.; ×3 (76).

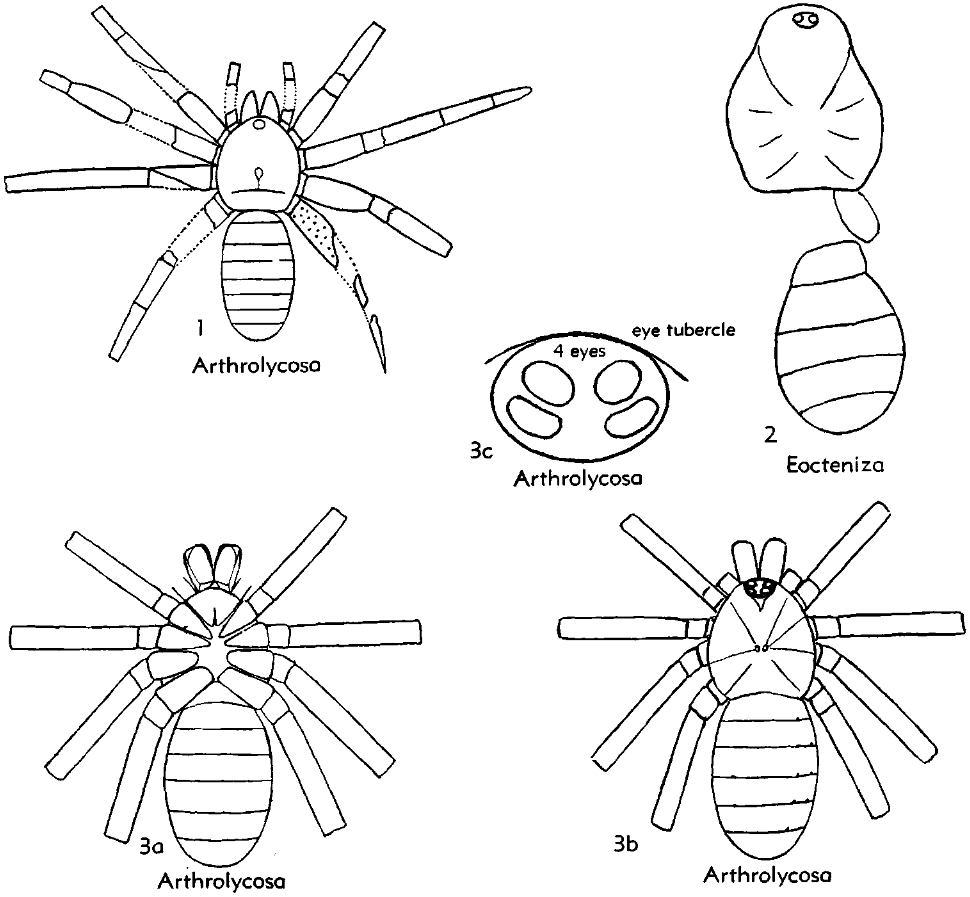


FIG. 98. Arthrolycosidae. *1, Arthrolycosa antiqua,* Penn., Ill., ×1.3; *2, Eocteniza silvicola,* U.Carb., Eng., ×3.5; *3, Arthrolycosa danielsi,* Penn., Ill.; *3a,b,* ventral and dorsal, ×2.3; *3c,* eye tubercle, ×16 (76).

Arthromygale Petrunkevitch, 1923 [**Arthrolycosa fortis* Fritsch, 1904]. Carapace about as wide as long, with convex front and sides, without eyes. Legs short and stout (45). *Carb.*, Eu.—Fig. 99,*3*. **A. fortis* (Fritsch), Czech.; ×1.7 (76).

Protocteniza Petrunkevitch, 1949 [**P. britannica*].

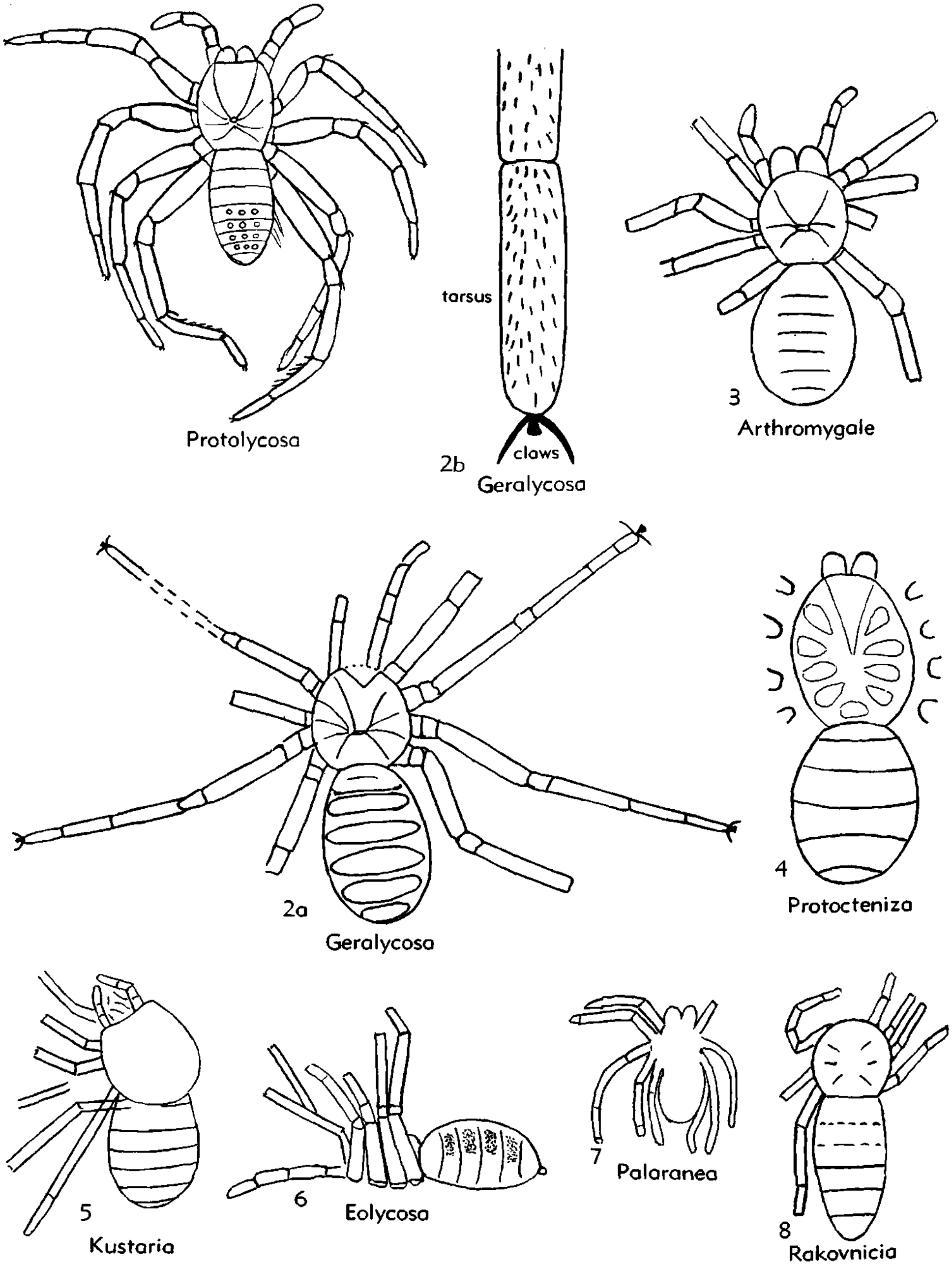


Fig. 99. Arthromygalidae. *1, Protolycosa anthracophila,* Carb., Ger., ×3 (66a). *2, Geralycosa fritschi,* U.Carb., Czech.; *2a,* ×2.3; *2b,* end of one of its legs, showing claws and arolium, ×13.5. *3, Arthromygale fortis,* U.Carb., Czech., ×1.7. *4, Protocteniza britannica,* U.Carb., Eng., ×7. *5, Kustaria carbonaria,* U.Carb., Czech, ×5.5. *6, Eolycosa lorenzi,* U.Carb., Czech., ×3.3. *7, Palaranea borassifoliae,* U.Carb., Czech., ×0.6. *8, Rakovnicia antiqua,* U.Carb., Czech., ×4.7 (76) (p. P133-P135).

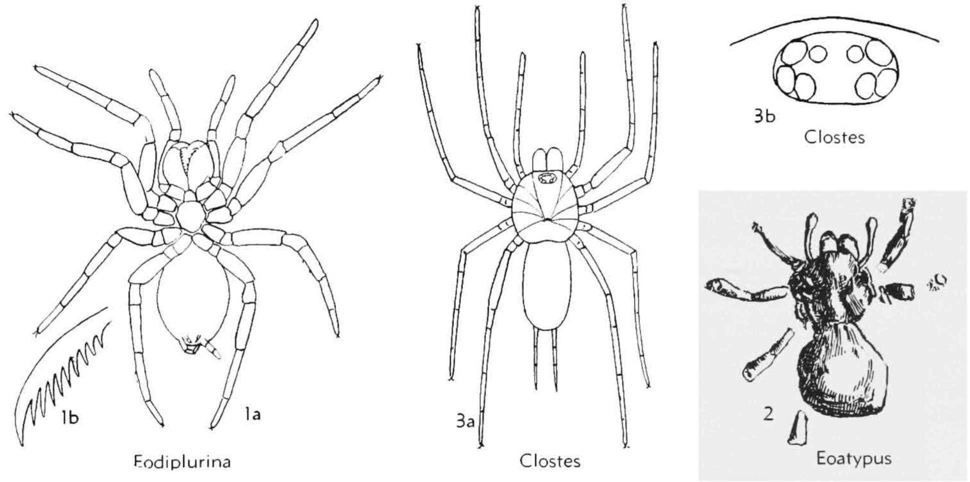


FIG. 100. Theraphosina. *1, Eodiplurina cockerelli,* Oligo., Colo. (Florissant); *1a,* ×6.5; *1b,* one of its claws, ×70 (76). *2, Eoatypus woodwardii,* Mio., Eng., ×3 (72). *3, Clostes priscus,* Oligo., Balt.; *3a,* ×5.5; *3b,* eye tubercle, ×20 (76) (p. P136).

Carapace considerably longer than wide (43). *Carb.,* Eu.—FIG. 99,*4*. **P. britannica,* Eng.; ×7 (76).

Palaranea FRITSCH, 1873 [**P. borassifoliae*]. Fourth leg as long as body. Order of legs 4321 (45). *Carb.,* Eu.—FIG. 99,*7*. **P. borassifoliae,* Czech.; outline of specimen as it appears impressed on leaf, ×0.6 (76).

Geralycosa KUŠTA, 1888 [**G. fritschi*]. Fourth leg longer than body by more than a fifth. Order of legs 4321. Tarsi with arolium (45). *Carb.,* Eu.—FIG. 99,*2*. **G. fritschi,* Czech.; *2a,* complete specimen, ×2.3; *2b,* tarsus with claws and arolium, ×13.5 (76).

Kustaria PETRUNKEVITCH, 1953 [**Scudderia carbonaria* KUŠTA, 1888]. Carapace with strongly convex posterior edge and slightly concave front (45). *Carb.,* Eu.—FIG. 99,*5*. **K. carbonaria* (KUŠTA), Czech.; ×5.5 (76).

Rakovnicia KUŠTA, 1884 [**R. antiqua*]. Carapace flat, with convex sides and front and truncated posterior edge. Abdomen twice as long as wide. Legs slender (45). *Carb.,* Eu.—FIG. 99,*8*. **R. antiqua,* Czech.; ×4.7 (76).

Eolycosa KUŠTA, 1885 [**E. lorenzi*]. Spinnerets terminal (45). *Carb.,* Eu.—FIG. 99,*6*. **E. lorenzi,* Czech.; ×3.3 (76).

Palaeocteniza HIRST, 1923 [**P. crassipes*]. Classification doubtful (17). *Dev.* (*Old Red Sandstone*), Scot.

Suborder THERAPHOSINA
Sundevall, 1830

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Theraphosae SUNDEVALL, 1830] [=Théraphoses WALCKENAER, 1805; Mygaliformes SIMON, 1864; Mygalomorphae POCOCK, 1893] [Type: *Theraphosa* WALCKENAER, 1805]

Chelicerae paraxial. Abdomen not segmented; 2 or 3 pairs of spinnerets. Two pairs of book lungs. Three or 4 pairs of cardiac ostia (36). *Oligo.-Rec.*

Family THERAPHOSIDAE Thorell, 1869

[=Aviculariidae SIMON, 1892][1]

Four pairs of cardiac ostia. Two pairs of spinnerets, posterior pair long, 3-jointed. Tarsi with 2 claws and claw tufts. *Oligo.-Rec.*

[1] The existing confusion of opinions concerning the status of the 2 generic names, *Mygale* and *Theraphosa,* is due to several causes, one of which is rooted in the historical change of the concept of the term *genus* and of its scope. LINNÉ did not use the term *family* in any way. He divided his orders directly into genera. DEGEER was the first to use the term *family,* but he placed it *under* the genus, dividing the genus into families, yet retaining binomial nomenclature for species, so that the family names appeared only in headings and the same genus in several families. WALCKENAER followed this principle. In 1802 he proposed the genus *Mygale*. In 1805 he proposed the genus *Theraphosa;* called "Théraphoses" all spiders with chelicerae of the type we call now paraxial, and subdivided them into 5 genera, the first of which is his *Mygale*. WALCKENAER did not mention the types of his genera, as that was not customary at his time. In 1850 C.L. KOCH restricted the genus *Mygale* to 2 species, *blondii* and *javanensis*. The name *Mygale* was found to be preoccupied by CUVIER for a mammal, so KOCH proposed for it the name *Scurria*. THORELL pointed out in 1869 that the name *Theraphosa* has priority, selected for its type the species *blondii* and erected the family Theraphosoidae which was later changed by POCOCK into Theraphosidae. SIMON retained in 1892 SUNDEVALL's name Theraphosae for the suborder, selected for the name of the family the genus *Avicularia* LAMARCK, 1818. Before that, in 1885, SIMON thought that the type of *Mygale* was really *M. fasciata* and not *M. blondii* and gave the name *Poecilotheria* as substitute for *Mygale* and *Scurria* which also proved to be preoccupied. In 1923 I divided SIMON's family Aviculariidae into 8 families, retaining the name Theraphosidae for one of them, following in this the example of POCOCK.

This family includes the largest spiders, known in America under the name of Tarantulae. A characteristic representative, *Poecilotheria regalis* Pocock from Madras, India, is shown in Fig. 95.

Eodiplurina Petrunkevitch, 1922 [**E. cockerelli*]. Legs spinose, in order 4123. Claws pectinated in a single row (35). *Oligo.,* N.Am.—Fig. 100,*1*. **E. cockerelli,* Colo.; *1a,* ventral side, ×6.5; *1b,* claw, ×70 (76).

Family DIPLURIDAE Pocock, 1894

Tarsi with 3 claws. Four pairs of cardiac ostia. Two or 3 pairs of spinnerets, posterior pair very long. *Oligo.-Rec.*

Clostes Menge, 1869 [**C. priscus*]. Four spinnerets. Upper claws dissimilar, order of legs 4123. Eyes on tubercle, anterior median eyes smallest. No spines on legs (37). *Oligo.*—Figs. 31,*3*, 100,*3*. **C. priscus,* Balt.; 31,*3*, dorsal side, ×8.4; 100,*3a*, dorsal side, ×5.5; 100,*3b*, tubercle with 8 eyes, ×20 (76).

THERAPHOSINA Incertae Sedis

Eoatypus McCook, 1888 [**E. woodwardi*]. *Eoc.,* Eu.—Fig. 100,*2*. **E. woodwardi,* Eng. (Wight); dorsal side, ×3 (72).

Suborder HYPOCHILINA Petrunkevitch, 1933

[*nom. correct.* Petr., herein (*pro* Hypochilomorphae Petr., 1933)] [Type: *Hypochilus* Marx, 1888]

Abdomen not segmented. Chelicerae di-

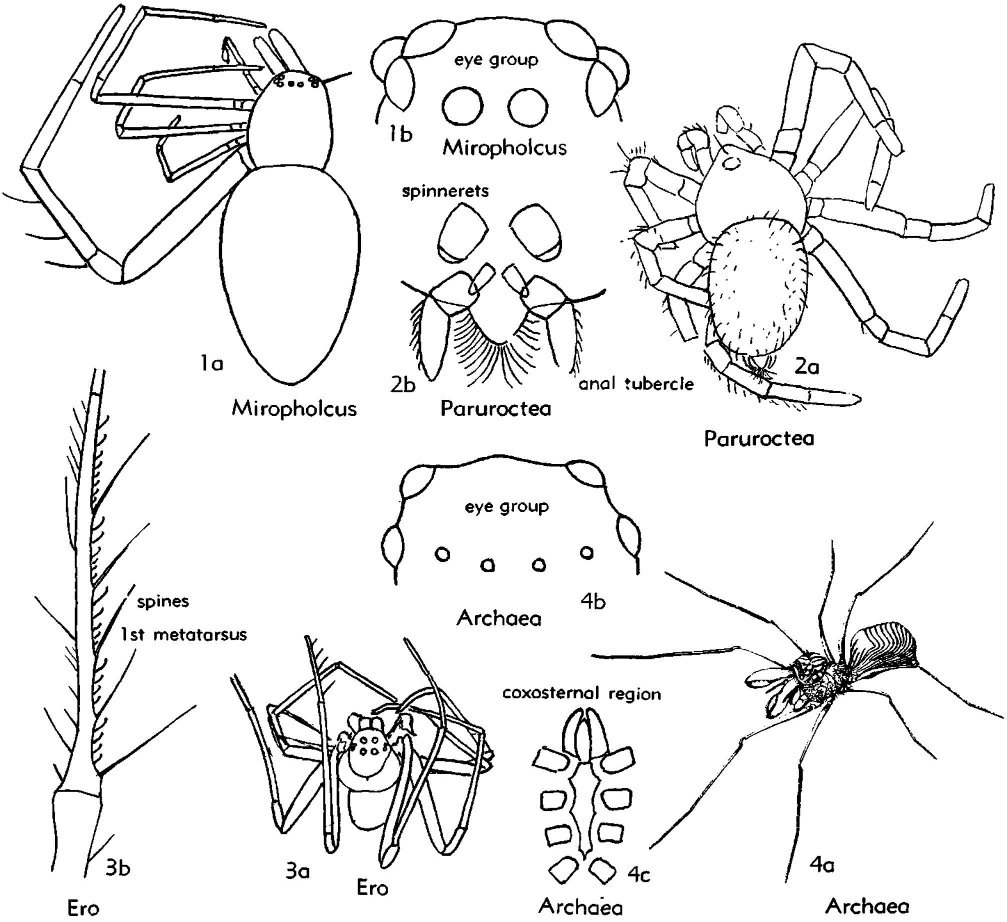


Fig. 101. Dipneumonina. *1, Miropholcus heteropus,* Oligo., Balt.; *1a,* ×20; *1b,* eye group, enlarged. *2, Paruroctea blauvelti,* Oligo., Balt.; *2a,* ×8.5; *2b,* spinnerets with anal tubercle, enlarged. *3, Ero permunda,* Oligo., Balt.; *3a,* ×5.2; *3b,* 1st metatarsus showing spines of 2 kinds, enlarged (76). *4, Archaea paradoxa,* Oligo., Balt.; *4a,* female, ×7.5 (71); *4b,* eye group, ×55; *4c,* coxosternal region, ×17 (76) (p. P138-P142).

axial. Two pairs of book lungs. Four pairs of cardiac ostia (36). *Rec.*

Suborder DIPNEUMONINA Latreille, 1817

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Dipneumones LATREILLE, 1817] [=Dipneumonomorphae PETR., 1933] [Type: *Araneus* CLERCK, 1757]

Abdomen not segmented. Chelicerae diaxial. Single pair of book lungs and one pair of tracheal tubes. Three or 2 pairs of cardiac ostia. *?Carb., Oligo.-Rec.*

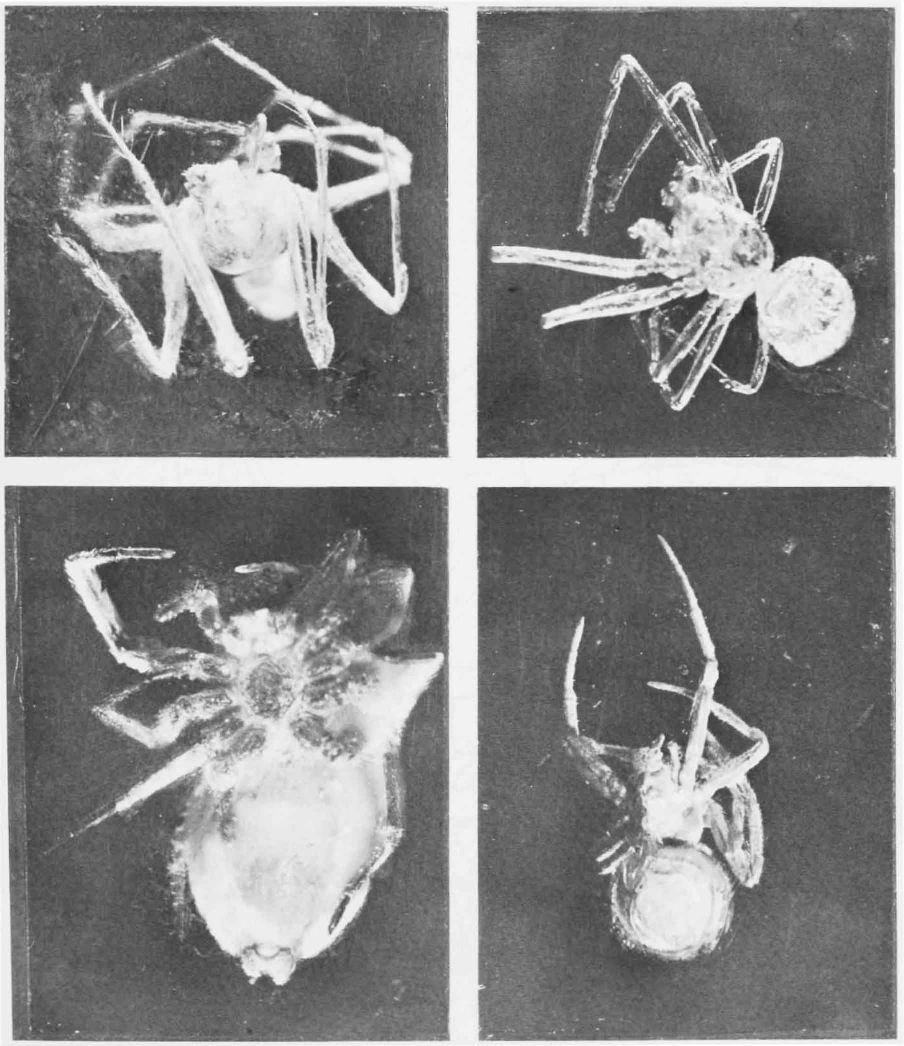
Division TRIONYCHI Petrunkevitch, 1933

Dipneumone spiders with 3 claws. Three pairs of cardiac ostia. *Oligo.-Rec.*

Superfamily HERSILIOIDEA Caporiacco, 1938

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Hersiliaeformia CAPORIACCO, 1938)]

Posterior spinnerets wide apart, with long



1. Ero permunda Petr. (Oligo.)

2. Acrometa cristata Petr. (Oligo.)

3. Auximus succini Petr. (Oligo.)

4. Eodipoena oculata Petr. (Oligo.)

FIG. 102. Dipneumonina, Oligo., Balt.; photographs of types. *1, Ero permunda,* ×8.2. *2, Acrometa cristata,* ×12. *3, Auximus succini,* ×8. *4, Eodipoena oculata,* ×6.4 (76) (p. P140-P145).

2nd joint. Four pairs of heterogeneous eyes. *Oligo.-Rec.*

Family UROCTEIDAE Simon, 1875

Six spinnerets. Anal tubercle large, with fringe of long hair. *Oligo.-Rec.*

Paruroctea PETRUNKEVITCH, 1942 [***P. blauvelti*]. First row of eyes recurved. Fourth tarsi with ventral spines (37). *Oligo.*, Eu.—FIG. 101,*2*. ***P. blauvelti***, Balt.; *2a*, dorsal side, ×8.5; *2b*, spinnerets and anal tubercle, much enlarged (76).

Family HERSILIIDAE Thorell, 1869

Head elevated. Posterior spinnerets very long, flexible. *Oligo.-Rec.*

Hersilia AUDOUIN, 1827 [**H. caudata*]. Clypeus very high. Metatarsi 2-jointed. *Oligo.-Rec.*—FIG. 105,*3*. **H. miranda* KOCH & BERENDT, Oligo., Balt.; ×2.1 (71).

Gerdia MENGE, 1869 [**G. myura*]. Anterior eyes half as large as posterior ones (74). *Oligo.*, Balt.

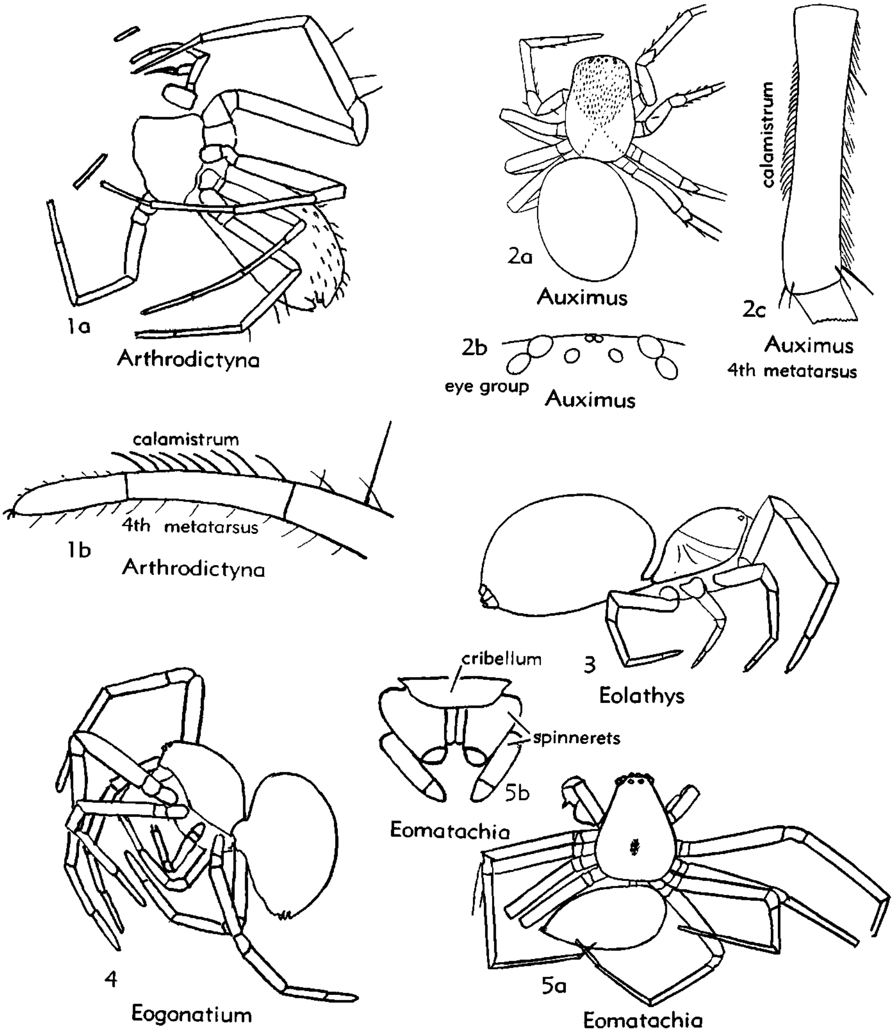


FIG. 103. Dipneumonina, Oligo., Balt. *1, Arthrodictyna segmentata; 1a,* ×25; *1b,* 4th metatarsus showing calamistrum, ×44. *2, Auximus fossilis; 2a,* ×4.6; *2b,* eye group, ×26; *2c,* 4th metatarsus showing calamistrum, ×26; *3, Eolathys succini,* ×11. *4, Eogonatium minutum,* ×24. *5, Eomatachia latifrons; 5a,* male, ×5; *5b,* its spinnerets, enlarged (76) (p. P140-P142).

Superfamily SCYTODOIDEA Caporiacco, 1938

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Scytodiformia CAPORIACCO, 1938)]

Tracheal system rudimentary. Lip fused with sternum. *Oligo.-Rec.*

Family PHOLCIDAE Simon, 1874

Lateral eyes in triads. Legs long and slender. *Oligo.-Rec.*—FIG. 96. *Artema mauricia,* a Recent representative of the family, ×2 (75).

Miropholcus PETRUNKEVITCH, 1942 [**M. heteropus*]. Eye group full width of head. Fourth pair of legs

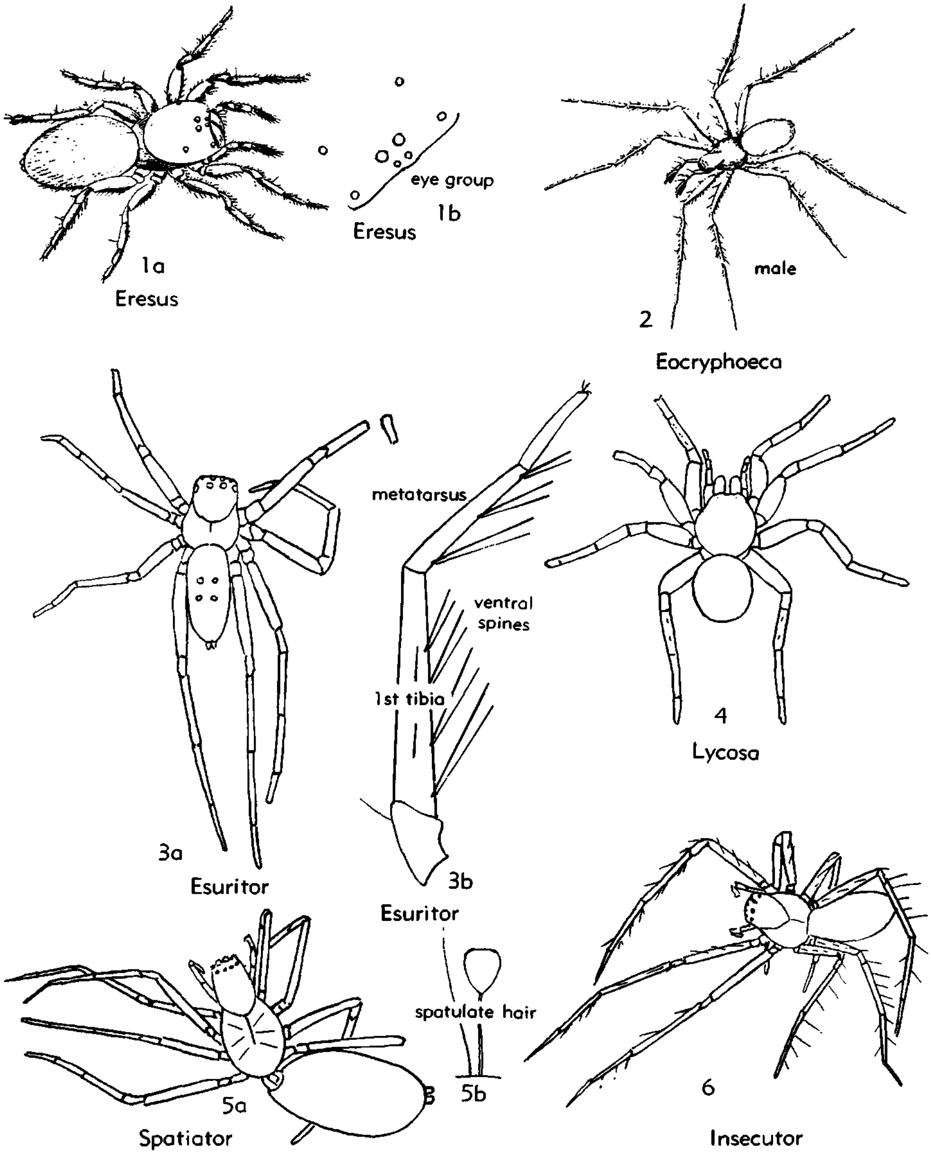


FIG. 104. Dipneumonina, Oligo. *1, Eresus monachus,* Balt.; *1a,* ×5; *1b,* eye group enlarged (71). *2, Eocryphoeca gracilipes,* Balt.; male, ×9 (71). *3, Esuritor longipes,* Balt.; *3a,* ×4.3; *3b,* 1st leg, showing ventral spines, ×14. *4, Lycosa florissanti,* Colo.; female, ×2.5. *5, Spatiator praeceps,* Balt.; *5a,* ×4.3; *5b,* spatulate hair, enlarged. *6, Insecutor aculeatus,* Balt.; ×6.5 (76) (p. P140-P141).

much stouter and longer than others (37). *Oligo.*, Eu.—FIG. 101,*1*. **M. heteropus*, Balt.; *1a*, dorsal side, ×26; *1b*, eye group, enlarged (76).

Superfamily ZODARIOIDEA Caporiacco, 1938

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Zodariiformia CAPORIACCO, 1938)]

Anterior and median spinnerets rudimentary or lacking. Third claw lacking in some species. *Oligo.-Rec.*

Family ZODARIIDAE Simon, 1892

First pair of legs not stouter than the others. *Oligo.-Rec.*

Anniculus PETRUNKEVITCH, 1942 [**A. balticus*]. Only 2 spinnerets, on pedestal. Sternum almost circular. Integuments with plumose hair (37). *Oligo.*, Eu.—FIG. 105,*1*. **A. balticus*, Balt.; *1a*, dorsal side, ×4.3; *1b*, spinnerets on pedestal, enlarged (76).

Family SPATIATORIDAE Petrunkevitch, 1942

Head separated from thorax by semicircular groove. Eyes in 2 rows. Six spinnerets, anterior pair stoutest and longest (37). *Oligo.*

Spatiator PETRUNKEVITCH, 1942 [**S. praeceps*]. Legs without spines, 4th pair longest. Spatulate hair present (37). *Oligo.*, Eu.—FIG. 104,*5*. **S. praeceps*, Balt.; *5a*, dorsal side of male, ×4.3; *5b*, spatulate hair from leg, enlarged (76).

Adorator PETRUNKEVITCH, 1942 [**A. brevipes*]. Legs spinose, 1st pair longest (37). *Oligo.*, Balt.

Superfamily LYCOSOIDEA Sundevall, 1833

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Lycosiformia CAPORIACCO, 1938, *nom. transl. ex* Lycosidae SUNDEVALL, 1833)]

Eyes in 2 or 3 rows. Tarsi without serrated bristles. *Oligo.-Rec.*

Family ERESIDAE C.L.Koch, 1837

Cribellum and calamistrum present. Eyes in 3 rows, homogeneous. *Oligo.-Rec.*

Eresus WALCKENAER, 1805 [**Aranea nigra* PETAGNA, 1787]. Posterior median eyes much larger than anterior median eyes. *Oligo.-Rec.*—FIG. 104,*1*. **E. monachus* KOCK & BERENDT, Oligo., Balt.; *1a*, female, ×5; *1b*, eye group, enlarged (71).

Family AMAUROBIIDAE C.L.Koch, 1868

Cribellum and calamistrum present. Eyes subequal, in 2 rows. *Oligo.-Rec.*

Amaurobius C.L. KOCH, 1837 [**Aranea fenestralis* STROEM, 1768]. Retromargin of chelicerae with 2 or 3 teeth (37). *Oligo.-Rec.* [*A. succini* PETRUNKEVITCH, Oligo., Balt.].

Auximus SIMON, 1892 [**A. dentichelis*]. Retromargin of chelicerae with 4 teeth. Anterior median eyes by far the smallest (37). *Oligo.-Rec.*—FIG. 102,*3*. *A. succini* PETRUNKEVITCH, Oligo., Balt.; photo of female, ventral side, ×8 (76).—FIG. 103,*2*. *A. fossilis* PETR., Oligo., Balt.; *2a*, holotype, ×4.6; *2b*, eye group, ×26; *2c*, 4th metatarsus with calamistrum, ×26 (76).

Family PSECHRIDAE Simon, 1892

Cribellum and calamistrum present. Three claws and claw tufts. Trichobothria few, on tarsi. *Oligo.-Rec.*

Eomatachia PETRUNKEVITCH, 1942 [**E. latifrons*]. Lateral eyes larger than median eyes. Cribellum entire (37). *Oligo.*, Eu.—FIG. 103,*5*. **E. latifrons*, Balt.; *5a*, dorsal side of male, ×5; *5b*, spinnerets with cribellum, enlarged (76).

Family AGELENIDAE C.L.Koch, 1837

[*nom. correct.* SIMON, 1875 (*pro* Agelenides C.L KOCH, 1837)] [=Agalenidae THORELL, 1869]

Six spinnerets, posterior pair longest, with 2nd joint cylindrical, long. Integument with plumose hair (37). *Oligo.-Rec.*

Agelena WALCKENAER, 1805 [**Araneus labyrinthicus* CLERCK, 1757]. Eyes homogeneous, in 2 strongly procurved rows (37). *Oligo.-Rec.* [*A. tabida* KOCH & BERENDT, Oligo., Balt.].

Eocryphoeca PETRUNKEVITCH, 1946 [**Tegenaria gracilipes* KOCH & BERENDT, 1954]. Anterior median eyes smallest. Second joint of posterior spinnerets conical, shorter than basal joint (40). *Oligo.*, Eu.—FIG. 104,*2*. **E. gracilipes* (KOCH & BERENDT), Balt.; male, ×9 (71).

Myro O. P. CAMBRIDGE, 1876 [**M. kerguelensis*]. Posterior spinnerets somewhat shorter than anterior ones (37). *Oligo.-Rec.* [*M. hirsutus* PETRUNKEVITCH, Oligo., Balt.].

Family INSECUTORIDAE Petrunkevitch, 1942

Spines numerous, long, erect. Sternum widely truncated in front. Eyes in 2 rows. *Oligo.*

Insecutor PETRUNKEVITCH, 1942 [**I. aculeatus*]. Anterior median eyes smallest. Quadrangle wider behind than in front (37). *Oligo.*, Eu.—FIG. 104,*6*. **I. aculeatus*, Balt.; immature female, ×6.5 (76).

Family PISAURIDAE Simon, 1897

Anterior eyes small; posterior row recurved and much wider than anterior row. Trochanters deeply notched. *Oligo.-Rec.*

Esuritor Petrunkevitch, 1942 [**E. spinipes*]. Ventral spines on anterior tibiae and metatarsi very long (37). *Oligo.*, Eu.—Fig. 104,*3*. **E. spinipes*, Balt.; *3a*, immature female, ×4.3; *3b*, distal half of 1st leg, showing tibial and metatarsal spines, ×14 (76).

Family LYCOSIDAE Sundevall, 1933

Eyes in 3 rows, 1st row formed by 4 small eyes. Trochanters deeply notched. *Oligo.-Rec.*

Lycosa Latreille, 1804 [**Aranea tarentula* Rossi, 1790]. Eyes of 2nd row separated by about their diameter. Legs stout, in order 4123 (35). *Oligo.-Rec.*—Fig. 104,*4*. *L. florissanti* Petrunkevitch, *Oligo.*, Colo.; female, ×2.5 (76).

Superfamily ARANEOIDEA Leach, 1815

[*nom. transl.* Petrunkevitch, herein (*ex* Araneides Leach, 1815)] [=Argyopiformia Caporiacco, 1938]

Eyes in 2 rows. Tarsi with serrated bris-

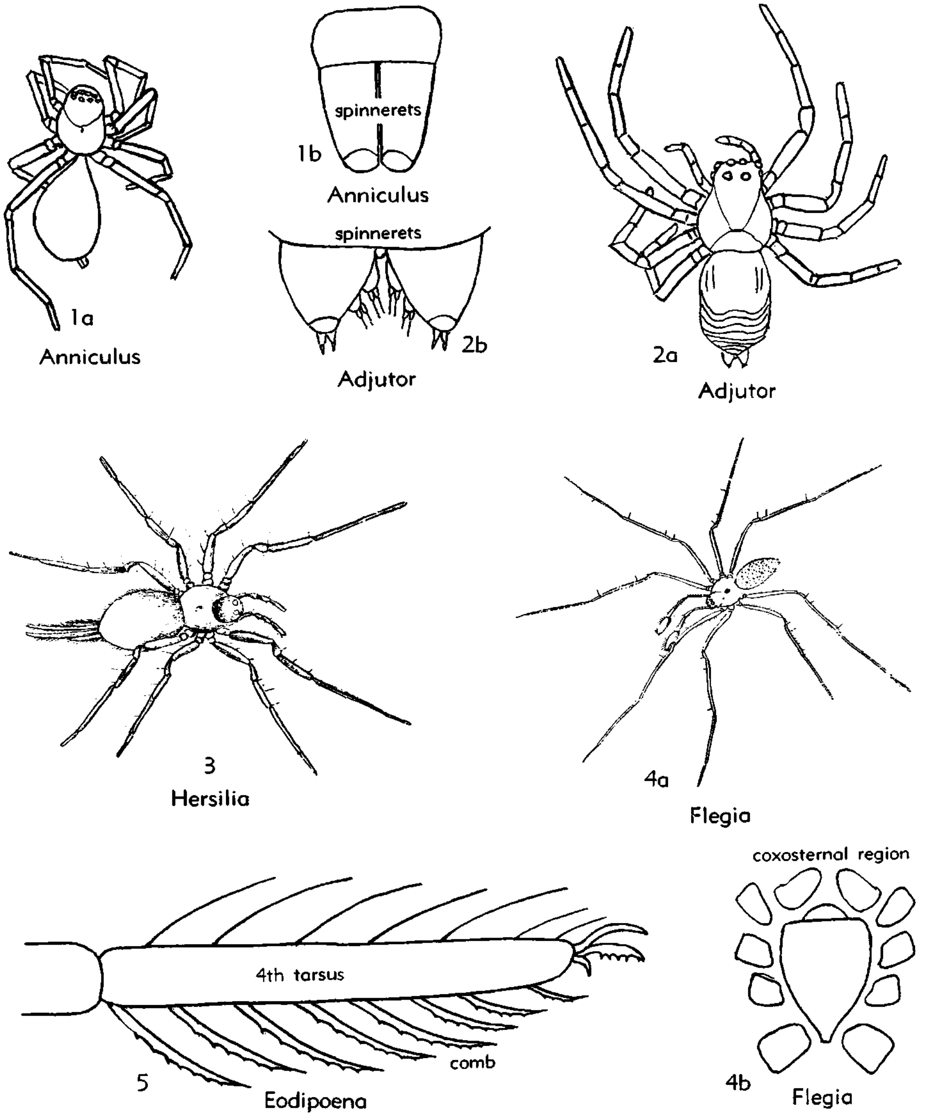


Fig. 105. Dipneumonina, Oligo., Balt. *1, Anniculus balticus; 1a*, ×4.3; *1b*, 2 spinnerets on pedestal, enlarged. *2, Adjutor mirabilis; 2a*, ×20; *2b*, spinnerets, enlarged (76). *3, Hersilia miranda*, ×2.1. *4, Flegia longimana; 4a*, male, ×3 (71); *4b*, its coxosternal region, ×15 (76). *5, Eodipoena oculata*, 4th metatarsus showing comb of serrated bristles, ×75 (76) (p. P138-P142).

tles. Pedipalpal coxae with maxillary serrula. *Oligo.-Rec.*

Family ARCHAEIDAE Koch & Berendt, 1854

Head elevated. Chelicerae inserted in an elliptic foramen far above mouth, strongly divergent. *Oligo.-Rec.*

Archaea Koch & Berendt, 1854 [**A. paradoxa*]. Sternum elongate. Maxillae converging over lip (37). *Oligo.-Rec.*—Fig. 101,*4*. **A. paradoxa,* Balt.; *4a,* female, ×7.5; *4b,* eye group, ×55; *4c,* coxosternal region, ×17 (76).

Family MIMETIDAE Simon, 1895

First and 2nd tibia and metatarsus with a row of long spines separated by much shorter, curved spines. *Oligo.-Rec.*

Ero C.L. Koch, 1837 [**Aranea tuberculata* DeGeer, 1778]. Posterior legs not much shorter than anterior ones (37). *Oligo.-Rec.*—Figs. 101,*3;* 102,*1*. *E. permunda* Petrunkevitch, Oligo., Balt.; 101, *3a,* male, ×5.2; 101,*3b,* 1st metatarsus showing row of spines of 2 kinds, ×20; 102,*1,* photo of holotype, ×8.2 (76).

Family ARTHRODICTYNIDAE Petrunkevitch, 1942

Cribellum and calamistrum present. Abdomen with imperfect segmentation (37). *Oligo.*

Arthrodictyna Petrunkevitch, 1942 [**A. segmentata*]. Cheliceral margins with scopula of 4 hairs. First coxae wide apart (37). *Oligo.,* Balt.—Fig. 103,*1*. **A. segmentata; 1a,* holotype, ×25; *1b,* end of 4th leg showing calamistrum on metatarsus, ×44 (76).

Family DICTYNIDAE Simon, 1874

Cribellum and calamistrum present. Abdomen not segmented. Tracheal system extends into cephalothorax. *Oligo.-Rec.*

Eolathys Petrunkevitch, 1950 [**E. succini*]. Quadrangle of median eyes much wider behind than in front and much wider than long (40). *Oligo.,* Eu.—Fig. 103,*3*. **E. succini,* Balt.; holotype, ×11 (76).

Family MICRYPHANTIDAE Bertkau, 1885

[=Erigonidae Simon, *nom. transl.* Petrunkevitch, 1939 (*ex* Erigoninae Simon, 1926)]

Tracheal system extends into cephalothorax. Tarsi with "drum." *Oligo.-Rec.*

Eogonatium Petrunkevitch, 1942 [**E. minutum*]. Legs without spines, with single trichobothrium on metatarsi, considerably beyond middle (37). *Oligo.,* Balt.—Fig. 103,*4*. **E. minutum;* holotype in side view, ×24 (76).

Family THERIDIIDAE Sundevall, 1833

Fourth tarsi with a "comb" of serrated bristles. Maxillae converging. Eyes heterogeneous, anterior median eyes diurnal. *Oligo.-Rec.*

Theridion Walckenaer, 1805 [**Araneus lineatus* Clerck, 1757] [=*Theridium auctt.*]. Abdomen ovoid with pointed posterior end. Fourth leg shorter than 1st (37). *Oligo.-Rec.* [*T. simplex* Koch & Berendt, Oligo., Balt.].

Flegia Koch & Berendt, 1854 [**F. longimana*]. Carapace flat. Quadrangle rectangular. First coxae wide apart. Femur of male palp as long as carapace. *Oligo.,* Eu.—Fig. 105,*4*. **F. longimana,* Balt.; *4a,* male, ×3; *4b,* coxosternal region, ×15 (76).

Eodipoena Petrunkevitch, 1942 [**E. oculata*]. Eyes equal. Eye group much narrower than head (37). *Oligo., Eu.*—Figs. 102,*4;* 105,*5*. **E. oculata,* Balt.; 102,*4,* photo of holotype, ×6.4; 105, *5,* 4th tarsus with "comb," ×75 (76).

Nactodipoena Petrunkevitch, 1942 [**N. dunbari*]. Eye group almost as wide as head. Posterior median eyes smaller than anterior median eyes (37). *Oligo.,* Balt.

Steatoda Sundevall, 1833 [**Aranea bipunctata* Linné, 1758]. Stridulatory organ between abdomen and carapace. Anterior median eyes larger than anterior lateral eyes (37). *Oligo.-Rec.* [*S. succini* Petrunkevitch, Balt.].

Municeps Petrunkevitch, 1942 [**M. pulcher*]. Eyes equal. Upper claws with single tooth (37). *Oligo.,* Balt.

Eomysmena Petrunkevitch, 1942 [**E. moritura*]. Posterior median eyes smallest. Upper claws smooth (37). *Oligo.,* Balt.

Family ADJUTORIDAE Petrunkevitch, 1942

Anterior spinnerets very stout. Legs with spines and very long trichobothria (37). *Oligo.*

Adjutor Petrunkevitch, 1942 [**A. mirabilis*]. Single trichobothrium on tibiae and metatarsi. Legs in order 1234. Third claw well developed (37). *Oligo.,* Eu.—Fig. 105,*2*. **A. mirabilis,* Balt.; *2a,* holotype, ×20; *2b,* spinnerets, enlarged (76).

Admissor Petrunkevitch, 1942 [**A. aculeatus*]. Anterior spinnerets not much stouter than posterior ones. Legs in order 2143 (37). *Oligo.,* Balt.

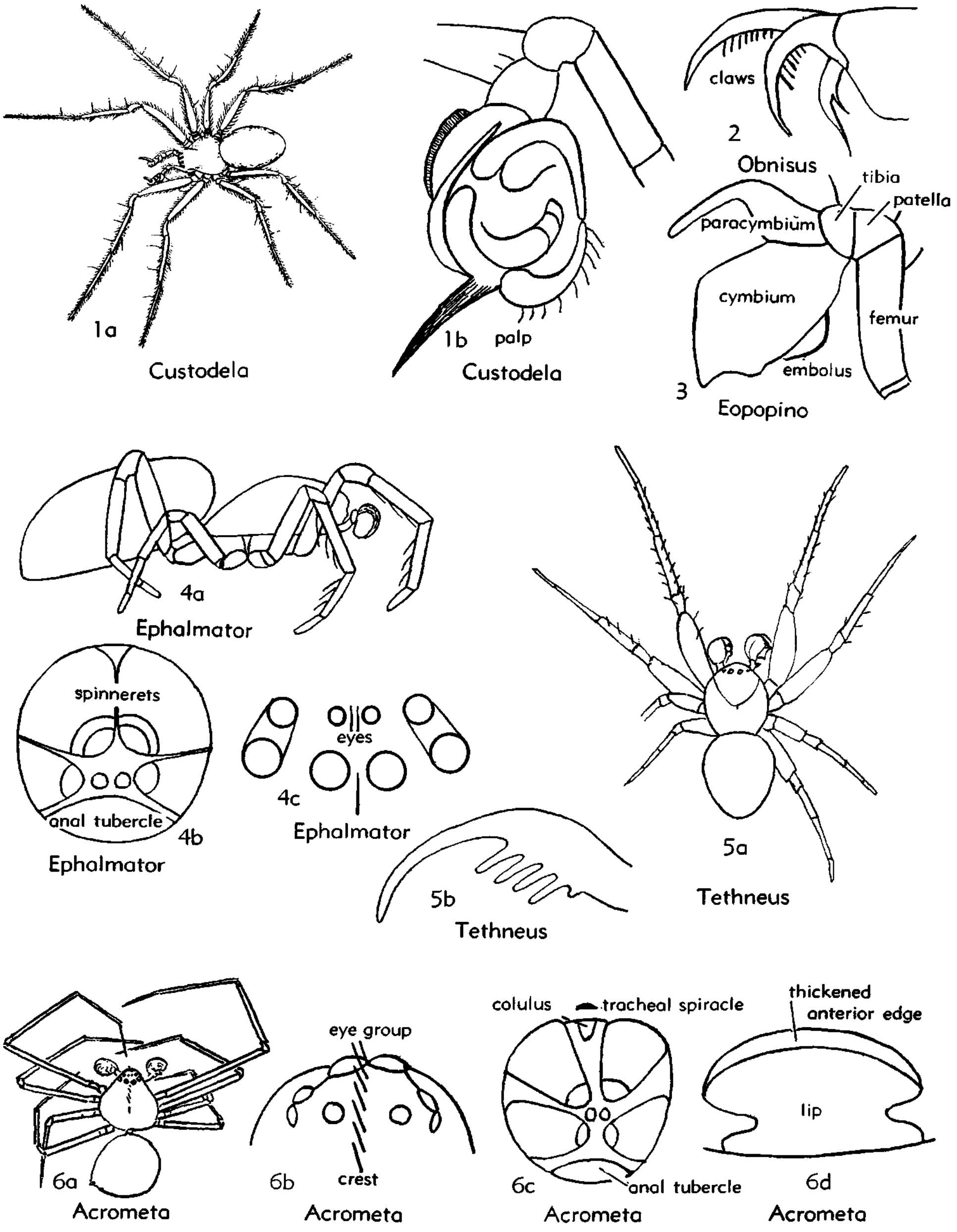


FIG. 106. Dipneumonina, Oligo. *1, Custodela cheiracantha,* Balt.; *1a,* male, ×3.3 (71); *1b,* its palp, enlarged (76). *2, Obnisus tenuipes,* Balt.; claws, enlarged. *3, Eopopino longipes,* Balt.; palp of male showing paracymbium and embolus, enlarged. *4, Ephalmator fossilis,* Balt.; *4a,* male, ×16; *4b,* its spinnerets, ×60; *4c,* its eye group, ×52. *5a, Tethneus robustus,* Colo.; male, ×3.3; *5b, Tethneus hentzi,* Colo.; claw, ×270. *6, Acrometa cristata,* Balt.; *6a,* male, ×8; *6b,* its eye group, ×25; *6c,* spinnerets, enlarged; *6d,* lip, showing thickened anterior edge, enlarged (76) (p. P144-P145).

Adjunctor PETRUNKEVITCH, 1942 [**A. similis*]. Several trichobothria on tibiae and metatarsi. Legs in order 4123. Third claw reduced to a thorn (37). *Oligo.*, Balt.

Family EPHALMATORIDAE Petrunkevitch, 1950

Anterior spinnerets much stouter than posterior ones. Chelicerae with transverse margins. First and 2nd tibia with several pairs of very long ventral spines. *Oligo.*

Ephalmator PETRUNKEVITCH, 1950 [**E. fossilis*]. Legs short, stout. Lateral eyes on common tubercle. Anterior median eyes smallest. Quadrangle much narrower in front (44). *Oligo.*, Eu.—FIG. 106,*4*. **E. fossilis,* Balt.; *4a,* holotype in side view, ×16; *4b*, spinnerets, ×60; *4c,* eye group, ×52 (76).

Family LINYPHIIDAE Dahl, 1913

Eyes heterogeneous. Chelicerae with oblique margins. Maxillae parallel. Legs slender, with 1 or 2 bristles, without spines. Pedipalp of male with paracymbium, of female with terminal claw. *Oligo.-Rec.*

Linyphia LATREILLE, 1804 [**Araneus triangularis* CLERCK, 1757]. Posterior eyes well separated. Margins of chelicerae with at least 3 teeth. *Oligo.-Rec.* [*L. seclusa* (SCUDDER), Oligo., Colo.].

Custodela PETRUNKEVITCH, 1942 [**Linyphia cheiracantha* KOCH & BERENDT, 1854]. Head higher than thorax. Order of legs 1243. Male palp with powerful spike directed forward (37). *Oligo.*, Eu.—FIGS. 31,*6* 106,*1*. **C. cheiracantha* (KOCH & BERENDT), Balt.; 31,*6*, photo of male, ×6; 106,*1a*, copy of figure of KOCH-B., ×3.3; *1b*, palp showing spike, enlarged (76).

Obnisus PETRUNKEVITCH, 1942 [**O. tenuipes*]. Carapace slightly narrowed in front. Legs in order 1243. Claws slightly dissimilar. Male palp with apophysis shaped like a pick-axe (37). *Oligo.*, Eu.—FIG. 106,*2*. *O. tenuipes,* Balt.; claws of 2nd leg, enlarged (76).

Eopopino PETRUNKEVITCH, 1942 [**E. longipes*]. Carapace almost circular. Lip much wider than long. Legs in order 1243 (37). *Oligo.*, Eu.—FIG. 106,*3*. **E. longipes,* Balt.; male palp, enlarged (76).

Meditrina PETRUNKEVITCH, 1942 [**M. circumvallata*]. Carapace with greatly thickened edges and pair of shoulder humps. Eyes on tubercles. Legs in order 1243 (37). *Oligo.*, Balt.

Malleator PETRUNKEVITCH, 1942 [**M. niger*]. Carapace almost circular. Legs in order 4123. Femur of male palp longer than carapace, tibia with terminal brush of long bristles (37). *Oligo.*, Balt.

Impulsor PETRUNKEVITCH, 1942 [**I. neglectus*]. Legs in order 4123. Lip pentagonal. Claws dissimilar (37). *Oligo.*, Balt.

Liticen PETRUNKEVITCH, 1942 [**L. setosus*]. Legs in order 1243, setose. All eyes on common tubercle (37). *Oligo.*, Balt.

Mystagogus PETRUNKEVITCH, 1942 [**M. glaber*] Legs in order 1243. Eyes on separate tubercles. Abdomen wider behind than in front (37). *Oligo.*, Balt.

Family ARANEIDAE Leach, 1819

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Araneadae LEACH, 1819)] [=Epeireides SUNDEVALL, 1833; Epeiridae BLACKWELL, 1859; Argiopidae SIMON, 1892]

Six spinnerets sitting in a circle or square, with colulus in front and anal tubercle behind. Lip with thickened anterior edge. Tarsi with spurious claws in addition to regular ones. Cheliceral margins oblique, with teeth. Maxillae parallel, wide in front. Legs with spines. Orb weavers. *Oligo.-Rec.*

Subfamily TETRAGNATHINAE Simon, 1892

Femora with single or double row of trichobothria. Chelicerae long. Body elongate. Orb web horizontal. *Oligo.-Rec.*

Tetragnatha LATREILLE, 1804 [**Aranea extensa* LINNÉ, 1757]. Chelicerae divergent, with long fangs. Abdomen 3 or 4 times longer than wide. *Oligo.-Rec.* [*T. tertiaria* SCUDDER, Oligo., Colo.].

Palaeopachygnatha PETRUNKEVITCH, 1922 [**P. scudderi*]. Abdomen oval. Carapace slightly longer than wide (37). *Oligo.*, Colo.

Palaeometa PETRUNKEVITCH, 1922 [**Theridium opertaneum* SCUDDER, 1890]. Carapace at least twice as long as wide. Eyes elevated (35). *Oligo.*, Colo.

Subfamily NEPHILINAE Simon, 1892

Metatarsus with tarsus longer than patella with tibia in all legs. Lip longer than wide. Body and legs long. Males many times smaller than females. Orb web vertical. *Oligo.-Rec.*

Nephila LEACH, 1815 [**Aranea maculata* FABRICIUS, 1793]. Carapace convex. Eye group almost as wide as head. Lateral eyes separated. *Oligo.-Rec.* [*N. pennatipes* SCUDDER, Oligo., Colo.].

Subfamily ARANEINAE Simon, 1892

Metatarsus with tarsus shorter than patella with tibia in all legs. Lip wider than long. Orb web vertical. *Oligo.-Rec.*

Epeira WALCKENAER, 1805 [**Aranea cornuta* LINNÉ, 1758]. First leg longer than 4th. Legs spinose; femora in females without ventral spines; tibiae and metatarsi in males with double row of ventral spines (37). *Oligo.-Rec.* [*E. vulcanalis* SCUDDER, Oligo., Colo.].

Tethneus SCUDDER, 1890 [**T. guyoti*]. First and 2nd femora very stout. Legs spinose (35). *Oligo.*, N.Am.—FIG. 106,*5a*. *T. robustus* PETRUNKEVITCH, Colo.; male, ×3.3 (76).—Fig. 106,*5b. T. hentzii* Scudder; claw of 1st left foot, ×270 (76).

Eustaloides Petrunkevitch, 1942 [**E. setosus*]. Carapace narrowed in front, with shoulder humps. Lateral eyes on common tubercle. Sternum triangular. *Oligo.,* Balt.

Subfamily METINAE Simon, 1892

Chelicerae with rudimentary boss. Sternum pointed behind. Legs with spines. *Oligo.-Rec.*

Acrometa Petrunkevitch, 1942 [**A. cristata*]. Carapace greatly narrowed in front, in middle twice as wide as eye group. Quadrangle of median eyes wider behind than in front. Male palp with spiral embolus (37). *Oligo.,* Eu.—Figs. 31,*4;* 102,*2;* 106,*6.* **A. cristata,* Balt.; 31,*4,* photo of male, ×12; 102,*2,* photo of holotype, ×12; 106, *6a,* dorsal side of male, ×8; 106,*6b,* eye group, ×25; 106,*6c,* spinnerets, enlarged; 106,*6d,* lip showing thickened edge, enlarged (76).

Theridiometa Petrunkevitch, 1942 [**T. edwardsi*].

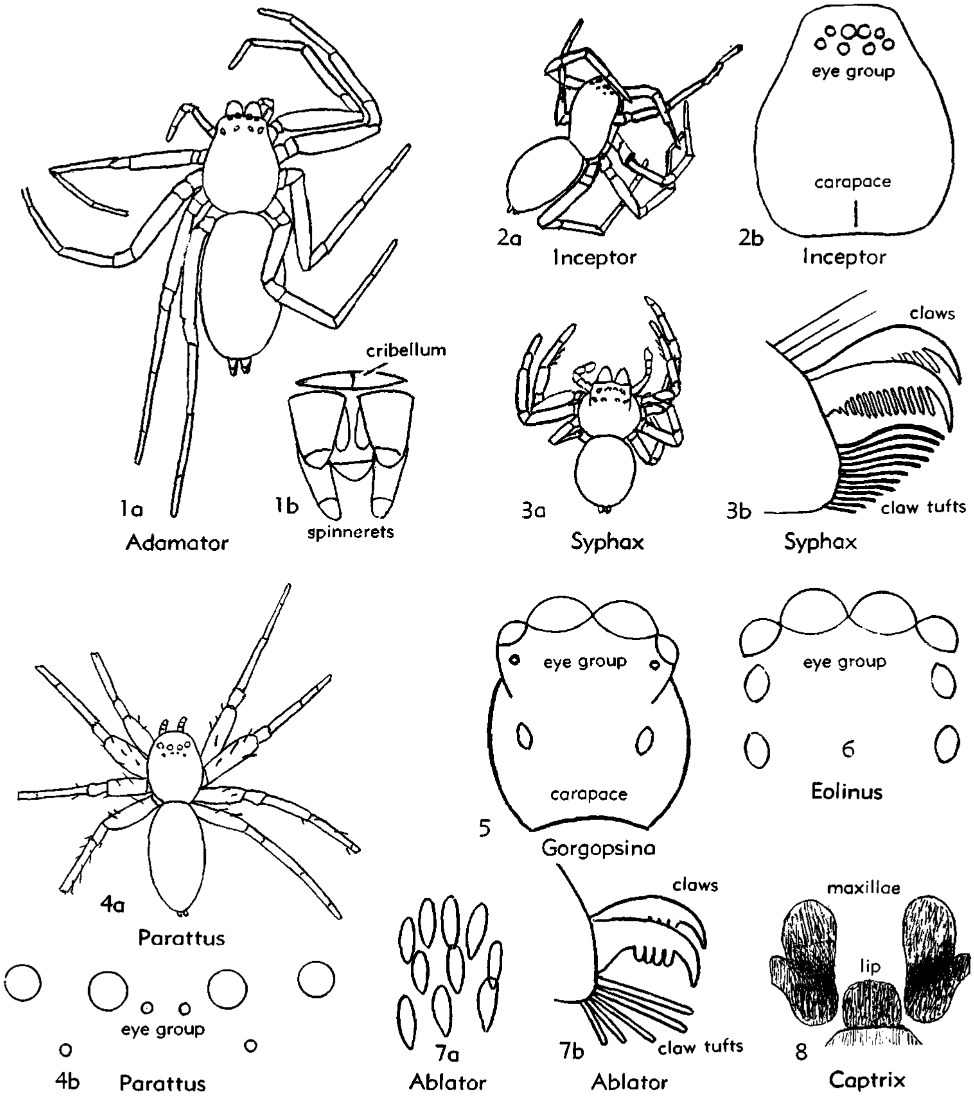


Fig. 107. Dipneumonina, Oligo. *1, Adamator succineus,* Balt.; *1a,* ×4; *1b,* its spinnerets with cribellum, enlarged. *2, Inceptor aculeatus,* Balt.; *2a,* ×10; *2b,* carapace, ×30. *3, Syphax crassipes,* Balt.; *3a,* ×4; *3b,* claws, enlarged. *4, Parattus evocatus,* Colo.; *4a,* ×3.3; *4b,* its eye group, ×29 (76). *5, Gorgopsina frenata,* Balt.; carapace of male, ×10. *6, Eolinus theryi,* Balt.; eye group, enlarged. *7, Ablator triguttatus,* Balt.; *7a,* scales, enlarged; *7b,* claws, enlarged (76). *8, Captrix lineata,* Balt., maxillae and lip, enlarged (76) (p. P146-P150).

Carapace narrowed in front. Eye group as wide as head (37). *Oligo.*, Balt.

Memoratrix Petrunkevitch, 1942 [**M. rydei*]. Carapace narrowed in front. First leg 9 times as long as carapace (37). *Oligo.*, Balt.

Subfamily THERIDIOSOMATINAE Simon, 1892

Sternum broadly truncated behind. Legs without spines. Third claw at least as long as upper claws. *Oligo.-Rec.*

Elucus Petrunkevitch, 1942 [**E. inermis*]. Head much wider than eye group. Clypeus as high as quadrangle. Sternum convex (37). *Oligo.*, Balt.

Superfamily ARCHAEOMETOIDEA Petrunkevitch, nov.

[*nom. transl.* Petrunkevitch, herein (*ex* Archaeometidae Petrunkevitch, 1949)]

Presumptive Trionychi with segmented abdomen. *Carb.*

Family ARCHAEOMETIDAE Petrunkevitch, 1949

Legs prograde. *Carb.*

Archaeometa Pocock, 1911 [**A. nephilina*]. Abdomen long, cylindrical. Carapace with almost parallel sides (45). *Carb.*, Eu.—Fig. 110,*2*. **A. nephilina*, Eng.; ×4.1 (76).

Arachnometa Petrunkevitch, 1949 [**A. tuberculata*]. Abdomen subconical. Carapace with strongly converging sides (45). *Carb.*, Eu.—Fig. 110,*1*. **A. tuberculata*, Eng.; ×4.1 (76).

Eopholcus Fritsch, 1904 [**E. pedatus*]. Abdomen almost globular. Carapace with pair of eyes (45). *Carb.*, Eu.—Fig. 110,*6*. **E. pedatus*, Czech., ×8.7 (76).

Division DIONYCHI Petrunkevitch, 1933

Dipneumone spiders with 2 claws and claw tufts. Three pairs of cardiac ostia. *Oligo.-Rec.*

Superfamily ZOROPSIDIOIDEA Simon, 1892

[*nom. correct.* Petrunkevitch, herein (*pro* Zoropidiformia Caporiacco, 1938, *nom. transl. ex* Zoropsidae Simon, 1892)]

Dionychi with cribellum and calamistrum. *Oligo.-Rec.*

Family ZOROPSIDAE Simon, 1892

Eyes homogeneous, in 2 rows. First and 2nd tarsi and metatarsi scopulate. Cribellum divided. *Oligo.-Rec.*

Adamator Petrunkevitch, 1942 [**A. succineus*]. Legs in order 4123. Both rows of eyes recurved, 2nd row much wider than 1st row (37). *Oligo.*, Eu.—Fig. 107,*1*. **A. succineus*, Balt.; *1a*, female, holotype, ×4; *1b*, spinnerets with divided cribellum, enlarged (76).

Superfamily THOMISOIDEA Sundevall, 1833

[*nom. correct.* Petrunkevitch, herein (*pro* Thomisiformia Caporiacco, 1938, *nom. transl. ex* Thomisidae Sundevall, 1833)]

Dionychi with laterigrade legs. Abdomen not segmented. *Oligo.-Rec.*

Family EUSPARASSIDAE Petrunkevitch, 1949

[=Sparassidae Bertkau, 1878]

Tarsi usually scopulate. Trichobothria numerous. Claws similar. *Oligo.-Rec.*

Subfamily EUSPARASSINAE Petrunkevitch, 1949

[=Sparassinae Simon, 1897]

Spinnerets normal. Ventral spines on anterior tibiae not unusually long. *Oligo.-Rec.*

Collacteus Petrunkevitch, 1942 [**C. captivus*]. Legs in order 4231. First and 2nd tarsi and metatarsi scopulate. *Oligo.*, Balt.

Caduceator Petrunkevitch, 1942 [**C. minutus*]. Legs in order 4213, without spines. Tarsi and metatarsi not scopulate (37). *Oligo.*, Eu.—Fig. 108,*1*. *C. quadrimaculatus* Petr., Balt.; *1a*, dorsal side showing coloration pattern, ×7.5; *1b*, eye group, ×45 (76).

Adulatrix Petrunkevitch, 1942 [**A. fusca*]. Legs in order 4213, with spines. First and 2nd tarsi and metatarsi scopulate (37). *Oligo.*, Balt.—Fig. 31,*5*. **A. fusca;* photo of ventral side of female, ×8.5 (76).

Zachria L.Koch, 1875 [**Z. flavicoma*]. Legs in order 2143. All tarsi scopulate. *Oligo.-Rec.* [*Z. peculiata* Petrunkevitch, Oligo., Balt.].

Subfamily SPARIANTHIDINAE Simon, 1897

Spinnerets on pedestal. Ventral spines on anterior tibiae and metatarsi very long and slender. *Oligo.-Rec.*

Eostasina Petrunkevitch, 1942 [**E. aculeata*]. Anterior metatarsi with 3 pairs of ventral spines (37). *Oligo.*, Balt.

Eostaianus Petrunkevitch, 1942 [**E. succini*]. Anterior metatarsi with 2 pairs of ventral spines (37). *Oligo.*, Balt.

Family SELENOPIDAE F.P.Cambridge, 1900

Body very flat. Eyes in 2 rows, 1st row with 6 eyes, 2nd row with 2 eyes. Eyes heterogeneous, posterior medians alone nocturnal. *Rec.*—Fig. 35. *Selenops* sp., a typical laterigrade spider from tropical Africa, ×6 (75).

Family THOMISIDAE Sundevall, 1833

Tarsi without scopula. Margins of chelicerae smooth, or with 2 or 3 teeth. Eyes homogeneous. Maxillae converging. *Oligo.-Rec.*

Subfamily STEPHANOPSINAE Simon, 1892

Anterior legs considerably longer than posterior ones; 1st leg longest. Hair simple. Claw tufts well developed. *Oligo.-Rec.*

Syphax KOCH & BERENDT, 1854 [**S. megacephalus*]. Head rectangular. Eyes on common tubercle. Quadrangle wider behind than in front (37). *Oligo.*, Eu.—FIGS. 31,*1*; 107,*3*. *S. crassipes* PETRUNKEVITCH, Balt.; 31,*1*, photo of male, ×6.5; 107,*3a*, dorsal side, ×4; 107,*3b*, claws and claw tufts, enlarged (76).

Facundia PETRUNKEVITCH, 1942 [**F. clara*]. First leg longest. Anterior median eyes much smaller than lateral eyes. Sternum suborbicular (37). *Oligo.*, Balt.

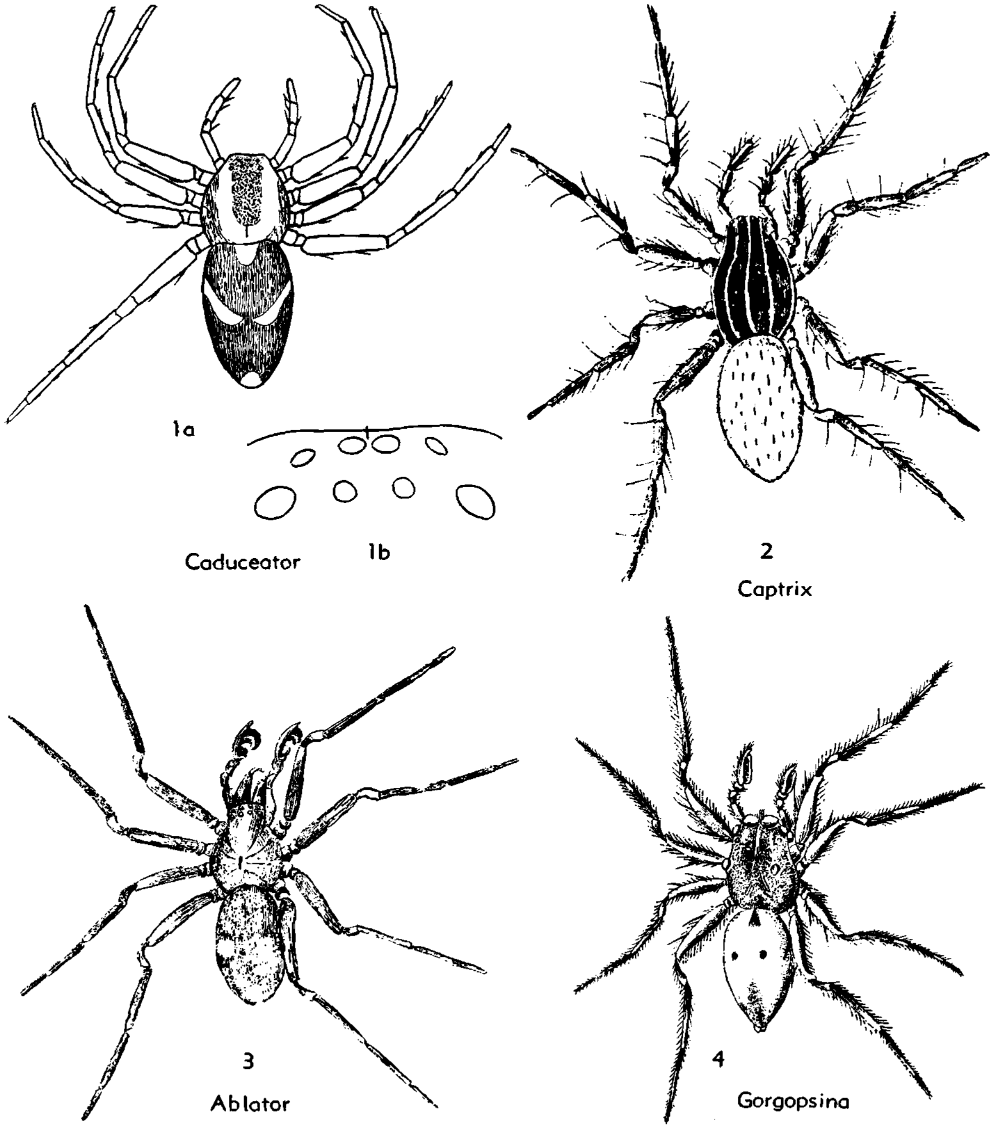


FIG. 108. Dipneumonina, Oligo., Balt. *1, Caduceator quadrimaculatus; 1a,* female, ×7.5; *1b,* its eye group, ×45 (76). *2, Captrix lineata,* ×7 (71). *3, Ablator triguttatus,* ×19 (71). *4, Gorgopsina melanocephala,* ×6 (71) (p. P146-P150).

Fiducia Petrunkevitch, 1942 [**F. tenuipes*]. First leg longest. Eyes of 1st row equal. Sternum triangular (37). *Oligo.*, Balt.

Subfamily THOMISINAE Sundevall, 1833

[*nom. transl.* Petrunkevitch, herein (*ex* Thomisidae Sundevall, 1833)] [=Misumeninae Simon *et auctt.*]

Second legs longest. *Oligo.-Rec.*

Thomisus Walckenaer, 1805 [**Aranea alba* Gmelin, 1788]. Face angular. Clypeus high. *Oligo.-Rec.* [*T. defossus* Scudder, Oligo., N.Am.(Colo.); *T. oeningensis* Heer, Mio., Switz.].

Misumena Latreille, 1804 [**Araneus vatius* Clerck, 1757]. Face obtusely truncate. Legs without spines (37). *Oligo.-Rec.* [*M. samlandica* Petrunkevitch, Oligo., Balt.].

Subfamily PHILODROMINAE Simon, 1892

Fourth legs longest. Integument with plumose or squamose hair. *Oligo.-Rec.*

Eothanatus Petrunkevitch, 1950 [**E. diritatis*]. Claw tufts present. Eyes sessile. *Oligo.*, Balt.

Medela Petrunkevitch, 1942 [**M. baltica*]. Claw tufts lacking. Eyes of 1st row smallest. Patella strongly angular. Hair simple. *Oligo.*, Balt.

Filiolella Petrunkevitch, *herein* [*nom. nov. pro Filiola* Petr., 1942 (ref. 37, p. 379) (*non* Barrande, 1881)] [**Filiola argentata* Petr., 1942]. Eyes subequal, on tubercle. Claw tufts lacking. Hair simple. *Oligo.*, Balt.

Superfamily PYRITARANEOIDEA Petrunkevitch, nov.

[*nom. transl.* Petrunkevitch, herein (*ex* Pyritaraneidae Petrunkevitch, 1953)]

Presumptive Dionychi with laterigrade legs and segmented abdomen. *Carb.*

Family PYRITARANEIDAE Petrunkevitch, 1953

Characters of superfamily. *Carb.*

Pyritaranea Fritsch, 1899 [**P. tubifera*]. Carapace longer than wide. Legs slender, long, in order 2134 (45). *Carb.*, Eu.—Fig. 110,*3*. **P. tubifera*, Czech.; dorsal side, ×22.5 (76).

Dinopilio Fritsch, 1904 [**D. gigas*]. Legs long, stout. Carapace not known (45). *Carb.*, Eu.—Fig. 110,*4*. **D. gigas;* holotype, ×1.5 (76).—Fig. 110, *5*. *D. parvus* Petrunkevitch, Eng.; ×2.5 (76).

Superfamily CLUBIONOIDEA Simon, 1895

[*nom. correct.* Petrunkevitch, herein (*pro* Clubioniformia Caporiacco, 1938, *nom. transl. ex* Clubionidae Simon, 1895] [=Clubioniformia (*partim*)+Gnaphosaeformia (*partim*) Caporiacco, 1938]

Eyes in 2 rows. Legs prograde. Tarsi scopulate. Trichobothria numerous, on tibiae, metatarsi and tarsi. *Oligo.-Rec.*

Family DRASSODIDAE Petrunkevitch, 1942

[=Gnaphosidae *auctt.*] [Name of family derived from *Drassodes* Westring, 1851, *nom. correct. pro Drassus* Walckenaer, 1805, of which it is a synonym; genotype of *Drassus* in doubt, changed twice, but of *Drassodes* undisputed. Family name Drassides Sundevall, 1833, used as Drassidae until 1949, has priority over Gnaphosidae]

Anterior spinnerets wide apart. Maxillae with oblique depression. Eyes heterogeneous. *Oligo.-Rec.*

Captrix Petrunkevitch, 1942 [**Textrix lineata* Koch & Berendt, 1854]. First row of eyes recurved, 2nd procurved. Quadrangle wider in front. *Oligo.*, Eu.—Figs. 107,*9*; 108,*2*. **C. lineata* (Koch & Berendt), Balt.; 107,*9*, lip and maxillae, enlarged (76); 108,*2*, female, ×7 (71).

Palaeodrassus Petrunkevitch, 1922 [**Titanoeca ingenua* Scudder, 1890]. Legs spinose, 4th leg longest. *Oligo.*, N.Am.(Colo.).

Family INCEPTORIDAE Petrunkevitch, 1942

Claw tufts wanting. Legs spinose, in order 4123. Cheliceral margins without teeth. *Oligo.*

Inceptor Petrunkevitch, 1942 [**I. aculeatus*]. Spines erect. Posterior median eyes half as large as anterior ones (37). *Oligo.*, Eu.—Fig. 107,*2*. **I. aculeatus*, Balt.; *2a*, holotype, ×10; *2b*, carapace with eyes, ×30 (76).

Family CLUBIONIDAE Simon, 1895

Anterior spinnerets contiguous. Eyes homogeneous, in 2 rows. Maxillae without oblique impression. *Oligo.-Rec.*

Subfamily CLUBIONINAE Simon, 1895

[*nom. transl.* Simon, 1903 (*ex* Clubionidae Simon, 1895)]

Terminal segment of posterior spinnerets conical. Maxillae constricted in middle. Integument with plumose hair. *Oligo.-Rec.*

Clubiona Latreille, 1804 [**Aranea holosericea* Linné, 1758 (=*Araneus pallidulus* Clerck, 1757)]. Maxillae parallel. Legs spinose, 4th leg longest. *Oligo.-Rec.* [*C. arcana* Scudder, Oligo., Colo.].

Eoversatrix Petrunkevitch, 1922 [**Clubiona eversa* Scudder, 1890]. Legs in order 1243. Hair simple (25). *Oligo.*, N.Am.(Colo.).

Eobumbratrix Petrunkevitch, 1922 [**Clubiona latebrosa* Scudder, 1890]. Legs in order 2431 (35). *Oligo.*, N.Am.(Colo.).

Eostentatrix Petrunkevitch, 1922 [**Clubiona ostentata* Scudder, 1890]. Legs in order 1423 (35). *Oligo.*, N.Am.(Colo.).

Subfamily MICARIINAE Simon, 1903

Terminal segment of posterior spinnerets rounded. Maxillae truncate in front. _Oligo.-Rec._

Massula PETRUNKEVITCH, 1942 [*_M. klebsi_]. Legs without scopulae. Maxillae with parallel sides. Hair simple. Order of legs 4123 (37). _Oligo._, Balt.

Ablator PETRUNKEVITCH, 1942 [*_Ocypete triguttata_ KOCH & BERENDT, 1854]. Legs with scopulae. Maxillae with ventrolateral protuberance. Legs in order 4123 (37). _Oligo._, Eu.—FIGS. 107,_7_; 108,_3_. *_A. triguttatus_ (KOCH & BERENDT), Balt.; 107,_7a_, scales from abdomen, enlarged; _7b_, claws and claw tufts enlarged (76); 108,_3_, male, ×19 (71).

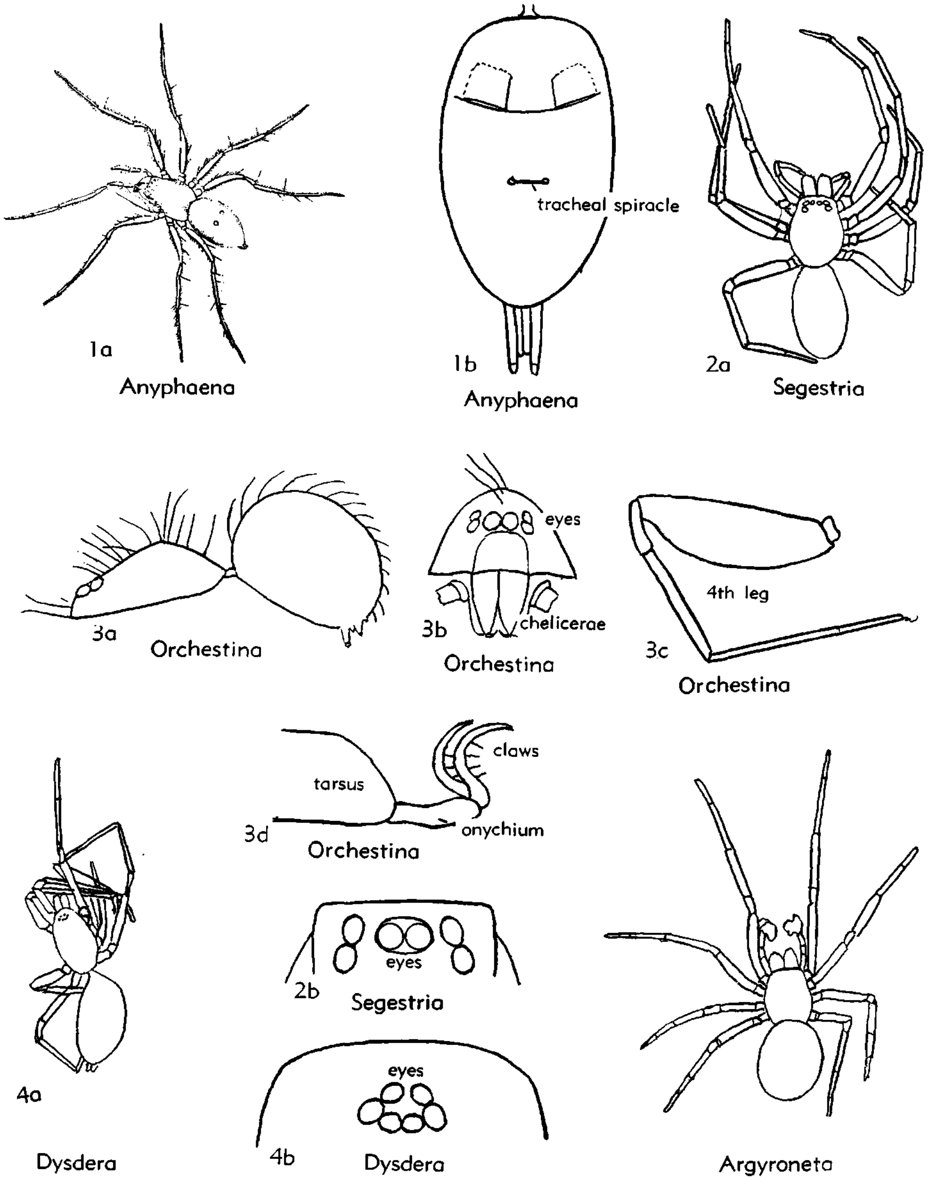


FIG. 109. Dipneumonina Quadrostiata. _1, Anyphaena fuscata,_ Oligo., Balt.; _1a,_ ×3 (71); _1b,_ ventral side of abdomen showing position of spiracle, ×20 (76). _2, Segestris elongata,_ Oligo., Balt.; _2a,_ ×6; _2b,_ eye group, enlarged. _3, Orchestina baltica,_ Oligo., Balt.; _3a,_ side view of body, ×20; _3b,_ face, ×40; _3c,_ 4th leg, ×90; _3d,_ claws on onychium, ×3,000. _4, Dysdera scobiculata,_ Oligo., Balt.; _4a,_ ×4; _4b,_ eye group, enlarged. _5, Argyroneta antiqua,_ Mio. (Brown Coal), Ger.; ×2 (76) (p. P151-P152).

Desultor Petrunkevitch, 1942 [**D. depressus*]. Eye group much narrower than head. Chelicerae geniculated. Order of legs 4123 (37). *Oligo.*, Balt.

Family PARATTIDAE Petrunkevitch, 1922

Eyes of 2nd row much smaller than those of 1st row. Posterior row strongly recurved and much shorter than anterior row. *Oligo.*

Parattus Scudder, 1890 [**P. resurrectus*]. Anterior eyes equidistant, slightly procurved (35). *Oligo.*, N.Am.—Fig. 107,*4b*. *P. oculatus* Petrunkevitch, Colo.; eye group, ×29 (76).—Fig. 107,*4a*. *P. evocatus* Scudder, Colo.; female, ×3.3 (76).

Superfamily SALTICOIDEA F.P.Cambridge, 1900

[*nom. correct.* Petrunkevitch, herein (*pro* Salticiformia Caporiacco, 1938, *nom. transl. ex* Salticidae F.P. Cambridge, 1900] [=Attidae *auctt.*]

Eyes in 3 or 4 rows, homogeneous. Legs adapted for jumping. Claw tufts well developed. Integument with simple hair and scales. *Oligo.-Rec.*

Family SALTICIDAE F.P. Cambridge, 1900

Eight eyes in 3 rows, 1st row with 4 large eyes. Legs spinose. *Oligo.-Rec.*

Subfamily HELIOPHANINAE Simon, 1903

Retromargin of chelicerae with single, pointed tooth. Sternum broadly truncate in front. Eyes of 2nd row almost equidistant from anterior and posterior lateral eyes. Fourth leg longer than 3rd. *Oligo.-Rec.*

Parevophrys Petrunkevitch, 1942 [**P. succini*]. Eyes of 2nd row small, with tuft of 4 stout bristles lateral to them. Anterior tibiae with lateral spines (37). *Oligo.*, Balt.

Subfamily GORGOPSININAE Petrunkevitch, 1942

[*nom. correct.* Petrunkevitch, herein (*pro* Gorgopidinae Petrunkevitch, 1942)]

Both margins of chelicerae smooth. Carapace transversely depressed between 2nd and 3rd row of eyes. Claw tufts dense. *Oligo.*

Gorgopsina Petrunkevitch, *nom. nov.* [*pro Gorgopis* Menge, 1854 (ref. 22, p. 93) (*non* Huebner, 1820)] [**Phidippus frenatus* Koch & Berendt, 1854]. Eyes of 2nd row small, situated on swollen base of anterior lateral eyes. Hair simple (37). *Oligo.*, Eu.—Fig. 107,*5*. **G. frenata* (Koch & Berendt), Balt.; carapace of male, ×10 (76).—Fig. 108,*4*. *G. melanocephala* (Koch & Berendt), Balt.; male, ×6 (71).

Subfamily BOETHINAE Simon, 1903

Retromargin of chelicerae with several teeth. Eyes of 2nd row subequal in size to those of 3rd row. *Oligo.-Rec.*

Eolinus Petrunkevitch, 1942 [**E. succineus*]. Legs in order 4132. First tibia without dorsal spines (37). *Oligo.*, Eu.—Fig. 31,*2*; 107,*6*. *E. theryi* Petr., Balt.; 31,*2*, photo of immature female, ×11; 107,*6*, eye group, enlarged (76).

Paralinus Petrunkevitch, 1942 [**P. crosbyi*]. Legs in order 4312. Tibiae with at least 2 dorsal spines (37). *Oligo.*, Balt.

Cenattus Petrunkevitch, 1942 [**C. exophthalmicus*]. Legs in order 4312. All eyes on pedestals. Third row of eyes wider than head (37). *Oligo.*, Balt.

SALTICIDAE Incertae sedis

Eoattopsis Petrunkevitch, *nom. nov.* [*pro Attopsis* Gourret, 1886 (Rec. Zool. Suisse, v. 4, p. 441) (*non* Heer, 1849)] [**A. hirsutus* Gourret, 1886]. Thorax higher than head. Second leg longest, 3rd leg shortest. *Oligo.*, Fr.

Attoides Brongniart, 1901 [**A. eresiformis*]. Carapace low and long. Eye group narrower behind than in front. Legs in order 1243. Tibia of male palp with long and straight, prolateral apophysis. *Oligo.*, Fr.

Steneattus Bronn, 1856, *nom. subst.* [*pro Leda* Koch & Berendt, 1854 (*non* Schumacher, 1817)] [**Leda promissa* Koch & Berendt, 1854]. Head with parallel sides, almost as wide as thorax. Sternum heart-shaped. Legs thin. *Oligo.*, Balt.

Propetes Menge, 1854 [*P. felinus* (first species of 5 listed)]. Only character mentioned: eyes of 2nd row almost as large as those of 3rd row. *Oligo.*, Balt.

Division QUADROSTIATI Petrunkevitch, 1933

Dipneumone spiders with 2 pairs of cardiac ostia. *Oligo.-Rec.*

Superfamily DYSDEROIDEA C.L.Koch, 1837

[*nom. correct.* Petrunkevitch, herein (*pro* Dysderaeformia Caporiacco, 1938, *nom. transl. ex* Dysderidae C.L Koch, 1837)]

A pair of tracheal spiracles close behind openings of book lungs. *Oligo.-Rec.*

Family SEGESTRIIDAE Petrunkevitch, 1933

Third pair of legs directed forward. Three claws. Six eyes, homogeneous, in 2 rows, 1st row of 4 eyes, the 2 eyes of posterior row wide apart. *Oligo.-Rec.*

Segestria LATREILLE, 1804 [**Aranea florentina* ROSSI, 1790]. Retromargin of chelicerae with 2 teeth (37). *Oligo.-Rec.*—FIG. 109,*2*. *S. elongata* KOCH & BERENDT, Oligo., Balt.; *2a,* female, ×6; *2b,* eye group, enlarged (76).

Family DYSDERIDAE C.L.Koch, 1837

Third pair of legs directed backward; 2 or 3 claws. Six eyes, homogeneous, arranged in a more or less closed, transverse ellipse. *Oligo.-Rec.*

Dysdera LATREILLE, 1804 [**D. erythrina*]. Two claws. Terminal segment of posterior spinnerets with several spinning tubes (37). *Oligo.-Rec.*—FIG. 109,*4*. *D. scobiculata* MENGE, Oligo., Balt.; *4a,* female, ×4; *4b,* eye group, enlarged (76).

Harpactes TEMPLETON, 1834 [**Aranea hombergi* SCOPOLI, 1763]. Three claws. Terminal segment of posterior spinnerets with a single spinning tube. *Oligo.-Rec.* [*H. extinctus* PETRUNKEVITCH, Oligo., Balt.].

Thereola PETRUNKEVITCH, *nom. nov.* [*pro Therea*

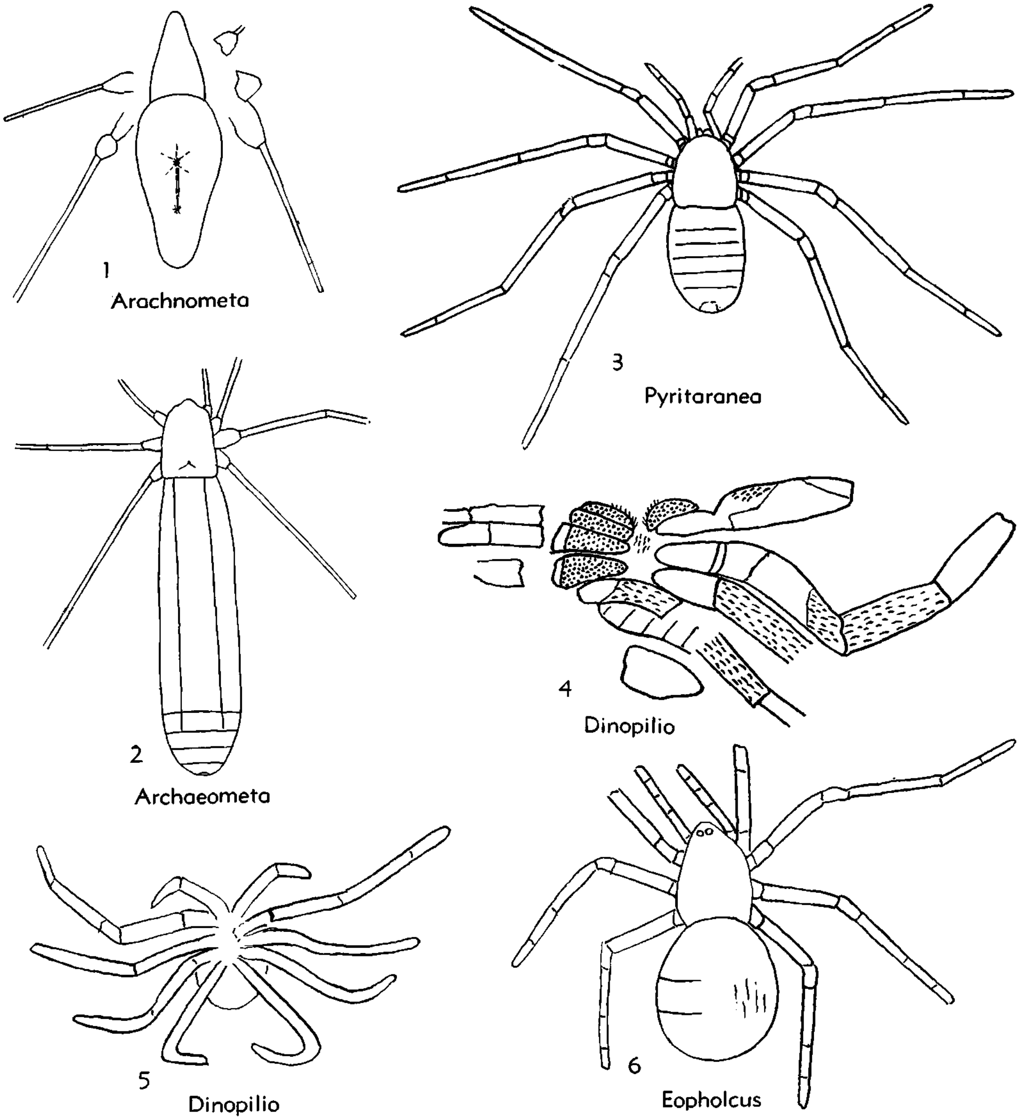


FIG. 110. Presumptive Dipneumonina, U.Carb. *1, Arachnometa tuberculata,* Eng.; ×4.1. *2, Archaeometa nephilina,* Eng.; ×4.1. *3, Pyritaranea tubifera,* Czech.; ×22.5. *4, Dinopilio gigas,* Czech.; ×1.5. *5, Dinopilio parvus,* Eng.; ×2.5. *6, Eopholcus pedatus,* Czech.; ×8.7 (76) (p. P146-P148).

KOCH & BERENDT, 1854 (ref. 22, p. 75) (*non* BILBERG, 1820)] [**T. petiolata*]. Anterior pair of eyes on a transversely elliptic tubercle. Claws not known. *Oligo.*, Balt.

Family OONOPIDAE Simon, 1892

Six eyes, homogeneous, nocturnal. Two claws on onychium. *Oligo.-Rec.*

Orchestina SIMON, 1892 [**O. pavesii*]. Abdomen with soft integument. Fourth pair of legs longest, adapted for jumping, with distended femur (37). *Oligo.-Rec.*—FIG. 109,*3*. *O. baltica* PETRUNKEVITCH, Oligo., Balt.; *3a,* side view of body, ×20; *3b,* face, ×40; *3c,* 4th leg, ×90; *3d,* claws, ×3,000 (76).

Superfamily ANYPHAENOIDEA Bertkau, 1878

[*nom. transl.* PETRUNKEVITCH, herein (*ex* Anyphaenidae BERTKAU, 1878)]

Tracheal spiracle single. Two claws. *Oligo.-Rec.*

Family ANYPHAENIDAE Bertkau, 1878

Eight eyes, homogeneous, sessile, in 2 rows. Tarsi scopulate. *Oligo.-Rec.*

Anyphaena SUNDEVALL, 1833 [**Aranea accentuata* WALCKENAER, 1802]. Retromargin of chelicerae with several teeth. Eyes of 1st row subequal (37). *Oligo.-Rec.*—FIG. 109,*1*. *A. fuscata* KOCH & BERENDT, Oligo., Balt.; *1a,* female, ×3 (71); *1b,* ventral side of abdomen, showing position of tracheal spiracle, ×20 (76).

Superfamily ARGYRONETOIDEA Menge, 1869

[*nom. transl.* PETRUNKEVITCH, herein (*ex* Argyronetidae MENGE, 1869)]

Tracheal spiracle single. Three claws. *Oligo.-Rec.*

Family ARGYRONETIDAE Menge, 1869

Aquatic spiders building a bell-shaped web under water. Eight eyes, heterogeneous, in 2 rows. *Mio.-Rec.*

Argyroneta LATREILLE, 1804 [**Aranea aquatica* LINNÉ, 1758]. Legs in order 4123. Retromargin of chelicerae with 2 teeth (37). *Mio.-Rec.*—FIG. 109,*5*. *A. antiqua* VAN HEYDEN, Mio., Ger.; male, ×2 (76).

Suborder APNEUMONINA Dahl, 1913

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Apneumones DAHL, 1913)] [Type: *Caponia* SIMON, 1887]

Araneida with diaxial chelicerae, 1 or 2 pairs of tracheal tubes in place of book lungs which are always lacking, and 2 pairs of cardiac ostia (36). No fossil spiders of this suborder have ever been found. *Rec.*

ARANEIDA INCERTAE SEDIS

Although all genera listed in this section have been placed by their respective authors in one or another family, none of them can now be placed in any known family, because their figures and descriptions are quite inadequate for correct placement. Even C. L. KOCH and MENGE, both very distinguished arachnologists of their time, are not exempt from this failure, because our knowledge has greatly progressed since their time. To list these genera in the families to which they were assigned by their authors, would be only misleading and contrary to scientific principles. For the same reason I have abstained from giving new names to such generic names as are preoccupied but cannot be placed. In absence of their type specimens which are reported to be lost or destroyed, a new name would be futile and contrary to all sense.

Amphiclotho GOURRET, 1886 [**A. breviuscula*]. *Oligo.*

Amphithomisus GOURRET, 1886 [**A. barbatus*]. *Oligo.*

Anandrus MENGE, 1856 (*nom. nud.*). *Oligo.*

Anatone MENGE, 1854 [**A. spinipes*]. *Oligo.*

Androgeus KOCH & BERENDT, 1854 [**A. militaris*]. *Oligo.*

Antopia MENGE, 1854 [**A. punctulata*]. *Oligo.*

Athera MENGE, 1856 [**A. exilis*]. *Oligo.*

Cercidiella GOURRET, 1886 [**C. aequisextana*]. *Oligo.*

Clubionella GOURRET, 1886 [**C. antiqua*]. *Oligo.*

Clya KOCH & BERENDT, 1854 [**C. lugubris*]. *Oligo.*

Clythia KOCH & BERENDT, 1854 [**C. alma*]. *Oligo.*

Corynitis MENGE, 1854 [**C. spinosa*]. *Oligo.*

Dielacata MENGE, 1856 (*nom. nud.*). *Oligo.*

Entomocephalus HOLL, 1829 [**E. formicoides*]. *Oligo.*

Eresioides GOURRET, 1886 [**E. orbicularis*]. *Oligo.*

Erithus MENGE, 1854 [**E. applanatus*]. *Oligo.*

Hersilioides GOURRET, 1886 [*H. thanatiformis*]. *Oligo.*

Heteromma MENGE, 1854 [**H. intersecta*]. *Oligo.*

Idmonia MENGE, 1854 [**I. virginea*]. *Oligo.*

Linoptes MENGE, 1854 [**L. oculeus*]. *Oligo.*

Lycosoides GOURRET, 1886 [**L. hersiliiformis*]. See *Trimeropus.*

Mastigusa MENGE, 1854 [**M. acuminata*]. *Oligo.*

Mizalia KOCH & BERENDT, 1854 [**M. punctulata*]. *Oligo.*

Ocia MENGE, 1854 (*nom. nud.*). *Oligo.*

Onca MENGE, 1854 [**O. pumila*]. *Oligo.*

Opisthophylax MENGE, 1856 [**O. exarata*]. *Oligo.*

Phalangopus MENGE, 1854 [*P. *subtilis*]. *Oligo.*

Prodysdera GOURRET, 1886 [*P. *intermedia*]. *Oligo.*

Protochersis GOURRET, 1886 [*P. *spinosus*]. *Oligo.*

Protolachesis GOURRET, 1886 [*P. *annulata*]. *Oligo.*

Protolycosa GOURRET, 1886 [*non.* RÖMER, 1866] [*P. *attiformis*]. *Oligo.*

Pseudothomisus GOURRET, 1886 [*P. *articulatus*]. *Oligo.*

Pytonyssa C.L. KOCH, 1837 [=*Gnaphosa* LATREILLE, 1804]. *Rec.*

Schellenbergia HEER, 1865 [*S. *rotundata*]. *Mio.*

Sphaeconia MENGE, 1854 [*S. *brevipes*]. *Oligo.*

Sosybius KOCH & BERENDT, 1854 [*S. *minor*]. *Oligo.*

Thyelia KOCH & BERENDT, 1854 [*T. *tristis*]. *Oligo.*

Trimeropus THORELL, 1891 [*nom. subst. pro Lycosoides* GOURRET, 1886 [*non* LUCAS, 1846)] [*L. *hersiliiformis*]. *Oligo.*

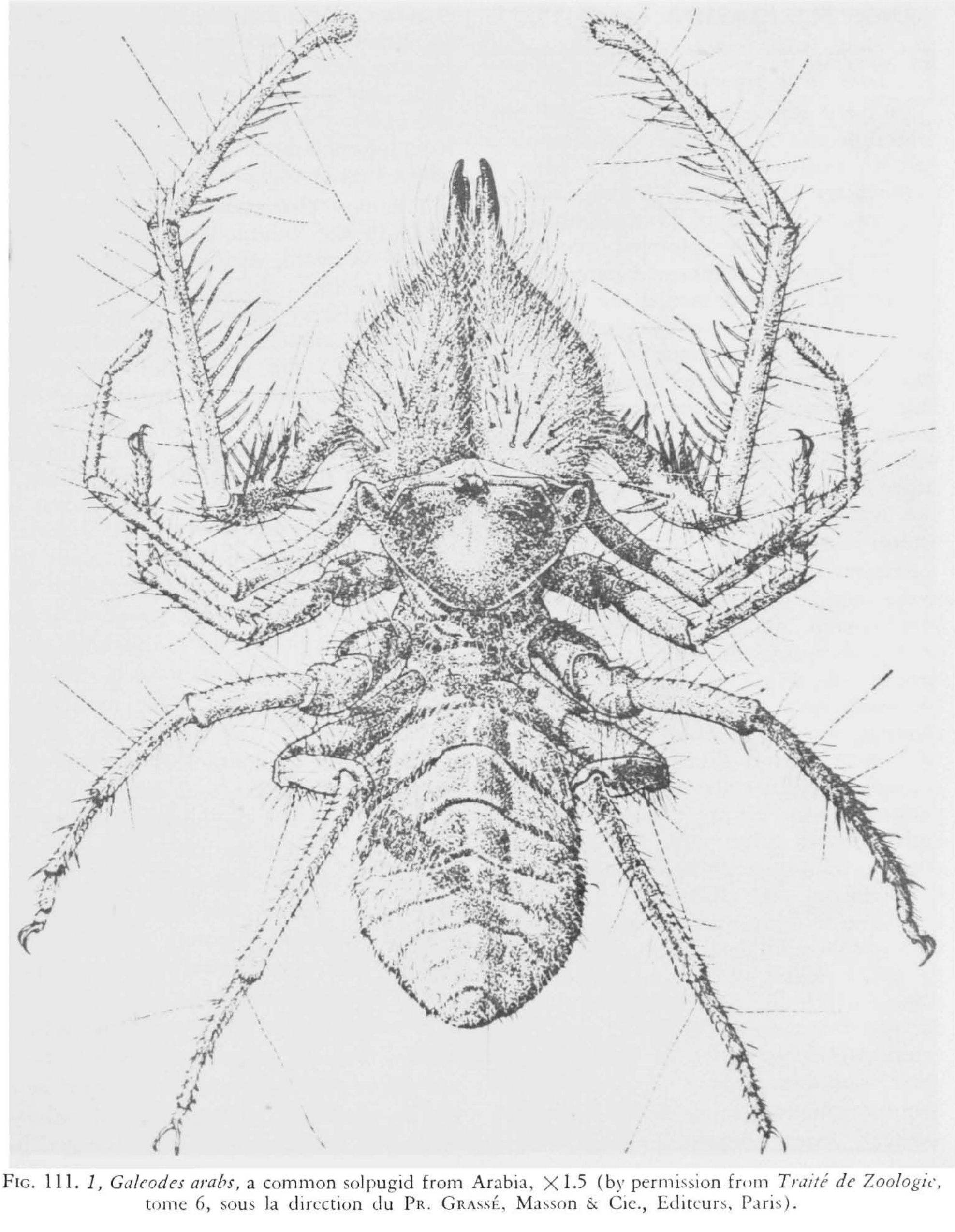


FIG. 111. *1, Galeodes arabs*, a common solpugid from Arabia, ×1.5 (by permission from *Traité de Zoologie*, tome 6, sous la direction du PR. GRASSÉ, Masson & Cie., Editeurs, Paris).

Superorder ROSTRATA Petrunkevitch, 1949

[Type: *Galeodes* OLIVIER, 1791] [=Mycetophorae LANKESTER, 1910]

Caulogastra with secondary mouth opening at end of beak formed by fusion of upper lip with deuterosternite. *Carb.-Rec.*

Order SOLPUGIDA Leach, 1815

[*nom. correct.*, PEARSE, 1936 (*pro* Solpugidea CAMBRIDGE, 1872, *pro* Solpugae C.L. KOCH, 1842, *pro* Fam. I. Solpugides LEACH, 1815)] [=Solifugae SUNDEVALL, 1833]

Carapace segmented, composed of propeltidium and 3 thoracic tergites, with a pair of median eyes and 1 or 2 pairs of rudimentary lateral eyes on propeltidium. Abdomen composed of 11 segments (Fig. 112,*2a*). Chelicerae 2-jointed, powerful, chelate. Pedipalpi pediform, 6-jointed. First pair of legs 7-jointed, tactile; the other legs 8-jointed, with a pair of long claws on an onychium. Ventral surface of 4th legs always with racket organs (malleoli) (Fig. 112,*2b*, showing anterior sternites of abdomen and 3 proximal joints of 4th legs with malleoli; Fig. 112,*2d*, malleolus enlarged). Anus on 11th (last) segment, slit-like, without operculum, terminal in some, ventral in others.

Respiration by means of tracheae opening to the outside by 7 spiracles, as follows: 1st pair between 2nd and 3rd coxae; 2nd pair on 3rd abdominal sternite; 3rd pair on 4th sternite; 7th, single opening on 5th sternite. No book lungs. Fore-gut with pumping pharynx, esophagus and rudimentary gizzard. Anterior end of rostrum (beak) with a brush of bristles serving as filtering apparatus. Cavity of rostrum serves as secondary mouth cavity with primary mouth opening into it at its base. Mid-gut with thoracenteron and chylenteron. Hind-gut short. Pair of coxal glands in cephalothorax, with openings on dorsal surface of pedipalpal coxae. Heart with 8 pairs of ostia, 2 pairs of which are in cephalothorax, 6 in abdomen. Nervous system with 5 abdominal neuromeres incorporated in thoracic ganglionic mass, remaining 5 pairs forming abdominal ganglionic mass in 6th abdominal segment. Sexes separate. In both sexes a single median genital opening on 2nd abdominal sternite. Oviparous. *Carb.-Rec.*

DISCUSSION

Solpugida are tropical and subtropical arachnids with a few species in moderate zones (Fig. 111, *Galeodes arabs*, ×1.4, from N.Africa and Arabia). They are swift runners and on account of their chelicerae were always feared and supposed to be poisonous. But none of them have poison glands. Like the majority of arachnids, they are carnivorous, feeding on insects. In mating the male uses the fingers of his chelicerae for the introduction of the spermatophores into the female genital opening, after having picked them up from the ground on which they were ejected by him.

The most characteristic external features are: (1) the enormous chelicerae, always directed forward, with movable finger ventral in position, the structure of the chelicerae furnishing secondary sexual characters by which males can be distinguished from females; (2) the shape and size of the propeltidium which, in conjunction with the chelicerae, gives the solpugids the appearance of an arthropod with a distinct head as in insects; (3) the shape of the 3 thoracic tergites which are independent of each other; (4) the stout pedipalpi with a blunt end bearing an adhesive organ; (5) the slender 1st legs, tactile in function and held upward; (6) the configuration of the coxosternal region (Fig. 112,*1*) with complete absence of externally visible thoracic sternites, 2nd and 3rd coxae meeting in median line; (7) the construction of the trochanters of 2nd, 3rd and 4th legs of 2 joints; (8) the clear segmentation of the abdomen; and (9) the possession of racket organs, not found in any other order of arachnids. In size Solpugida vary from 9 to 70 mm. Recent Solpugida are divided into 10 families, 134 genera and about 600 species. The only known fossil species is placed here provisionally in a Recent family. It is probable that it belongs to an extinct family, but its preservation is not good enough to permit the erection of a new family. Its placement in the family Galeodidae is entirely arbitrary and was motivated by the fact that this family has a wide Old-World distribution.

Family GALEODIDAE Pocock, 1897

Anus terminal. A pair of small claws at end of 1st tarsus. *Carb.-Rec.*

Protosolpuga PETRUNKEVITCH, 1913 [**P. carbonaria*]. Eyes lacking. Pedipalpi stout and long. *Penn.*, N.Am.—FIG. 112,*3*. **P. carbonaria,* Ill.; ×2 (drawing corrected from original after re-examination of holotype) (76).

Superorder PODOGONA Cook, 1899

[Type: *Ricinoides* EWING, 1929 (=*Cryptostemma* GUÉRIN, 1838)] [=Cucullifera PETRUNKEVITCH, 1945]

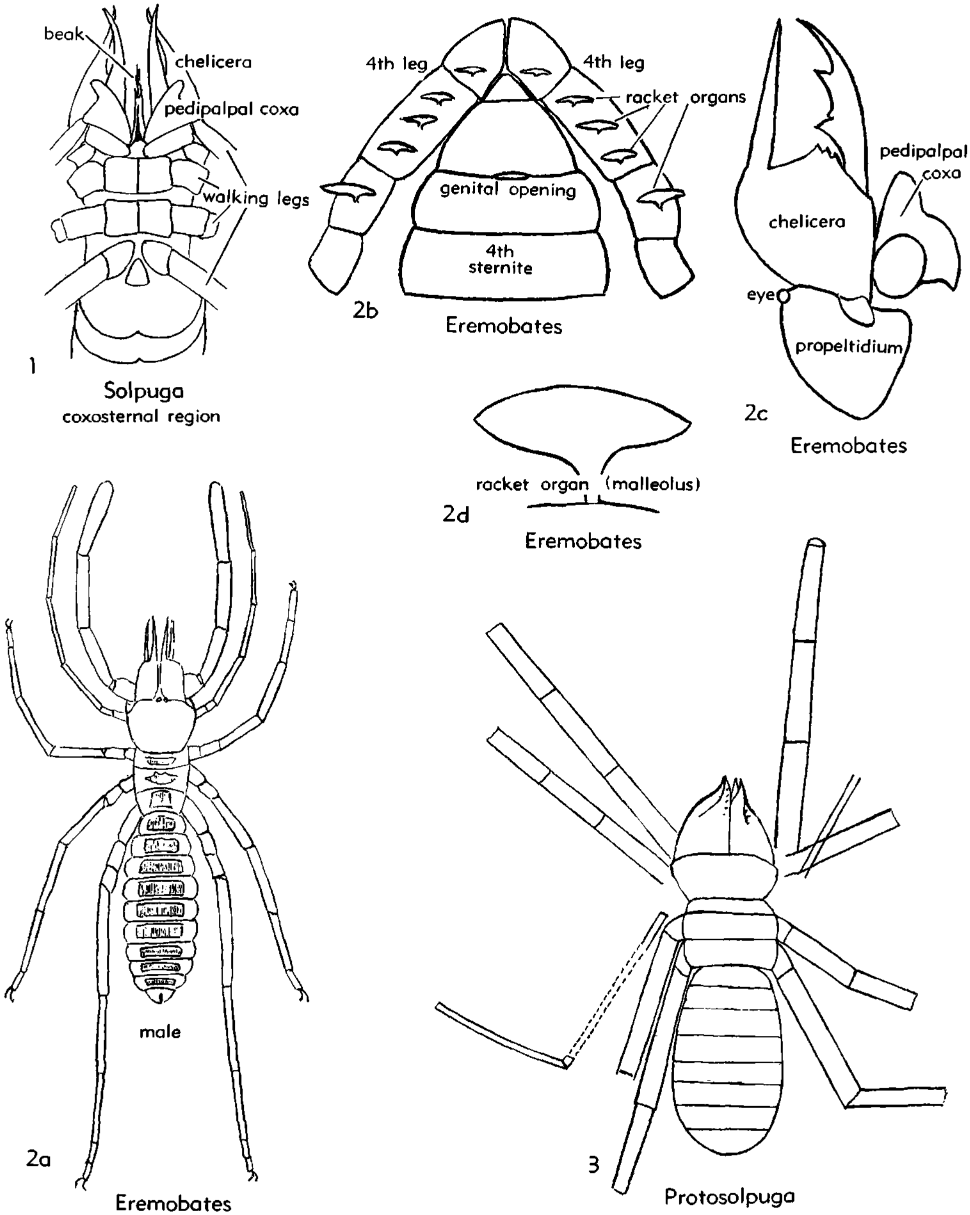


FIG. 112. *1, Solpuga venator,* Rec., S.Afr.; coxosternal region. *2, Eremobates pallipes,* Rec., USA; *2a,* adult; *2b,* proximal segments of 4th legs with racket organs; *2c,* side view of propeltidium and right chelicera; *2d,* racket organ enlarged. *3, Protosolpuga carbonaria,* Penn., Ill.; ×3 (76).

Caulogastra with movable plate (cucullus) in front of the carapace. *Carb.-Rec.*

Order RICINULEIDA Thorell, 1892

[*nom. correct.* PETRUNKEVITCH, herein (*pro* Ricinulei THORELL, 1892)] [Type: *Ricinoides* EWING, 1929] [=Rhinogastra COOK, 1899)]

Carapace entire, with a cucullus articulated to its anterior edge and capable of covering chelicerae from below (Fig. 113, *Cryptocellus foedus* female, dorsal side, ×10). Eyes wanting. First abdominal embryonic segment completely lost; abdomen of adult composed of 9 segments, the 1st of which (embryonic 2nd) forms petiolus and is concealed under dorsal anterior edge of following segment. Last 3 segments reduced to a pygidium. Chelicerae 2-jointed, chelate (Fig. 114,*1,* coxosternal region of *Cryprocellus dorotheae* GERTSCH, enlarged), their movable finger lateral and longer than immobile one. Pedipalpi 6-jointed, chelate, their coxae fused in median line, forming with the upper lip a camarostome similar to that in Thelyphonida and Schizomida. Pedipalpal tibia longest of the 6 joints, chela small, with movable finger longer than immobile one. First pair of legs 7-jointed, with single-jointed trochanter and tarsus; 2nd pair also with single-jointed trochanter, but with 5-jointed tarsus; 3rd pair with 2-jointed trochanter and 4-jointed tarsus; 4th pair also with 2-jointed trochanter, but 5-jointed tarsus. Only 4th coxae movable. Metatarsus and tarsus of 3rd pair of legs in males modified as organs of copulation and have the shape of a scoop, presumably to hold sperm. At end of all tarsi a pair of curved, smooth claws concealed in a depression of the tip. Body and legs heavily sclerotized. Sexes separate. Oviparous. Tropical and subtropical arachnids from 4 to 10 mm. in size. *Carb.-Rec.*

DISCUSSION

The juncture between the cephalothorax and the abdomen is accomplished by the 1st (embryonic 2nd) abdominal segment, and the abdomen is held in position by a

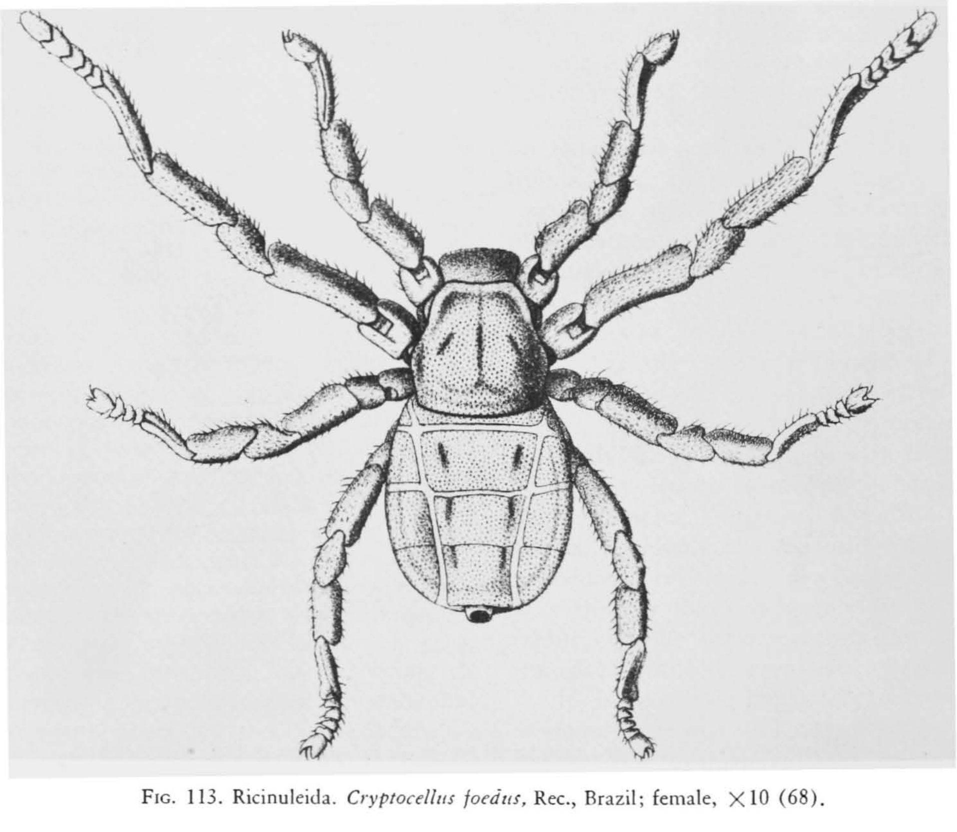


FIG. 113. Ricinuleida. *Cryptocellus foedus,* Rec., Brazil; female, ×10 (68).

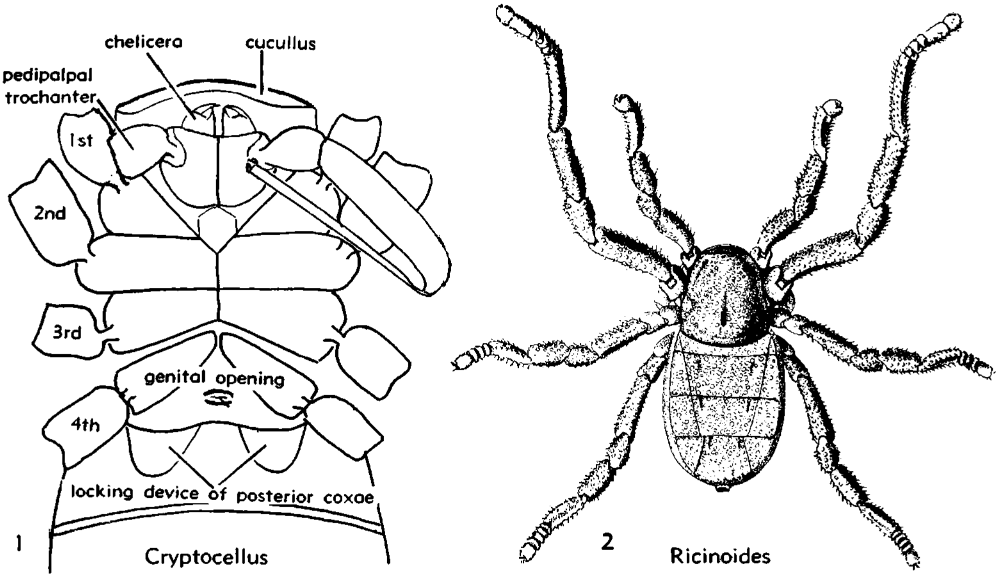


FIG. 114. Ricinuleida. *1, Cryptocellus dorotheae,* Rec., Tex.; coxosternal region, enlarged (76). *2, Ricinoides karschii,* Rec., Afr.; female, ×5 (68).

ridge of the posterior edge of the carapace fitting into a transverse groove on the 2nd (1st visible) abdominal tergite, which is in reality the tergite of the 3rd embryonic segment. The coupling is aided by the 4th coxae fitting into a pair of pouches of the postgenital sternite (Fig. 114,*1*). In consequence of such coupling, the animal appears to have a broad juncture between the carapace and the abdomen, and the 1st visible tergite looks like the true 1st tergite, whereas it is the tergite of the 2nd (embryonic 3rd) segment. Thus in all Recent Ricinuleida, and in the Carboniferous ones of the family Poliocheridae, only 4 tergites are visible, longitudinally divided by a pair of grooves into a median and a pair of lateral plates. The sternites are entire in Recent Ricinuleida and fossil Poliocheridae. On the other hand, in fossil Curculioididae the back of the abdomen, with exception of the pygidium, is covered by a single shield which is longitudinally divided by a median line, thus giving the arachnid the appearance of an insect with a pair of elytra (Fig. 115,*2b*). At the same time their 3rd, 4th and 5th abdominal sternites are subdivided by a pair of longitudinal lines into a median and a pair of lateral plates (Fig. 115,*2a*). The pygidium is always composed of 3 cylindrical segments which are telescoped in Recent species, but fully exposed in fossil ones.

As in Camarostomata, the mouth opens into the camarostome which serves as filter. The pharynx is quite rudimentary, the esophagus short. It opens into a true, pumping gizzard (according to my own, not yet published observations). The diverticles of the mid-gut are almost entirely restricted to the abdomen where they represent a true chylenteron, although arranged more or less longitudinally. Respiration is accomplished by tracheae which open by a pair of spiracles above 3rd coxae. Nervous system entirely concentrated in the cephalothorax. Nothing is known of the life and development of Ricinuleida, except that they pass through a 6-legged larval stage.

Ricinuleida are a small order represented by a single Recent family with 2 genera and 16 species and 2 fossil families with 2 genera and 9 species. Both Carboniferous families are extinct. The differences between the Carboniferous family Curculioididae and the Recent family Ricinoididae are great and it seems certain that the former represent the end of a special evolutionary line. The Carboniferous Poliocheridae are in many respects closely related to the Recent Ricinoididae. Their abdomen has the

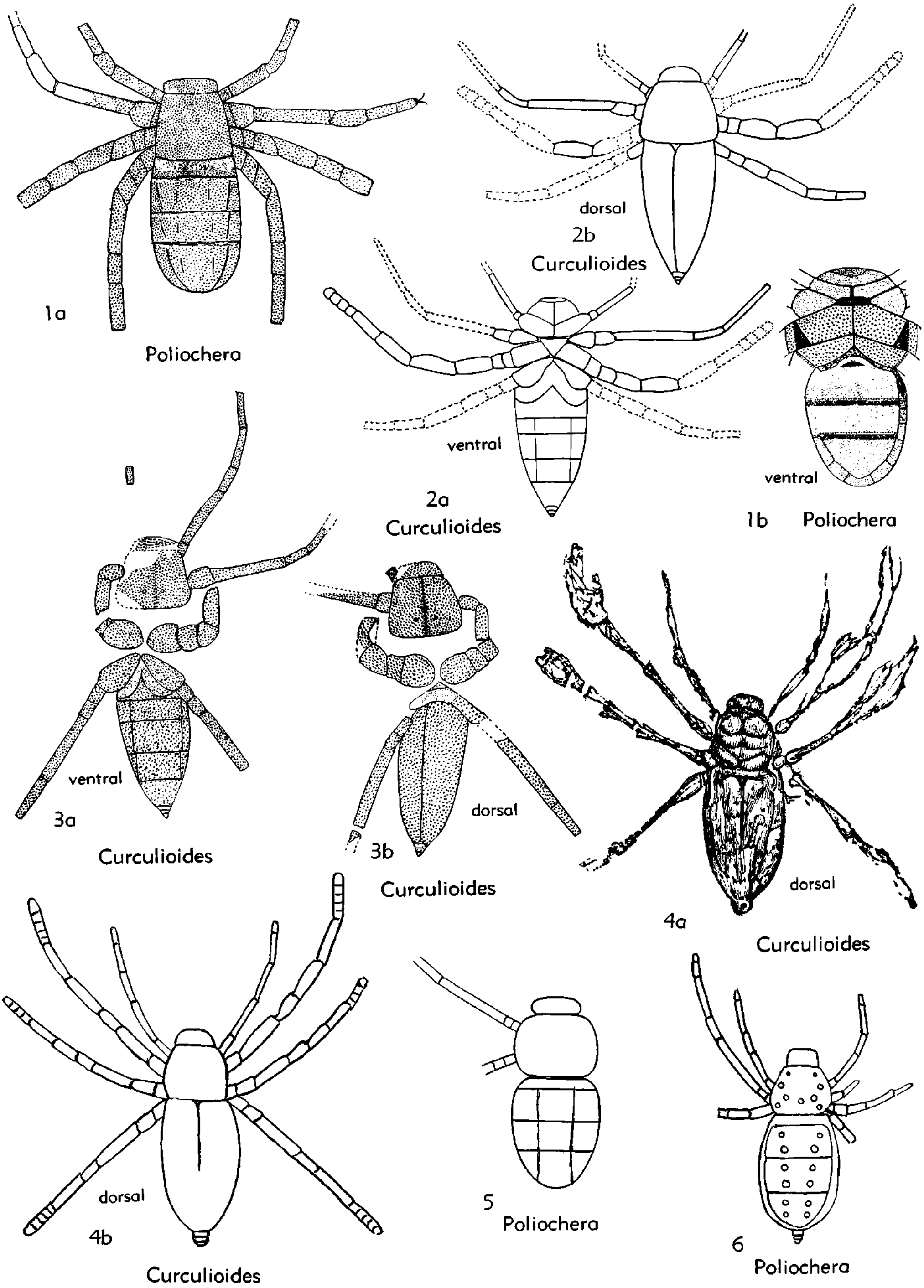


FIG. 115. Ricinuleida. *1, Poliochera punctulata,* Penn., Ill.; *1a,* dorsal, ×2; *1b,* ventral, ×2 (76). *2, Curculioides granulatus,* Penn., Ill.; *2a,b,* ventral and dorsal, ×1.5 (76). *3, Curculioides eltringhami,* Carb., Eng.; *3a,b,* ventral and dorsal, ×1.5 (76). *4, Curculioides ansticii,* Carb., Eng.; *4a,* BUCKLAND's original figure, ×1.9; *4b,* dorsal surface, restored, ×1.9 (76). *5, Poliochera glabra,* Penn., Ill.; ×2. *6, Poliochera alticeps,* Carb., Eng.; ×2.8 (76) (p. P159).

same type of segmentation with similar dorsal grooves dividing the tergites and similarly undivided sternites. The coupling between the cephalothorax and the abdomen is the same in all Ricinuleida. The chief visible character separating the Recent from the fossil Ricinuleida is furnished by the configuration of their coxosternal region. In Ricinoididae the 1st pair of coxae is clearly separated (Fig. 114,*1*), the 2nd and 3rd coxae are in contact with each other and all 3 pairs immobile. The 4th coxae are free and mobile. In both fossil families the 2nd coxae are clearly separated (Fig. 115,*1b,2a*), while the 1st coxae are usually in contact with each other in the median line. The 2 fossil families are easily distinguished by the structure of their abdomen.

Family POLIOCHERIDAE Scudder, 1884

Abdominal tergites subdivided by a pair of longitudinal grooves or lines into a median and a pair of lateral fields. Sternites entire. *Carb.*

Poliochera SCUDDER, 1884 [**P. punctulata*]. *Carb.*, Eu.-N.Am.—FIG. 115,*1*. **P. punctulata*, Ill.; *1a*, dorsal side, ×2; *1b*, ventral side, ×2 (76).—FIG. 115,*5*. *P. glabra* PETRUNKEVITCH, Ill.; dorsal side, ×2.—FIG. 115,*6*. *P. alticeps* POCOCK, Eng.; dorsal side, ×2.8 (76).

Family CURCULIOIDIDAE Cockerell, 1916

[=Holotergidae PETRUNKEVITCH, 1913]

Abdomen with a single dorsal shield longitudinally divided by a median line. Sternites divided by a pair of lines into a median and a pair of lateral fields. *Carb.*

Curculioides BUCKLAND, 1837 [**C. ansticii*] (45). *Carb.*, Eu.-N.Am.—FIG. 115,*4*. **C. ansticii*, Eng.; *4a*, dorsal side, ×1.9 (BUCKLAND's original figure) (65); *4b*, same (reconstr.), ×1.9 (76).—FIG. 115,*3*. *C. eltringhami* PETRUNKEVITCH, Eng.;

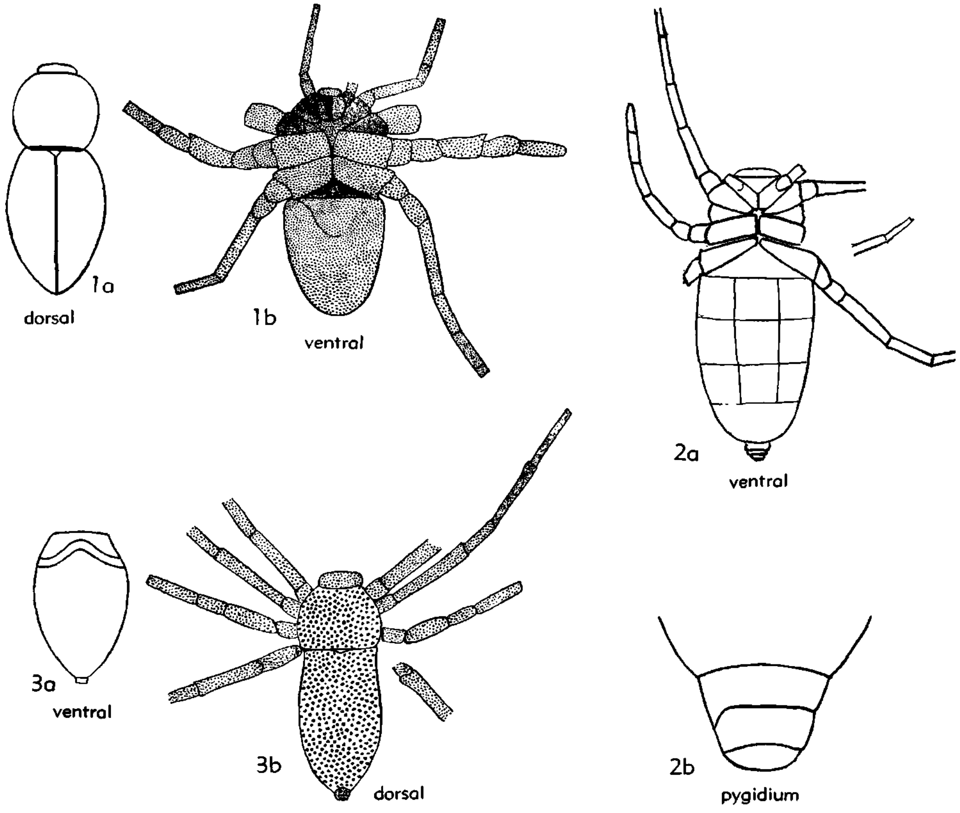


FIG. 116. Ricinuleida. *1*, *Curculioides scaber*, Penn., Ill.; *1a,b*, dorsal and ventral, ×2. *2*, *Curculioides gracilis*, Penn., Ill.; *2a*, ventral, ×2.2; *2b*, pygidium, ×14. *3*, *Curculioides sulcatus*, Penn., Ill.; *3a,b*, ventral and dorsal, ×1.7 (76) (p. P160).

3a, ventral side, ×1.5; *3b,* dorsal side, ×1.5 (76).—Fig. 115,*2*. *C. granulatus* Petr., Eng.; *2a,* ventral side, ×1.5; *2b,* dorsal side, ×1.5 (76).—Fig. 116,*1*. *C. scaber* (Scudder), Ill.; *1a,* dorsal side of body, ×2; *1b,* ventral side with legs, ×2 (76).—Fig. 116,*2*. *C. gracilis* Petr., Ill.; *2a,* ventral side, ×2.2; *2b,* pygidium, ×14 (76).—Fig. 116, *3*. *C. sulcatus* (Melander), Ill.; *3a,* ventral side of abdomen, ×1.7; *3b,* dorsal side of holotype, ×1.7 (76).

Family RICINOIDIDAE Ewing, 1929

[Type: *Ricinoides* Ewing, 1929]
[=Cryptostemmidae Westwood, 1874]

First coxae separated, 2nd and 3rd coxae contiguous. Abdomen as in Poliocheridae. *Rec.*

Ricinoides Ewing, 1929 [**Cryptostemma westermannii* Guérin, 1838]. *Rec.*—Fig. 114,*2*. *R. karschii* (Hansen & Sörensen), Afr.; female, ×5 (68).

GENERIC NAMES OF ARACHNIDA PLACED IN WRONG ORDERS AND INADEQUATELY DESCRIBED

Amphitrogulus Gourret, 1886 [**A. sternalis*], placed in Phalangiida, is an inadequately described spider. *Oligo.*, Eu.

Phalangillum Gourret, 1886 [**P. hirsutum*], placed in Phalangiida, is an inadequately described spider. *Oligo.*, Eu.

GENERIC NAMES WRONGLY PLACED IN ARACHNIDA

Hasseltides Weyenbergh, 1869 [*pro Hasseltia* Weyenbergh, 1869] [**Hasseltia primigenia* Weyenbergh, 1869], placed in Phalangiida, is a crinoid (*Saccocoma*). *Jur.*, Eu.

Phalangites Münster, 1839 [**P. priscus*] [=*Palpipes* Roth, 1851 (obj.)], placed in Phalangiida, is a crustacean larva.

Pleurolycosa Fritsch, 1904 [**Arthrolycosa prolifera* Fritsch, 1899], placed in Araneida, is quite unidentifiable.

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