COMPARATIVE STUDIES IN CHELICERATA IV. APATELLATA, ARACHNIDA, SCORPIONIDA, XIPHOSURA

by

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Key words: Amblypygi; Apatellata; Arachnida; Araneida; Chelicerata; evolution; Holopeltida; morphology; Pseudoscorpionida; Schizomida; Scorpionida; Solifugae; Uropygi; Xiphosura.

A comparative study is made of four chelicerate classes: Apatellata (Solifugae and Pseudoscorpionida), Arachnida s. str. (both groups of Uropygi, i.e. Holopeltida and Schizomida, Amblypygi and Araneida), Scorpionida and Xiphosura. Methods, principles and terminology, adopted in this paper, correspond with those of parts I-III of the present series of comparative studies in Chelicerata. Special attention is paid to segmentation of the body, respiratory organs, orifices of coxal glands, mouthparts, and appendages. The evolution of these structures is studied, and the relationships of the chelicerate classes and subclasses are reinvestigated and discussed.

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CONTENTS

I. INTRODUCTION

In continuation of the previous papers in the present series (Van der Hammen, 1979, 1982, 1985a; see also Van der Hammen, 1977a, 1985b), a comparative study is made of representatives of four chelicerate classes: Apatellata (Solifugae and Pseudoscorpionida), Arachnida (both groups of Uropygi, i.e. Holopeltida and Schizomida, Amblypygi and Araneida), Scorpionida and Xiphosura. In contradistinction to the previous papers in the series, the descriptions of the representatives are not complete; because of want of time, they are restricted to segmentation of the body, respiratory organs, orifices of coxal glands, mouthparts, and appendages. The evolution of these structures is further studied, and the relationships of the chelicerate classes and subsclasses are reinvestigated and discussed. In order to facilitate comparison, the methods of study, the principles of description, the orientation of illustrations, the notations and the terminology, are in accordance with those of the previous papers. Terminology is based on the Glossary of Acarological Terminology (Van der Hammen, 1976, 1980). Theoretical views, which influenced my approach in the study of evolution and classification, are expounded in separate studies (Van der Hammen, 1981a, 1981b, 1983, in press 1 and in press 2).

II. MATERIAL

The present paper is based on material of the following seven groups (with the exception of Uropygi and Araneida, only one representative of each group is studied).

Solifugae: *Pseudocleobis andinus* (Pocock), Hormito del Gringo, Mendoza, Argentina, December 1977 (I am grateful to Dr. E.A. Maury, Buenos Aires, for sending me this material).

Pseudoscorpionida: *Chthonius (Chthonius) tenuis* L. Koch, Mongaillard, Coulounieix, Dordogne, France, 3 September 1959.

Uropygi (Schizomida): *Trithyreus* spec., Auki Island (Padaido Islands), former Netherlands New Guinea (now Indonesia), 2 March 1954. Uropygi (Holopeltida): *Tetrabalius seticauda* (Doleschall), Latuhalat, Ambon, former Netherlands East Indies (now Indonesia), April 1922.

Amblypygi: *Heterophrynus alces* Pocock. Guyana Placer (situated on a branch of the Saramacca river, NW of Kabel), Surinam, October 1911.

Araneida: *Liphistius desultor* Schiödte, Penang, Malaya, 28 February 1963; *Segestria senoculata* (Linnaeus), Barneveld, The Netherlands, 4 March 1943;

Araneus quadratus Clerck, National Park "De Hoge Veluwe", The Netherlands, September-October 1946.

Scorpionida: *Euscorpius carpathicus* (Linnaeus), Rovinj, Yugoslavia, 14 April 1937.

Xiphosura: *Limulus polyphemus* (Linnaeus), Woods Hole, Massachusetts, U.S.A., August 1924.

III. SEGMENTATION OF THE BODY

The body of the groups studied in the present paper consists of two tagmata, prosoma and opisthosoma, as in other Chelicerata. The prosoma comprises an unknown number of precheliceral metameres and the segments I-VI. The opisthosoma consists of 10-13 segments, whilst in several groups a so-called telson (the flagellum of Uropygi, the sting of Scorpionida, and the tail of Xiphosura) is present; the term telson is used here as a neutral descriptive term indicating a structure which is, as yet, not completely understood. Segmentation of the prosoma is generally incomplete or indistinct in the dorsal part (prodorsum); with the exception of most Araneida, the opisthosomatic segmentation is still recognizable. Segment VII, the first opisthosomatic segment, has generally been subject to regression. The genital orifice is always associated with segment VIII. In most cases, the current interpretation of chelicerate segmentation should be confirmed by studies of the opisthosomatic musculature and the embryonic development. The segmented body of the groups studied here, is represented in lateral view in figs. 1-3.

Data with reference to Solifugid segmentation have been summarized by Kästner (1933: 195-204, figs. 271-279), Roewer (1932: 29-44, 93-101, figs. 13-33, 83-91), and Millot & Vachon (1949b: 483-491, figs. 243-247). The segmentation of *Pseudocleobis andinus* is represented in fig. 1A. The Solifugid prodorsum (the dorsal part of the prosoma) generally consists of two main sclerites (propeltidium and postpeltidium), whilst smaller sclerites can be present in the soft skin between them. These smaller sclerites are, for instance, particularly distinct in *Solpuga* (see Roewer, 1932: figs. 25-26); they are generally named anterior and posterior arcs, and the arrangement in *Solpuga* suggests that they constitute arthrodial sclerites, and must be connected with the articulation of the prodorsum. The subdivided condition of the prodorsum is generally regarded as primitive; Weygoldt & Paulus (1979: 89) suggested that it could also be secondary. The ventral region of the prosoma is occupied by the coxae of the appendages. The Solifugid opisthosoma comprises the segments VII-XVII. Each opisthosomatic segment generally

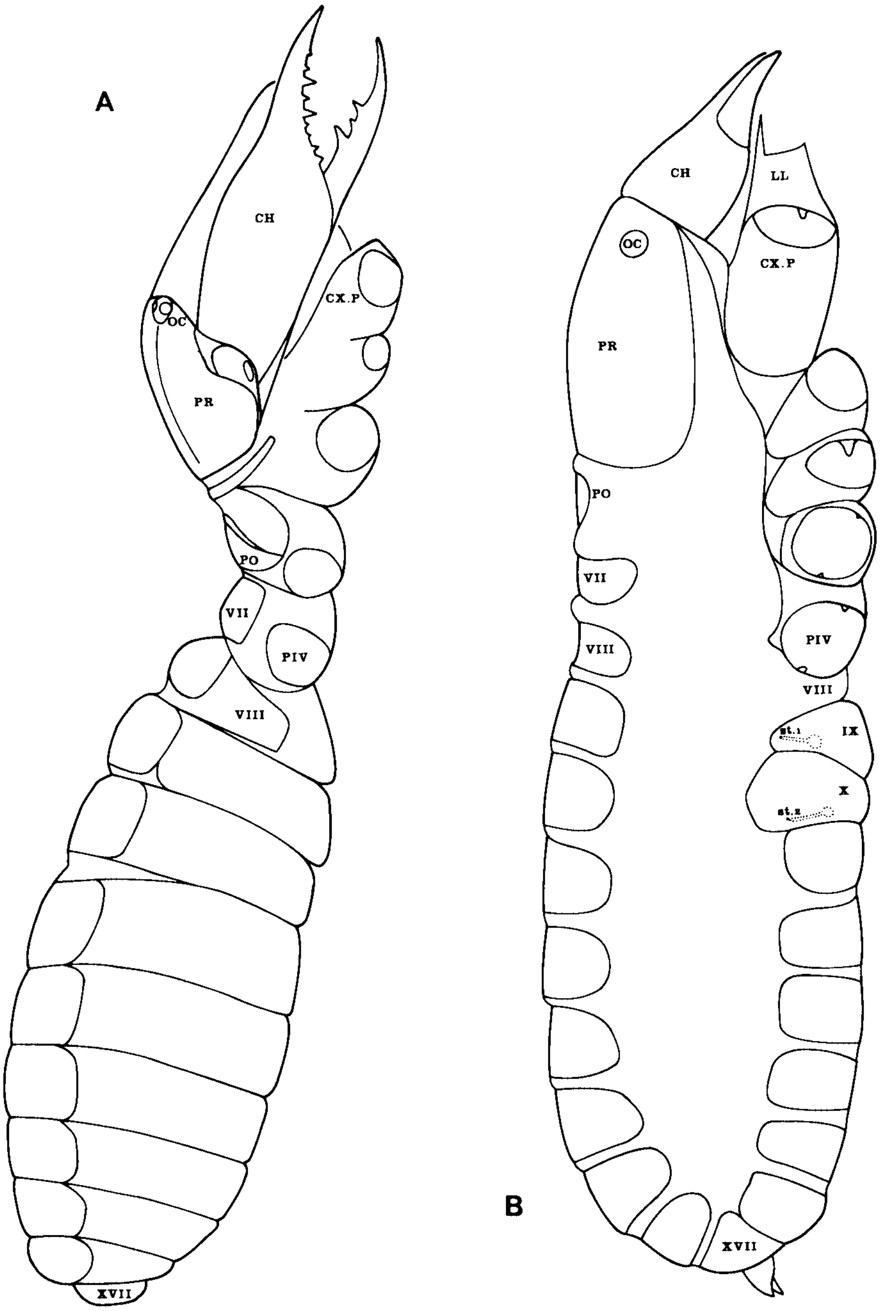

Fig. 1. Representatives of the two groups of Apatellata (Solifugae and Pseudoscorpionida) in lateral view (palp and legs, with the exception of the coxae, removed); A, Solifugae: *Pseudocleobis andinus* (Pocock), adult; B, Pseudoscorpionida: *Chthonius (Chthonius) tenuis* L. Koch, adult; A, × 11; B, × 73.

consists of a tergite, a sternite, and a large pleural region of soft skin; the succesive tergites and sternites are also connected by soft skin. The longitudinal genital opening is supposed to be bordered by homologues of the opisthosomatic appendages of segment VIII. Segment XVII (the anal segment) is constituted by a single sclerite. According to Millot & Vachon (1949b: 486), the sclerite generally named metapeltidium (and attributed to the prodorsum) constitutes the tergite of segment VII, whilst the small sternite anterior to the genital segment (and between coxae IV) is regarded by these authors as the sternite of segment VII (Millot & Vachon, 1949b: 491). The anal opening (in segment XVII) is more or less terminal, with the exception of species of the family Rhagodidae, in which it has a more ventral position.

An important study of Pseudoscorpionid morphology, including segmentation, was published by Chamberlin (1931; see particularly pp. 27-40 and figs. 2-7). Data with reference to Pseudoscorpionid segmentation have been summarized by Beier (1932: 119-124, figs. 159-165) and Vachon (1949: 438-442, figs. 197-201). The segmentation of *Chthonius (Chthonius) tenuis* is represented in fig. 1B; this species belongs to the family Chthoniidae, which is generally regarded as one of the most primitive Pseudoscorpionid families. Although the Pseudoscorpionid prodorsum is generally described as undivided and presenting only one or two furrows, the condition in *Chthonius (Chthonius) tenuis* is here regarded as distinctly consisting of two sclerites: propeltidium and postpeltidium. The postpeltidium is regarded in literature as the first opisthosomatic tergite. In dorsal view, however, propeltidium and postpeltidium distinctly constitute a unity, separated from the opisthosoma by a narrowing. The subdivision of the prodorsum in Chthoniidae (and probably also in some other families), and the consequent misinterpretation of the border between prosoma and opisthosoma, could account for the supposed differences in the position of this border in relation to the coxae of the legs. The ventral surface of the prosoma is nearly completely occupied by the coxae of the appendages. The Pseudoscorpionid opisthosoma comprises the segments VII-XVIII. As in Solifugae, each opisthosomatic segment generally consists of a tergite, a sternite, and a large pleural region of soft skin (the successive tergites and sternites are also connected by soft skin). Segment VII is represented dorsally by a distinct tergite and ventrally by a triangular sternite situated between coxae IV. The dorsal and ventral parts of the segments VIII-XVI have corresponding positions, which condition distinctly demonstrates that the postpeltidium belongs to the prosoma. Vachon (1949: 442) supposed that the ventral region of segment VIII includes homologues of opisthosomatic appendages. The sternite and tergite of segment XVII have fused, and the anal segment (XVIII) is reduced to a circum-anal ring (the anal opening is represented by a transverse slit surrounded by the more or less membraneous tergite and sternite). The position of the anal opening is more or less terminal.

A comparison of figs. 1A and 1B distinctly demonstrates that similarities in segmentation of the two groups of Apatellata (Solifugae and Pseudoscorpionida) are evident, and that the differences in number of segments (seventeen in Solifugae, eighteen in Pseudoscorpionida) can easily be explained by the regression of segment XVIII.

Data with reference to Uropygid segmentation have been summarized by Kästner (1932: 4-7, figs. 4, 5, 9) and Millot (1949a: 534-536, figs. 288-291). The two groups of Uropygi (Schizomida and Holopeltida) are treated here separately, particularly because of differences in the structure of prodorsum and flagellum; a species of Schizomida is represented, in lateral view, in fig. 2A, a species of Holopeltida in fig. 2B.

The Schizomid prodorsum is generally regarded as being subdivided into a relatively large propeltidium, a mesopeltidium consisting of two small sclerites, and a metapeltidium. The two sclerites constituting the so-called mesopeltidium are here regarded as arthrodial sclerites (see also fig. 17E), and the two other sclerites are now called pro- and postpeltidium. The ventral surface of the prosoma is for the greater part occupied by the coxae of the legs; there is a triangular sternite between the coxae of legs I and II (the sternite between the coxae of legs IV could represent the sternite of segment VII). The opisthosoma consists of the segments VII-XVIII and a telson (flagellum). Segment VII is distinctly narrowed, and consists of a small tergite and probably also of a narrowed sternite (the triangular sternite between coxae IV). Segments VIII-XV each consist of a tergite and a sternite, connected by pleural regions of soft skin. The genital opening is a slit at the posterior border of sternite VIII. The segments XVI-XVIII constitute a distinctly narrowed metasoma, in which tergites and sternites are not differentiated. The telson is represented by a short flagellum which can be subdivided into a small number of segments and sections. The anal opening is terminal in segment XVIII, ventral to the base of the flagellum.

The Holopeltid prodorsum is represented by a large, undivided sclerite; the ventral surface of the prosoma resembles that of the Schizomida (it is for the greater part occupied by the coxae of the appendages; there is a triangular sternite between the coxae of legs I-II). The Holopeltid opisthosoma consists of the segments VII-XVIII; segment VII is narrowed, the genital opening is a transverse slit at the posterior border of sternite VIII, segments VIII-XV each consist of a tergite and a sternite separated by a pleural region of soft skin, and the segments XVI-XVIII constitute a narrow metasoma in which

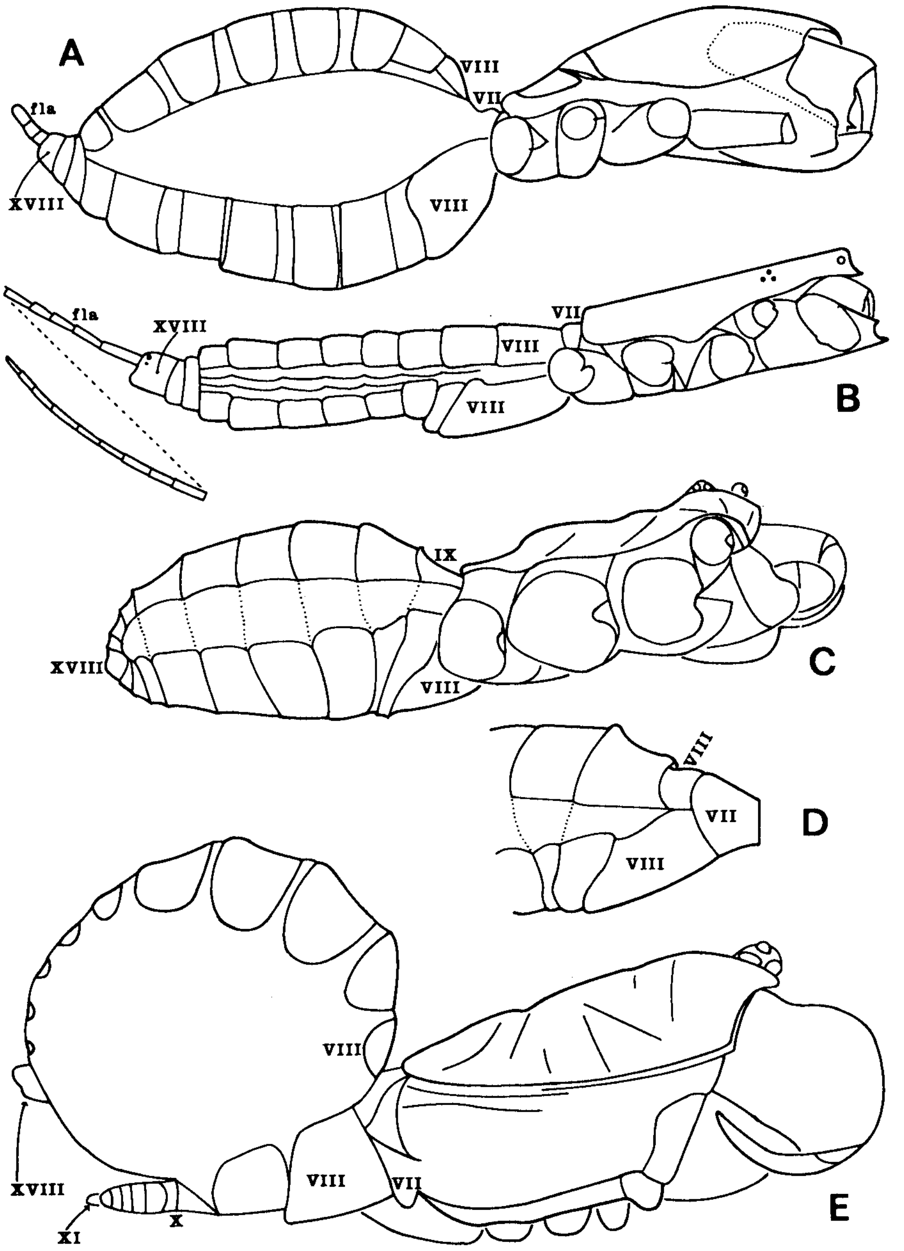

Fig. 2. Representatives of the three groups of Arachnida s. str. (Uropygi, Amblypygi and Araneida) in lateral view (palp and legs, with the exception of the coxae, removed); A, Uropygi (Schizomida): *Trithyreus* spec., adult female; B, Uropygi (Holopeltida): *Tetrabalius seticauda* (Doleschall), adult male; C, D, Amblypygi: *Heterophrynus alces* Pocock, adult (D, anterior part of separated opisthosoma; orientation slightly different from C); E, Araneida: *Liphistius desultor* Schiödte, adult female (coxae of the right side also removed); A, × 32.7; B-E, × 3.8.

tergites and sternites are not differentiated. The Holopeltid telson (flagellum) is long and subdivided into a great number of small segments. The anal opening is terminal in segment XVIII, ventral to the base of the telson.

Data with reference to Amblypygid segmentation have been summarized by Kästner (1932: 4-7, figs. 7-8) and Millot (1949b: 564-565, figs. 318-320). A species of Amblypygi is represented, in lateral view, in fig. 2C, D. The Amblypygid prodorsum consists of a single, large prodorsal shield. The ventral surface of the prosoma is occupied by a sternum (constituted by the sternites of the segments III-VI) surrounded by the coxae of the appendages. The opisthosoma consists of the segments VII-XVIII. Segment VII is narrowed; its tergite is hidden by the prodorsum (compare figs. 2C and 2D) and its sternite is represented by a triangular sclerite between coxae IV. The tergite of segment VIII is small and hidden by the prodorsal shield; its sternite is much larger, whilst the genital opening is a transverse slit at its posterior border. Segments IX-XVII each consist of a tergite and a sternite, separated by a pleural region of soft skin; the sternites of segments IX and X are distinctly shortened. In segment XVIII, tergite and sternite are not distinctly differentiated; the anal opening is terminal in this segment. In Amblypygi, segments XV-XVIII do not constitute a narrowed metasoma, whilst a telson is not present.

Data with reference to the constitution of the Araneid body have been summarized by Gerhardt & Kästner (1937: 398-408, figs. 488-505) and Millot (1949c: 590-600, figs. 350-365). Although vestiges of segmentation can be found in various groups of spiders (and particularly in the first instars), true segmentation is found in the spider family Liphistiidae only. A species of *Liphistius* is represented, in lateral view, in fig. 2E. The dorsal surface of the Araneid prosoma is constituted by a single prodorsal shield. The ventral surface of the prosoma is constituted by a sternum; part of the ventral prosomatic surface can also be occupied by the coxae of the appendages (such as in *Liphistius*). The Araneid opisthosoma is constituted by the segments VII-XVIII. Segment VII constitutes a narrow pedicel. The dorsal parts of the segments VIII-XVIII are represented by isolated sclerites. The genital opening is ventrally represented by a transverse slit at the posterior border of segment VIII. The two pairs of spinnerets (this number is reduced in other spiders) represent the opisthosomatic appendages of segments X and XI. Segment XVIII is constituted by the anal tubercle.

In all Arachnida s. str. (Uropygi, Amblypygi, Araneida) the body is constituted by precheliceral metameres and the segments I-XVIII. The genital orifice is a transverse slit at the posterior border of segment VIII, and the anus has a terminal position in segment XVIII. Important differences are con-

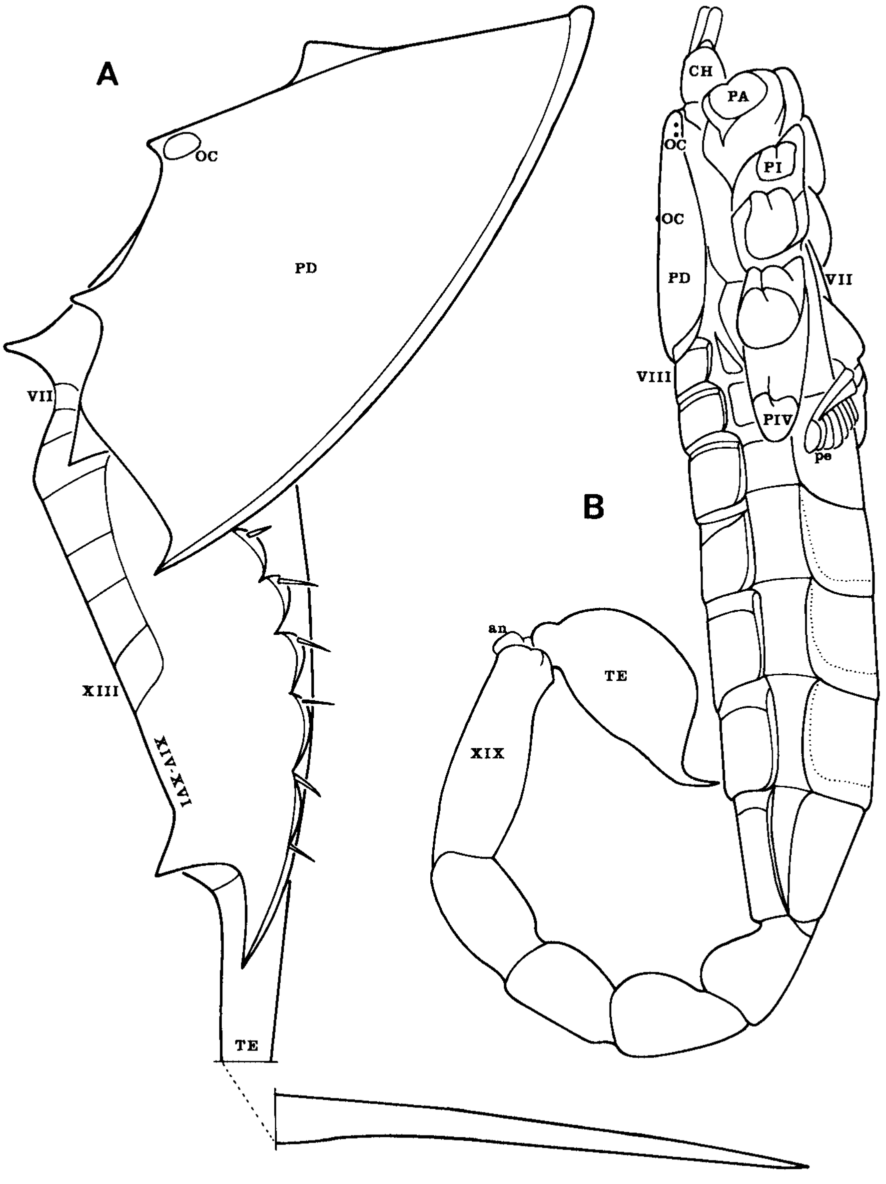

Fig. 3. Representatives of Xiphosura and Scorpionida in lateral view; A, Xiphosura: *Limulus polyphemus* (Linnaeus), juvenile specimen; B, Scorpionida: *Euscorpius carpathicus* (Linnaeus), adult male (palp and legs, with the exception of the coxae, removed); A, × 3.4; B, × 8.4.

stituted by the condition of the prodorsum (subdivided in Uropygi Schizomida, entire in Uropygi Holopeltida, Amblypygi and Araneida) and the telson (present in Uropygi, absent in Amblypygi and Araneida).

Data with reference to the constitution and segmentation of the Scorpionid body have been summarized by Kästner (1940: 119-125, figs. 91-93) and Millot & Vachon (1949a: 387-391, figs. 158-160). A species of Scorpionida is represented, in lateral view, in fig. 3B. The Scorpionid prodorsum is constituted by a single prodorsal shield. The ventral surface of the prosoma is occupied by the coxae of the appendages. The opisthosoma consists of the segments VII-XIX and a telson. The sternite between the coxae of legs IV is attributed here to segment VII; the tergite of segment VII is no more recognizable (segment VII is present in the embryo). The segments VIII-XIV each present a separate tergite, segments X-XIV moreover a separate sternite; tergites and sternites are connected by a pleural region of soft skin. Ventrally, segment VIII is represented by the genital operculum which is supposed to be homologous with the opisthosomatic appendages of this segment. Segment IX is represented ventrally by a plate on which the combs or pectines (homologous with the opisthosomatic appendages of segment IX) are inserted. Segments VII-XIV constitute the so-called mesosoma, a pseudotagma. Segments XV-XIX (which are distinctly narrowed) and the telson constitute the so-called metasoma, another pseudotagma; because of the absence of pleural soft skin, these segments do not present separate tergites and sternites. The Scorpionid telson is represented by the sting. The anal opening has a terminal position in segment XIX, ventral to the telson. It may be remarked here that Weygoldt & Paulus (1979: 87-88, fig. 2) attributed the higher number of Scorpionid segments (nineteen) to a supposed subdivision of the sternite of segment VIII. Such a subdivision is not in agreement with Lankester's so-called laws of metamerism, notably his ninth law (see Lankester, 1904: 536-538), according to which new metameres are added only at the anterior border of the telson. Weygoldt & Paulus regarded a number of nineteen segments as aberrant among Chelicerata, although it is also mentioned for Anactinotrichida (see Van der Hammen, 1970: 4-5. fig. 1B).

Data with reference to the constitution of the Xiphosurid body have been summarized by Gerhardt (1935: 50-53, figs. 32-33) and Fage (1949: 220-222, figs. 1-3). A species of Xiphosura is represented, in lateral view, in fig. 3A. The Xiphosurid prodorsum is constituted by a single, large prodorsal sclerite. The ventral surface of the prosoma is constituted by the coxae of the appendages and a narrow sternum (posterior to the mouth). The ventral region of the opisthosoma consists of: an anterior part with homologues of seven pairs of opisthosomatic appendages, viz., the chilaria (segment VII, with advanced

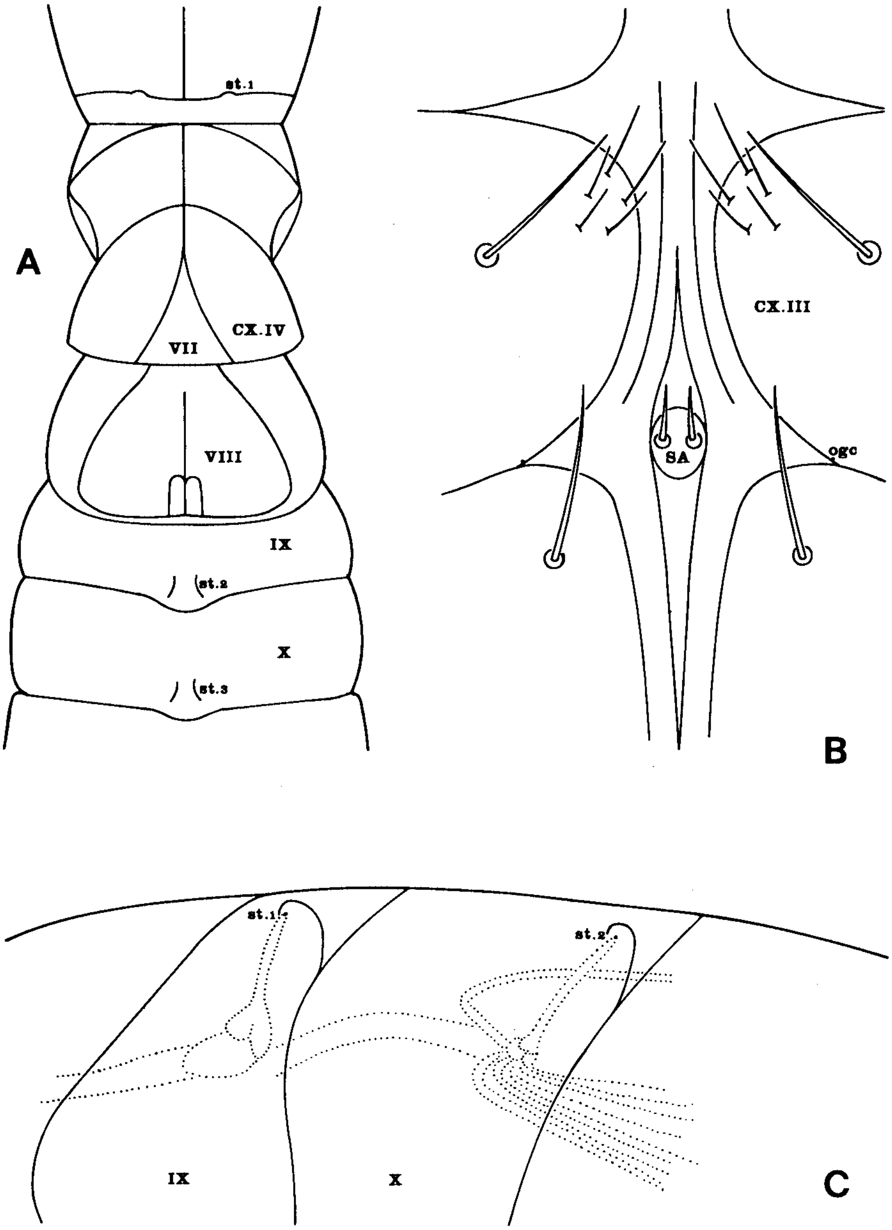

Fig. 4. Representatives of the two groups of Apatellata in ventral view; A, Solifugae: *Pseudocleobis andinus* (Pocock), posterior part of prosoma and anterior part of opisthosoma, ventral view; B, C, Pseudoscorpionida: *Chthonius (Chthonius) tenuis* L. Koch; B, ventral view of part of coxisternal region; C, ventral (oblique) view of left part of opisthosoma with segments IX and X and stigmata 1 and 2; A, × 14; B, × 591; C, × 318.

position), the genital operculum (segment VIII) and five pairs of branchial appendages (segments IX-XIII); and a posterior part with a large tail or telson. The dorsal part of segment VII is represented by a small area of soft skin. The segments VIII-XIII are dorsally recognizable by the presence of furrows (and muscle insertions) in the median part, and by the presence of six pairs of lateral spines. Because the posterior part of the opisthosoma of some extinct Xiphosura consists of three segments and a telson, the segments XIV-XVI are supposed to have been incorporated in the posterior part of the opisthosoma of extant Xiphosura, without leaving any trace of segmentation (see Størmer, 1955: 14-23, figs. 11-16). The Xiphosurid anal opening is terminal, ventral to the base of the telson.

IV. RESPIRATORY ORGANS

The Solifugid respiratory system (see Kästner, 1933: 257-266, figs. 334-341) is represented by a vast system of tracheae and three pairs of stigmata (a posterior unpaired stigma is, moreover, present in the families Galeodidae and Hexisopodidae). The anterior pair of stigmata is prosomatic, the other stigmata are opisthosomatic (fig. 4A). The prosomatic stigmata are situated near the posterior border of coxae II, the two pairs of opisthosomatic stigmata are situated near the posterior border of the sternites of segments IX and X respectively (the unpaired stigma of Galeodidae and Hexisopodidae is near the posterior border of sternite XI). The Solifugid opisthosomatic respiratory organs could have arisen from homologues of opisthosomatic appendages, although in the course of embryonic development the rudiments of these appendages disappear before the development of the stigmata.

The Pseudoscorpionid respiratory system consists of tracheae and two pairs of stigmata situated near the posterior border of sternites IX and X respectively (figs. 1B, 4C). The stigmata have a more lateral position than the opisthosomatic stigmata of the Solifugae, but could be homologous with those of the corresponding segments (IX and X); in that case, the occurrence of stigmata in segments IX and X could be a shared character of the Apatellata.

The Uropygid respiratory organs are represented by booklungs and stigmata with ventral position: one pair (stigmata in segment VIII) in Schizomida (fig. 5A), two pairs (stigmata in segments VIII and IX) in Holopeltida (fig. 5B). The Amblypygid respiratory system (fig. 5C) is also represented by booklungs and paired stigmata with ventral position (in segments VIII and IX); a pair of small evaginable ventral sacs, with unknown

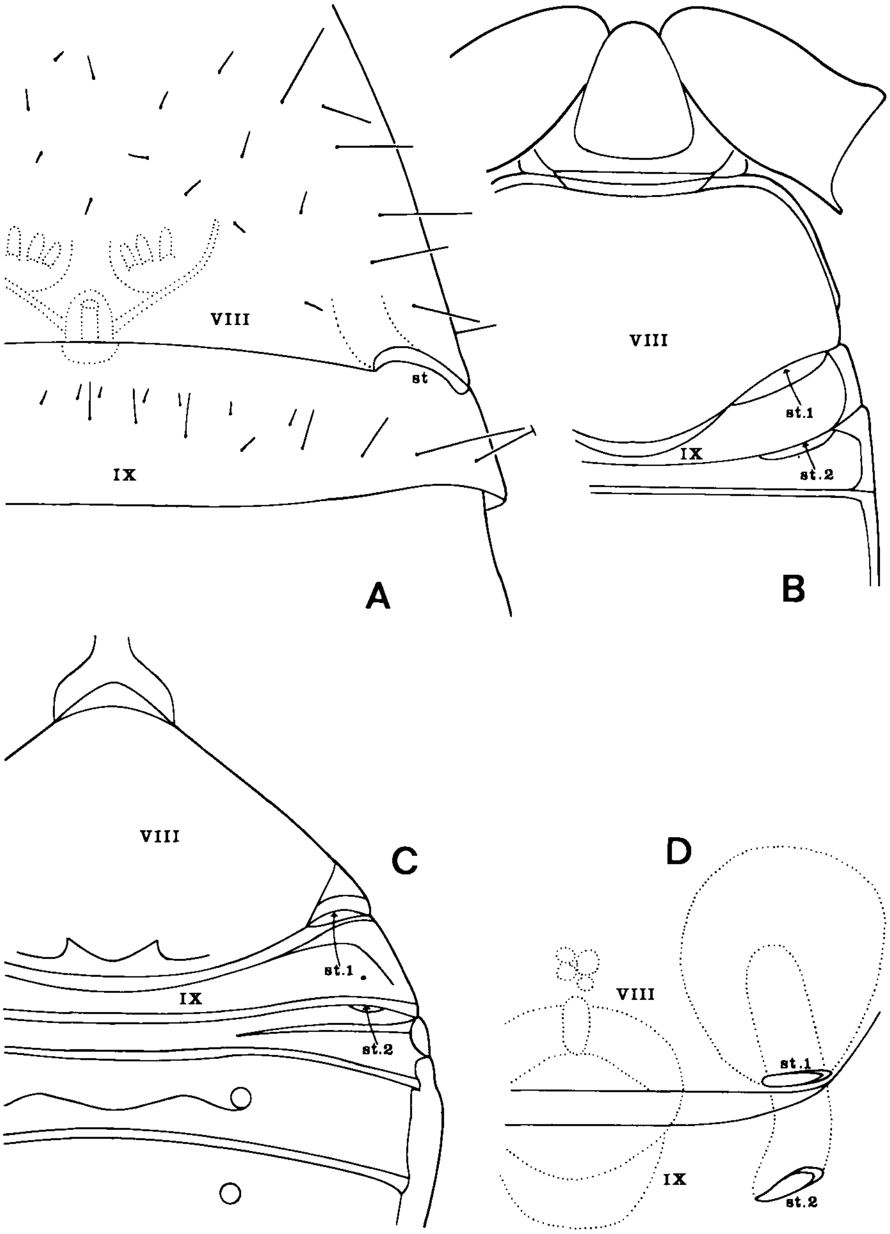

Fig. 5. Anterior part of opisthosoma of representatives of the three groups of Arachnida s. str. in ventral view; A, Uropygi (Schizomida): *Trithyreus* spec., adult female; B, Uropygi (Holopeltida): *Tetrabalius seticauda* (Doleschall), adult female; C, Amblypygi: *Heterophrynus alces* Pocock, adult; D, Araneida: *Segestria senoculata* (Linnaeus), adult female; A, × 159; B, C, × 9.5; C, × 49.5.

function, can also be present in the Amblypygid segment IX (see Millot, 1949b: 572-573, fig. 332). The respiratory system of Araneida (fig. 5D) is represented by paired stigmata with ventral position in segments VIII and IX, associated with either booklungs or tracheae. It is generally accepted that booklungs have arisen, in the course of evolution, from gills, and are homologous with opisthosomatic appendages; it is supposed that the Araneid tracheae have replaced the booklungs in the course of evolution. Evidently,

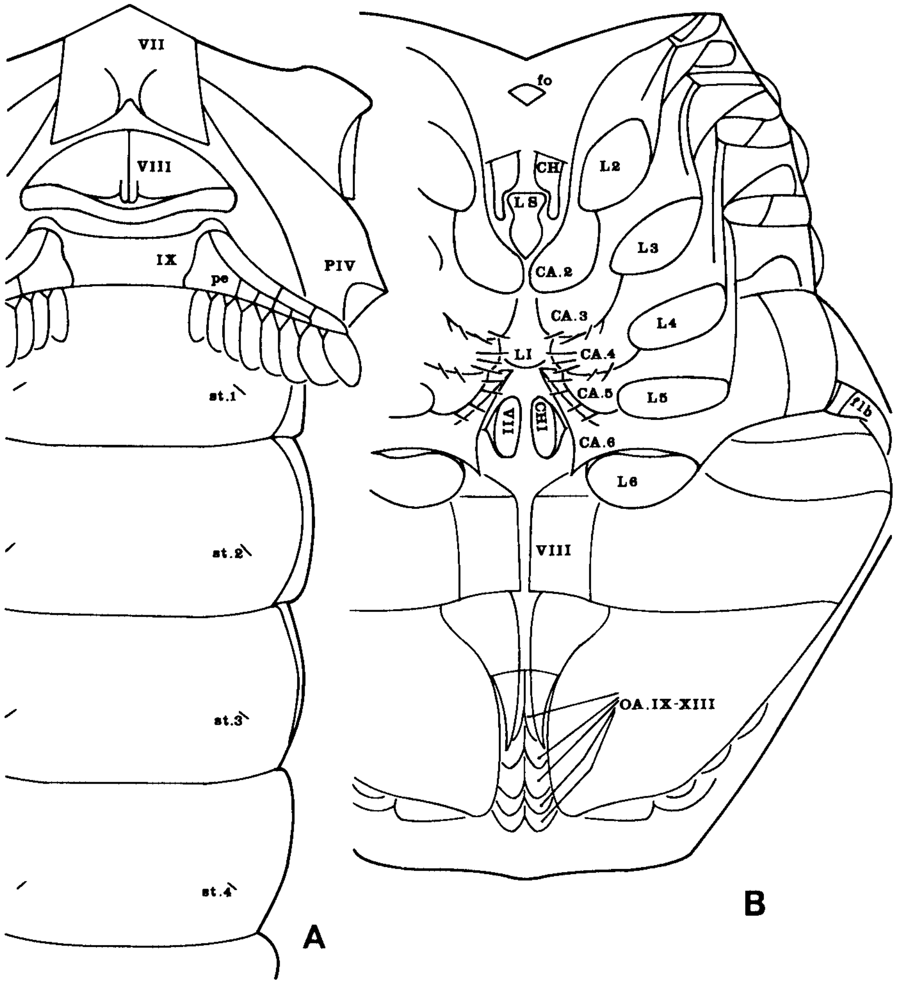

Fig. 6. Representatives of Scorpionida and Xiphosura in ventral view; A, *Euscorpius carpathicus* (Linnaeus), adult male, ventral view of posterior part of prosoma and anterior part of opisthosoma; B, *Limulus polyphemus* (Linnaeus), juvenile specimen, ventral view of prosoma and anterior part of opisthosoma; A, × 13.5; B, × 5.1.

all Arachnida s. str. are characterized by the presence of homologous respiratory organs, of which one pair has disappeared in Schizomida. The small evaginable sacs, known from some Amblypygi, could represent the opisthosomatic endites of segment IX.

The Scorpionid respiratory system consists of four pairs of booklungs and the associated four pairs of stigmata with ventral position in the segments X-XIII (fig. 6A). It is generally accepted that these booklungs have arisen, in the course of evolution, from opisthosomatic branchial appendages. As mentioned above, the opisthosomatic appendages of the segments VIII and IX are represented by the genital operculum and the combs or pectines respectively.

Xiphosura constitute the only extant group of Chelicerata characterized by the presence of gills. Five pairs of gills are carried in this group by the opisthosomatic appendages of the segments IX-XIII (fig. 6B). As mentioned above, the opisthosomatic appendages of the segments VII-VIII are represented by the so-called chilaria and the genital operculum respectively.

In the groups of Chelicerata, dealt with in the present paper, respiratory organs are either represented by, or originate from, opisthosomatic appendages carrying gills (Arachnida s. str., Scorpionida, Xiphosura), or are supposed to originate from non-branchial opisthosomatic appendages (Apatellata).

V. ORIFICES OF COXAL GLANDS

Orifices of coxal glands are usually extremely small and difficult to discover, although studies of the internal anatomy (Buxton, 1913, 1917) have indicated their approximate positions. In the present section, an attempt is made to locate the exact position of the orifices, and to study their possible association with sternapophyses and taenidia (for definitions of these terms, see: Van der Hammen, 1980: 149-150, 154).

According to Kästner (1933: 253-254, figs. 326, 331) and Millot & Vachon (1949b: 507, figs. 265-266) the coxal gland of Solifugae, with its sacculus, labyrinth and duct, occupies a region extending from the segments II-VI. The gland probably belongs to segment III (the segment of leg I). According to Kästner the orifice is dorsal, at the base of the palpal coxa (I have not succeeded in discovering this orifice; in fig. 8D I have represented a supposed orifice, of uncertain identity, near the base of the palpal coxa. The duct of the gland is, according to Kästner, close to the lateral wall of the prosoma and, because of this, resembles the podocephalic canal of those Actinotrichida where it is internal.

The Pseudoscorpionid coxal gland (Beier, 1932: 160; Vachon, 1949: 457) belongs to segment V (the segment of leg III) and the orifice is at the posterior paraxial border of coxa III (fig. 4B). In *Chthonius* the orifice is associated with a small setiferous tubercle which is here homologized with a (vestigial) sternapophysis. In several groups of Chelicerata (Anactinotrichida, Ricinulei, Uropygi, Amblypygi) sternapophyses are associated with the taenidia of coxal glands. Evidently, the position of the coxal gland, as well as that of its orifice, are entirely different in the two groups of Apatellata.

The Uropygid coxal gland (Kästner, 1932: 37-38, figs. 52, 54; Millot, 1949a: 550-551, fig. 310), with its two sacculi, labyrinth and duct, extends from segment IV to segment VI; it is probably the result of a fusion of two or more glands. The orifice of the gland is paraxial, at the base of coxa I (figs. 7A, B, 10B). In Schizomida as well as Holopeltida it is associated with a taenidium and a setiferous sternapophysis. The taenidia of both sides are connected with an unpaired intercoxal gutter (also a taenidium), with ventral position, which forms part of the mouthparts and is situated between the palpal coxae. The long setae of the sternapophysis are normally lying in the intercoxal gutter, exactly as in the case of sternapophyses and subcapitular gutter in the two groups of Cryptognomae (Anactinotrichida and Ricinulei).

The Amblypygi (Kästner, 1932: 37-39, fig. 53; Millot, 1949b: 576-577, figs. 338, 339) are characterized by the presence of one or two coxal glands: a large one in segment III, and a smaller one (present in the family Charontidae only) in segment V. The orifice of the last-mentioned gland, if present, is paraxial, at the posterior border of coxae III. The orifice of the first-mentioned gland (fig. 7E, F) is paraxial, at the base of coxa I. It is associated with a taenidium and a sternapophysis. The Amblypygid sternum generally presents three sternapophyses, of which those associated with coxae II and III are more or less vestigial (they could originally have been associated with the coxal glands of the segments IV and V).

In Araneida one or two pairs of coxal glands are present (Gerhardt & Kästner, 1937: 461-462, figs. 569-572; Millot, 1949c: 654). The anterior pair, present in all Araneida, belongs to segment III; its orifice is paraxial, at the base of coxa I (fig. 7C, D). The posterior gland, present in Liphistiidae and Mygalomorphae, belongs to segment V; its orifice is at the base of coxa III. In *Segestria senoculata* the orifice of the coxal gland is associated with a taenidium; Araneid coxal glands are not associated with sternapophyses.

Important differences, pertaining to the position of the coxal glands and their orifices, between the three groups of Arachnida s. str. (and even within the groups), are evident. Originally, the three groups together have probably been characterized by the presence of glands in the segments III and V (or III-

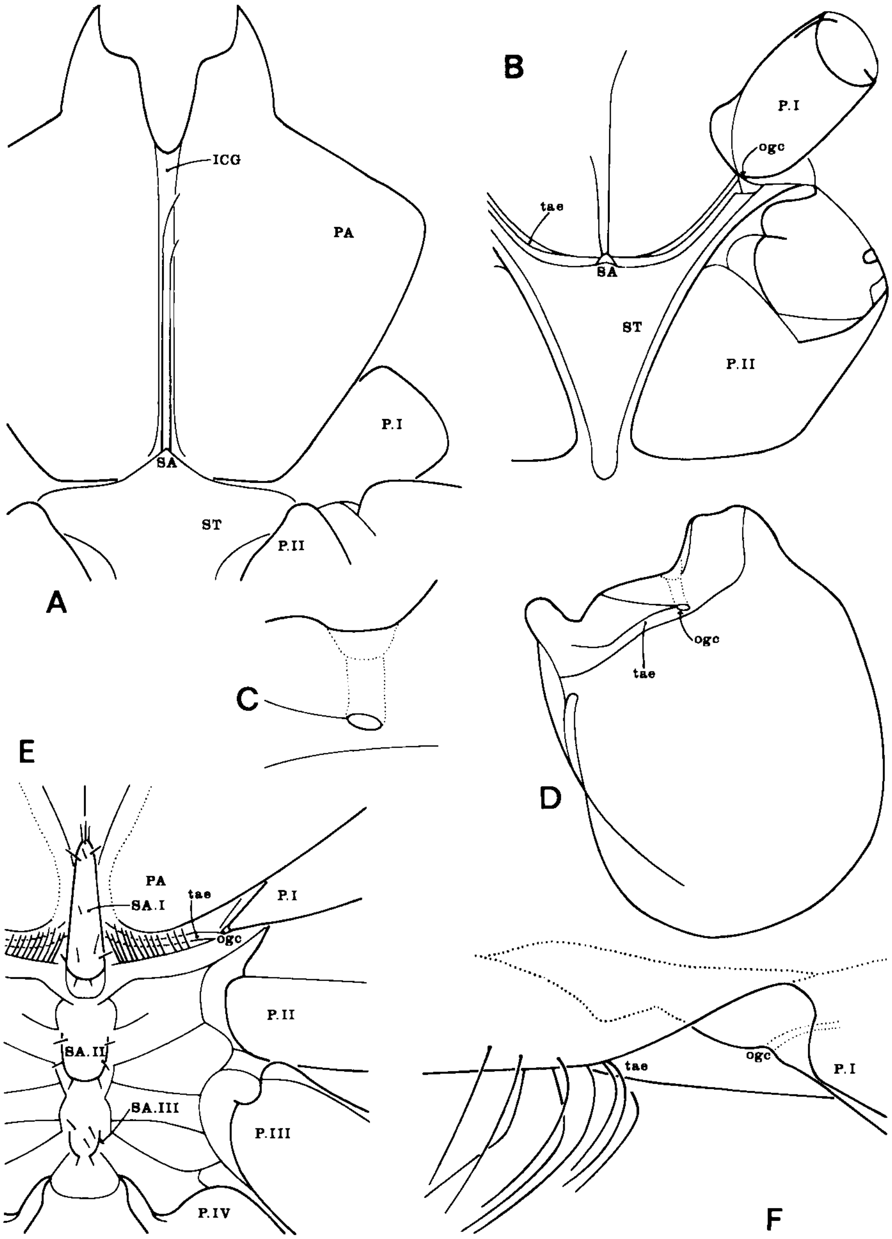

Fig. 7. Coxal and sternal region of Arachnida s. str.; A, B, *Tetrabalius seticauda* (Doleschall), adult male; A, ventral view of anterior part of coxal and sternal region; B, anteroventral view of coxal and sternal region of legs I and II; C, D, *Segestria senoculata* (Linnaeus), adult female; C, orifice of coxal gland (detail of D); D, basal view of right coxa I (the upper part of the figure is dorsal, the left part anterior); E, F, *Heterophrynus alces* Pocock, adult; E, ventral view of coxal and sternal region with sternapophyses I-III; F, posterior view of coxal and sternal region of right leg I, with orifice of coxal gland and taenidium (the upper part of the figure is dorsal); A, B, E, × 12.8; C, × 250.8; D, F, × 83.6.

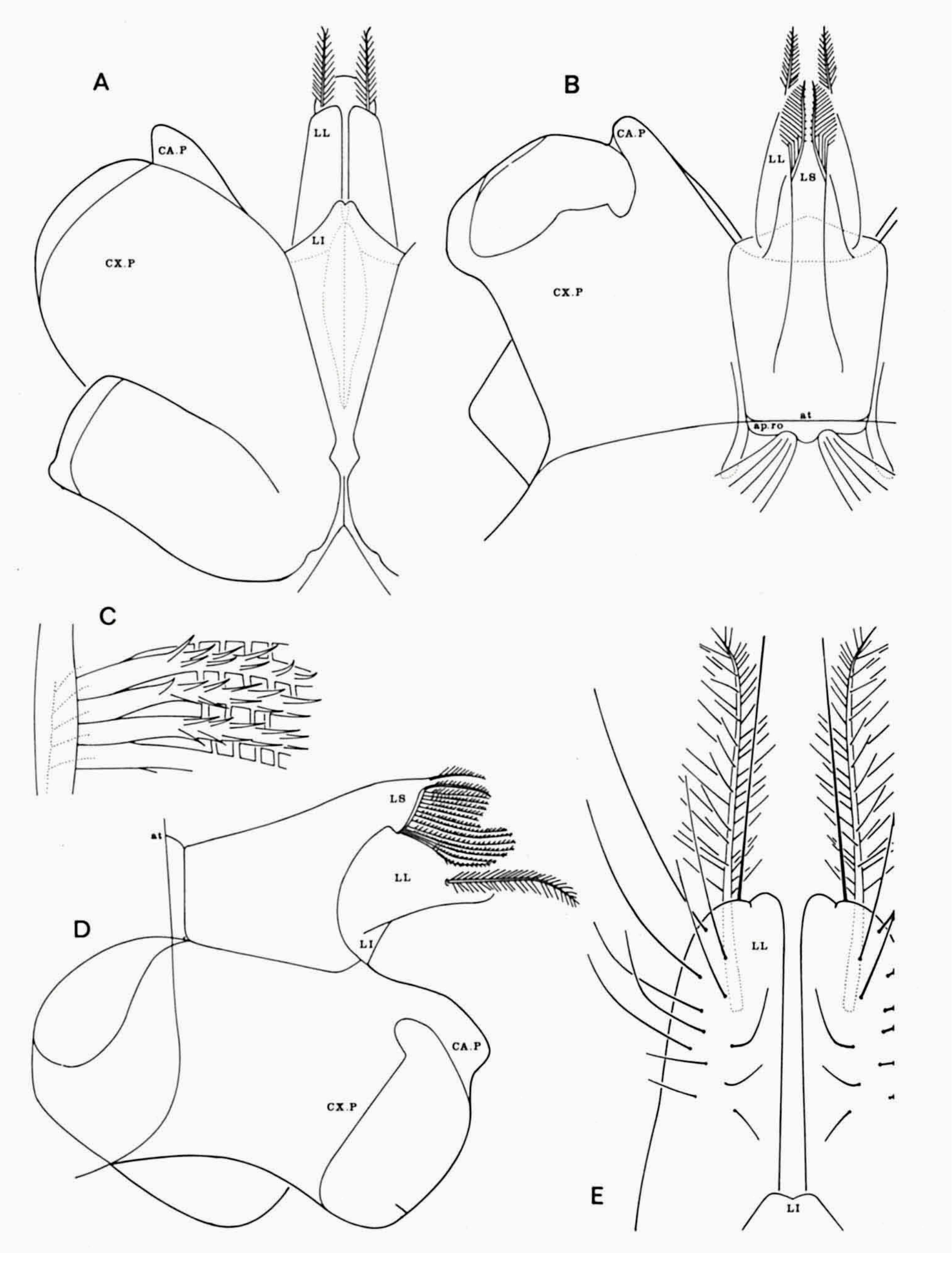

Fig. 8. *Pseudocleobis andinus* (Pocock), rostrosoma of adult; A, ventral view; B, dorsal view; C, basal part of some of the anastomosed setae of the labrum, lateral view; D, lateral (oblique) view; E, ventral view of lateral lips (in A, B, and D, all setae, with the exception of the large distal setae of the labrum, are omitted); A, B, D, × 33; C, × 198; E, × 106.

V); the orifices of these glands must originally, in all three groups, have been associated with sternapophyses.

The Scorpionid coxal gland (Kästner, 1940: 163-164, figs. 139-140; Millot & Vachon, 1949a: 412, fig. 182) belongs to segment V; the orifice is paraxial, at the base of coxa III (fig. 13C).

The Xiphosurid coxal gland (Gerhardt, 1935: 79-80, fig. 58; Fage, 1949: 233; Patten & Hazen, 1900) originates from a fusion of the glands of segments II-V. The orifice (fig. 14B) is at the posterior border of the coxa of limb 5 (homologous with coxa III of other Chelicerata); it is associated with a taenidium. This orifice was first described (but not figured) by Tower (1900).

VI. MOUTHPARTS

The Solifugid mouthparts (see Roewer, 1932: 44-58, figs. 33-51) comprise the chelicerae and the so-called rostrum (here termed rostrosoma). The last-mentioned structure consists of the labrum and the lateral lips, and includes the mouth and the pharynx. A dorsal view of the Solifugid rostrosoma is represented in fig. 8B, a ventral view in fig. 8A, and a lateral view in fig. 8D. The labrum is characterized by the presence, in the distal part, of anastomosed setae (fig. 8C); its dorsal surface is a prolongation of the cervix which has fused with the palpal coxae. The cheliceral frame is attached to the posterior border of the cervix, according to the line *at*. The interior prolongation of the cervix (posterior to *at*) is constituted by the rostrosomatic apodeme, the place of insertion of muscles. The labium, which probably represents the sternal part of segment II, has a ventral position between the coxae of the palpi (to which it is attached). The basal part of the lateral lips has fused with labrum and labium; these lips present many large setae, among which a pair of plumose setae (fig. 8E). The palpal coxae present a small coxapophysis.

The Pseudoscorpionid mouthparts (see Chamberlin, 1931: 95-112, figs. 22-26) comprise the chelicerae and the rostrosoma (as in Solifugae). The rostrosoma consists of the labrum, the labium and the lateral lips, and includes the mouth and the pharynx. A dorsal view of the Pseudoscorpionid rostrosoma is represented in fig. 9B, a ventral view in fig. 9A; a lateral view of the mouthparts is represented in fig. 9C. The dorsal surface of the labrum is a continuation of the cervix (which has fused with the palpal coxae). The cheliceral frame is attached to the posterior border of the cervix according to the line *at*. The interior prolongation of the cervix (posterior to *at*) is constituted by the relatively long and narrow rostrosomatic apodeme (the place

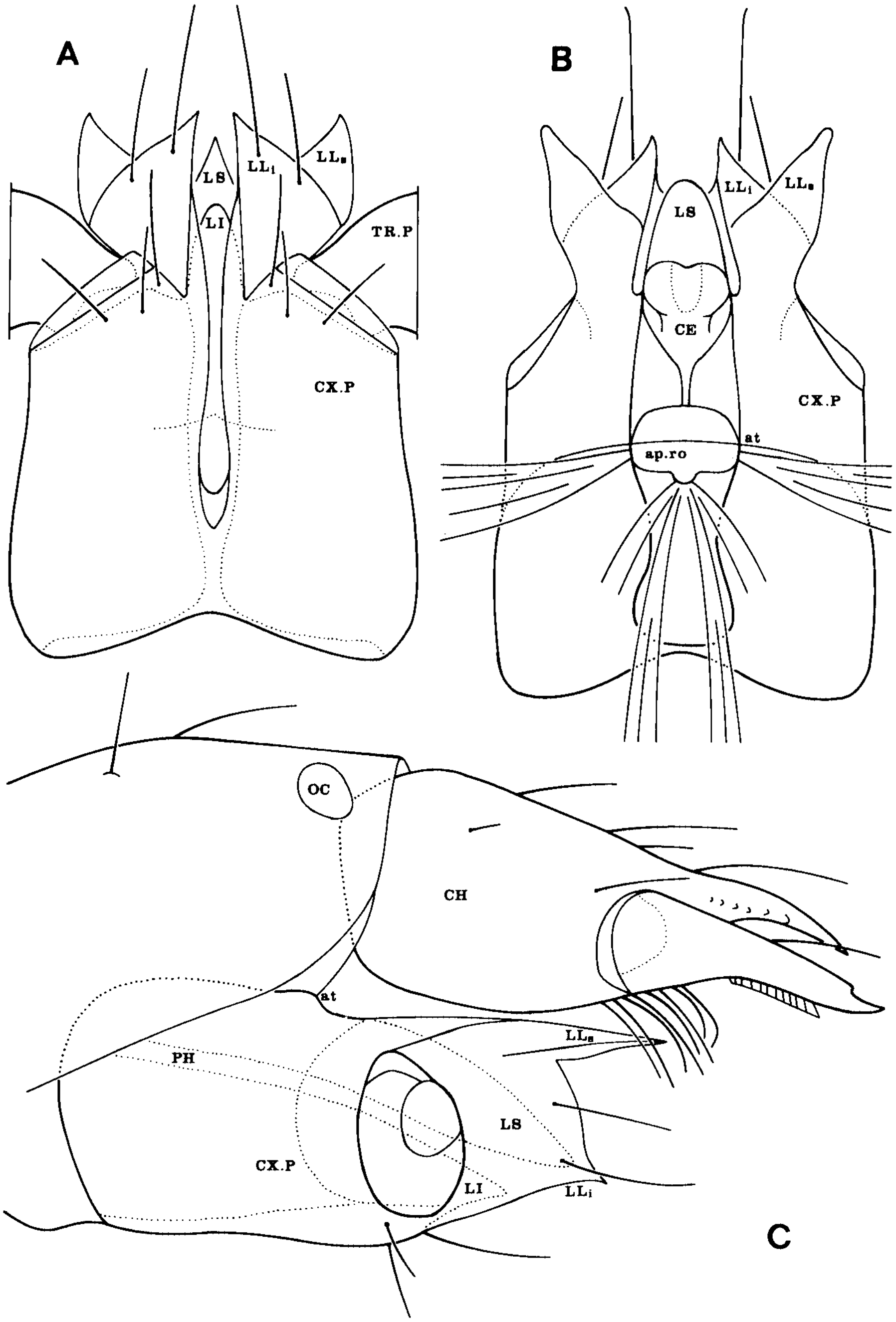

Fig. 9. *Chthonius (Chthonius) tenuis* L. Koch, mouthparts of adult; A, ventral view of rostrosoma; B, dorsal view of rostrosoma; C, lateral view; A-C, × 141.

of insertion of muscles). The labium, which could represent the sternal part of segment II, has a ventral position between the coxae of the palp. The large lateral lips present a superior and an inferior projection; their basal parts are attached to the palpal coxae and to labrum and labium. The pharynx is characterized by the presence of a pharyngeal pump.

The fundamental structure of the mouthparts of both groups of Apatellata (Solifugae and Pseudoscorpionida) is evidently very similar. In both groups the mouthparts include a rostrosoma (consisting of labrum, cervix, rostrosomatic apodeme, lateral lips and labium) of which the base has fused with the palpal coxae.

The Schizomid mouthparts comprise (besides the chelicerae): the labrum, the cervix (posteriorly bordered by the line of attachment of the cheliceral frame), median and lateral apodemes, the coxapophyses of the palpi, an intercoxal gutter (with ventral position, between the fused palpal coxae) and a labium; there are no lateral lips. A dorsal view of the mouthparts (chelicerae removed) is represented in fig. 10A, a ventral in fig. 10B, and a lateral in fig. 10C. The unpaired median apodeme is long and narrow, and muscles are inserted on it. The paired lateral apodemes are a continuation of the internal apodeme of the palpal coxa (homonomous with the anterior coxal apodeme of all Arachnida s. str.), and palpal muscles are attached to it. The coxapophyses of the palp present a dorsal brush. As mentioned above, the intercoxal gutter is associated with the sternapophyses and the orifices of the coxal glands (as in Cryptognomae). The labium is an anterior extension of the bottom of the intercoxal gutter, and is laterally fused with the palpal coxapophyses; an orifice of a labial gland is visible in ventral view (fig. 10D).

The Holopeltid mouthparts are very similar to those of the Schizomida. They are represented, in dorsal view (after removal of the chelicerae), in fig. 11A; in this figure, the attachment of palpal muscles to the lateral apodeme (the anterior apodeme of the palpal coxa) is also represented. The similarity of the mouthparts in Schizomida and Holopeltida demonstrates again the close relationship of the two groups of Uropygi.

The Amblypygid mouthparts are very simple, and comprise (besides the chelicerae): a small labrum (cervix not distinctly differentiated), and the coxae and coxapophyses of the palp. There is no labium and there are no lateral lips. A ventral view of the mouthparts is represented in fig. 11B, a longitudinal (nearly sagittal) section in fig. 11C. The position of the mouth is rostral. The mouthparts are associated with the anterior sternapophyses and the orifices of the coxal glands.

The rather simple Araneid mouthparts comprise (besides the chelicerae): the labrum and the cervix, the coxapophyses of the palp (not present in

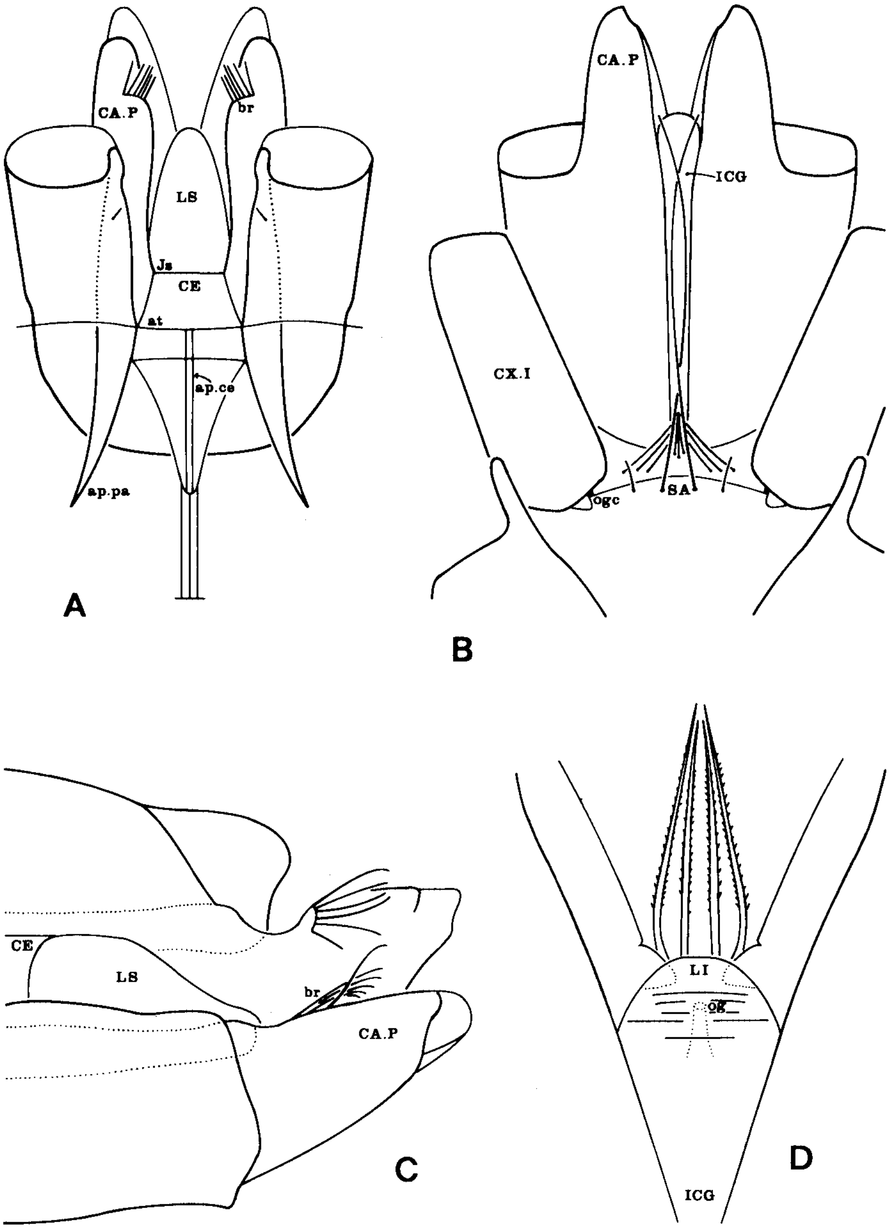

Fig. 10. *Trithyreus* spec., mouthparts of adult female; A, dorsal view; B, ventral view; C, oblique laterodorsal view; D, ventral view of labium and adjacent parts of coxapophyses and intercoxal gutter; A-B, × 88; C, × 141; D, × 295.

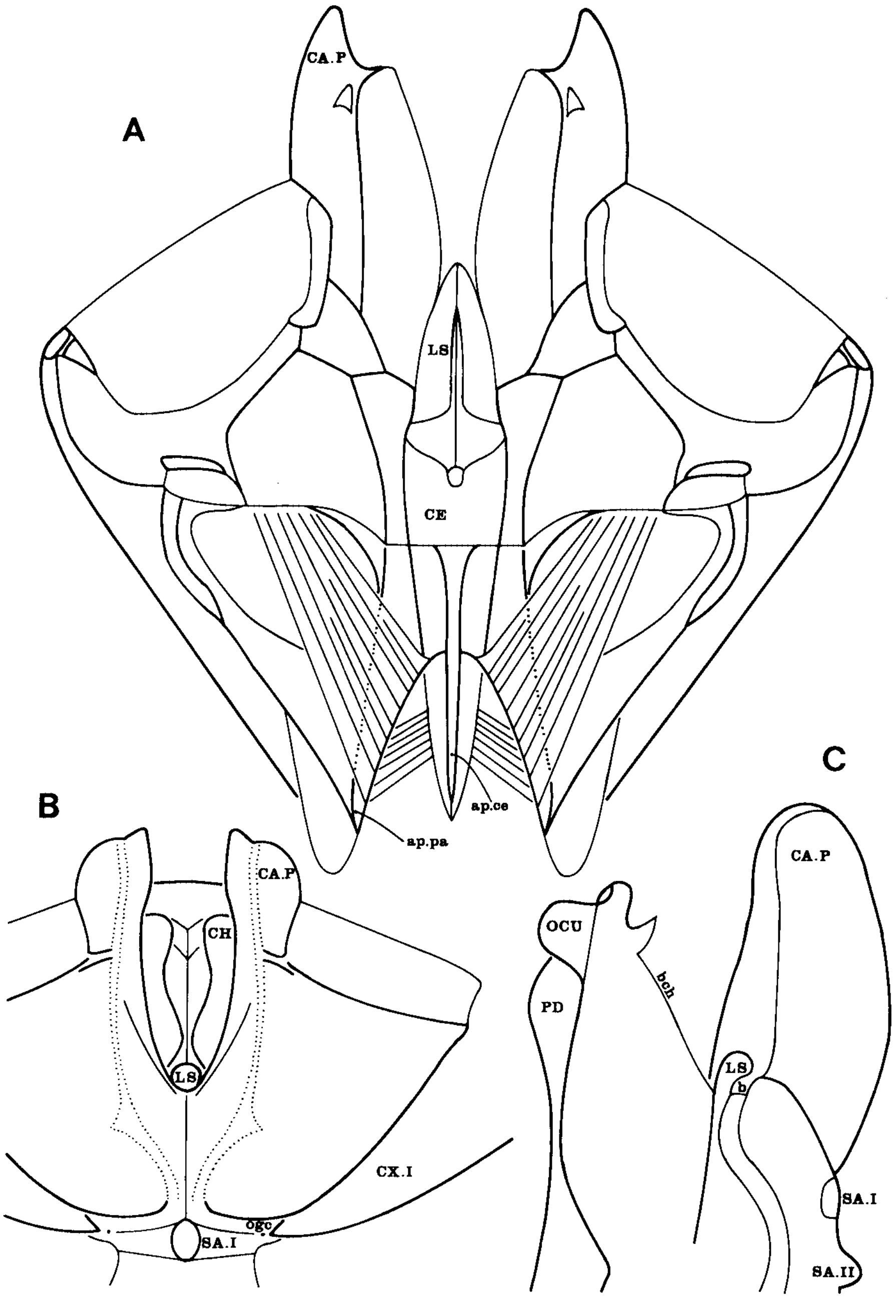

Fig. 11. Mouthparts of Arachnida s. str.; A, Uropygi (Holopeltida): *Tetrabalius seticauda* (Doleschall), adult male, dorsal view of mouthparts (chelicerae removed); B, C, Amblypygi: *Heterophrynus alces* Pocock, adult; B, anteroventral (oblique) view of mouthparts (sternapophysis I cut off); C, longitudinal section of mouthparts (chelicerae removed); A, × 20.3; B, C, × 4.8.

Liphistiidae and many Mygalomorphae), the palpal coxae, and the labium; there are no lateral lips. The mouthparts of *Segestria senoculata* are represented in dorsal and ventral view, and in a longitudinal section, in fig. 12A-C. A longitudinal section of the mouthparts of *Araneus quadratus* is represented in fig. 12D, a ventral view of the mouthparts of *Liphistius desultor* in fig. 12E. The position of the mouth is more or less rostral (fig. 12C); in many higher Araneida (fig. 12D), however, the chelicerae, the labrum and the labium (including the preoral cavity) are curved downwards, although the mouth has preserved its original position. The Araneid labium is generally regarded as representing the sternite of segment II. The absence of the palpal coxapophyses (fig. 12E) in more primitive groups of Araneida could point to the secondary origin of these apophyses, or to a suppression (they are present in Uropygi and Amblypygi).

Evidently, in all Arachnida s. str. the structure of the mouthparts is rather simple, and lateral lips are not present.

The Scorpionid mouthparts are characterized, in particular, by the ventral position of the mouth (as a result of a backward translocation) and by the participation of the coxapophyses of legs I and II in ingestion. For this type of mouthparts (also found in Opilionida and Xiphosura) I recently introduced the term myliosoma (Van der Hammen, 1985a: 25); it is associated with coxisternal food-intake. Scorpionid mouthparts are represented in dorsal view in fig. 13A, in ventral view in fig. 13B, and in longitudinal (nearly sagittal) section in fig. 13D. The mouthparts include (besides the chelicerae): labrum, cervix, palpal coxae, labium (a prosomatic sternite) and the coxapophyses of legs I and II (there are no palpal coxapophyses). The pharynx is bent in ventral direction, in association with the ventral position of the mouth. The orifices of the coxal glands, at the base of coxae III, could be associated with the mouthparts.

Xiphosura are characterized by the presence of a myliosoma, and by the participation of the coxapophyses of limbs 2-6 in food-intake (the coxapophyses of limbs 2-5 are associated with the mouth). A ventral view of the Xiphosurid mouthparts is represented in fig. 6B, a longitudinal (nearly sagittal) section in fig. 14A. Xiphosura differ from all other groups of Chelicerata by the absence of a pharynx; the foregut consists of oesophagus and crop, and is separated by a valve from the midgut (fig. 14A). The oesophagus is curved back in such a way that the labrum is ventral to the mouth, the labium dorsal; the oesophageal ganglia have been subject to a similar translocation. The chelicerae articulate with the labrum; there is no cheliceral frame (the cheliceral frame is present in all other Chelicerata). The Xiphosurid labium represents the fused prosomatic sternites.

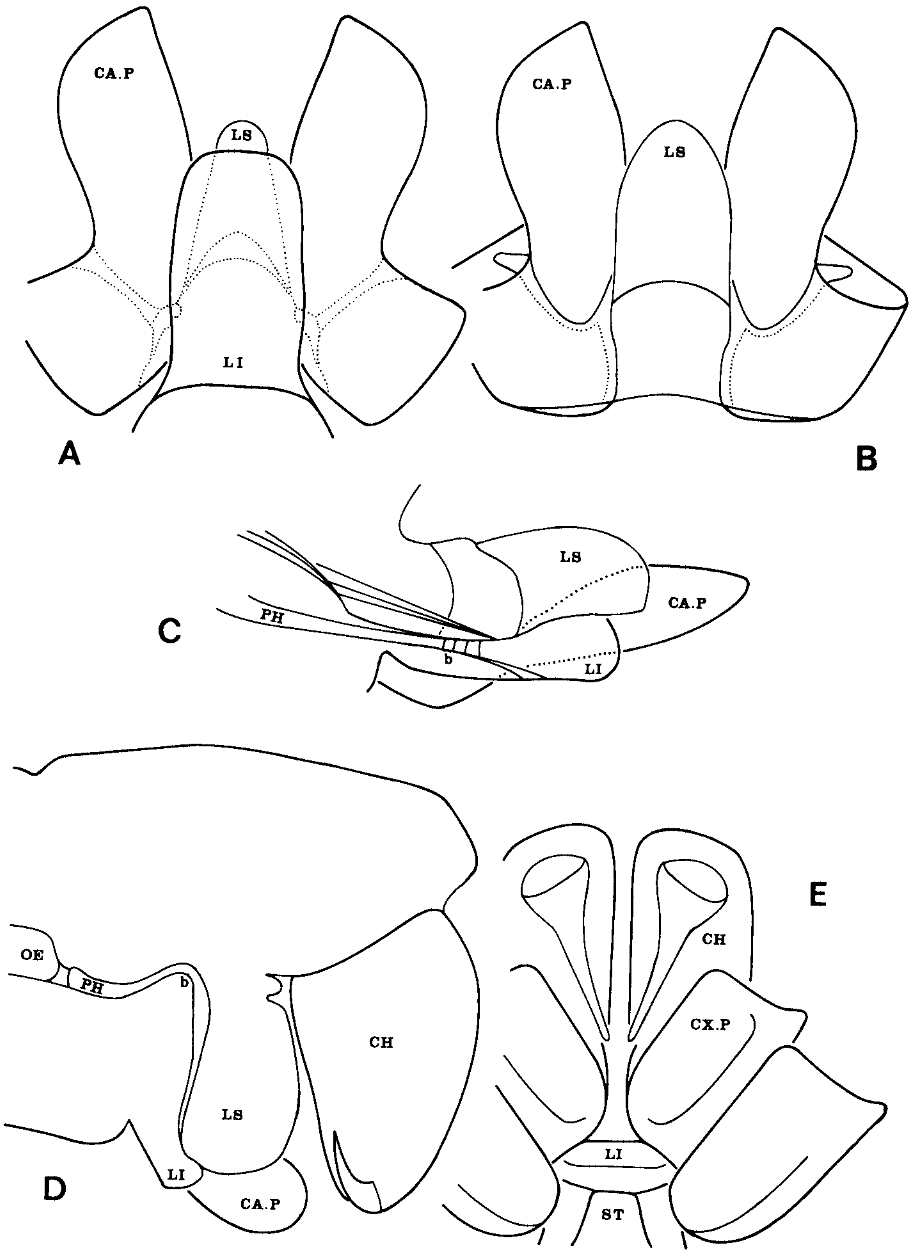

Fig. 12. Mouthparts of Araneida; A-C, *Segestria senoculata* (Linnaeus), adult female; A, ventral view; B, dorsal view; C, longitudinal section; D, *Araneus quadratus* Clerck, adult female, longitudinal section; E, *Liphistius desultor* Schiödte, adult female, ventral view; A-C, × 44; D, × 20.3; E, × 5.1.

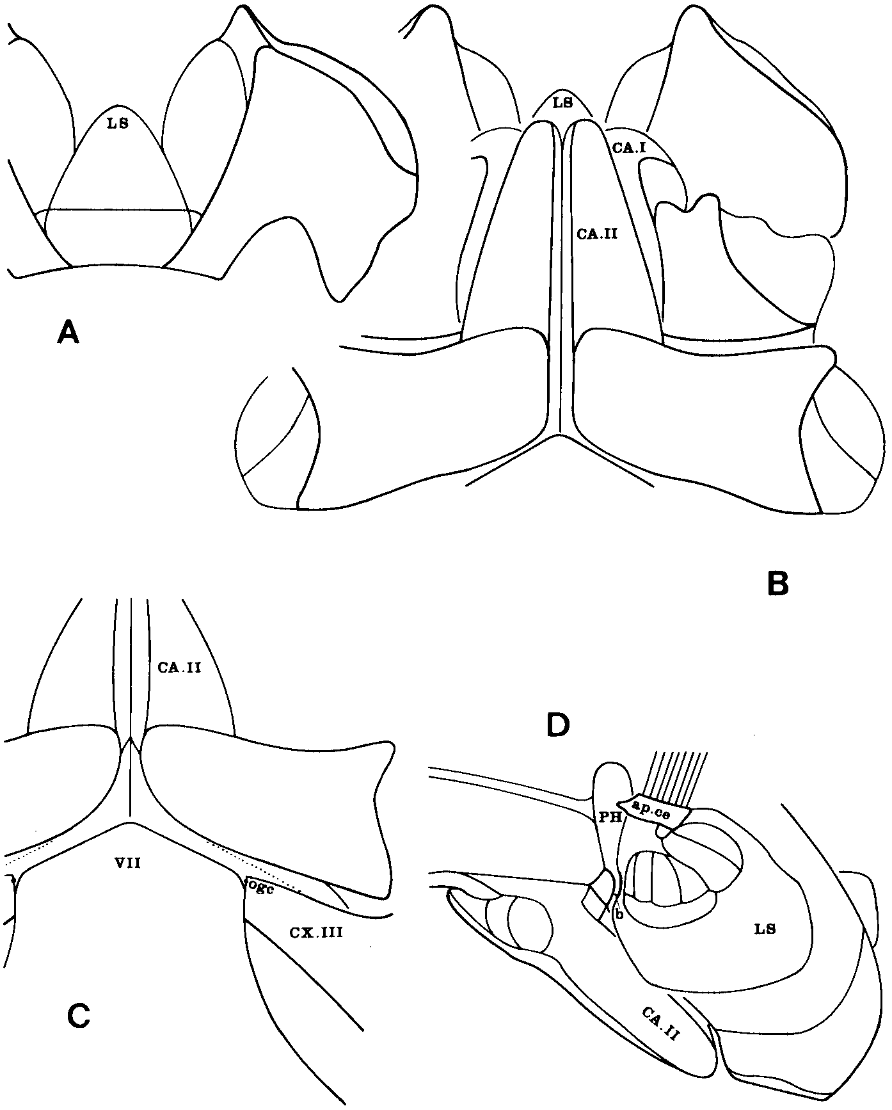

Fig. 13. *Euscorpius carpathicus* (Linnaeus); A, B, mouthparts of adult female; A, dorsal view of external parts (chelicerae removed); B, ventral view; C, coxisternal region of adult male, ventral view; D, longitudinal (nearly sagittal) section of mouthparts of adult female; A-D, × 20.3.

In the groups of Chelicerata, studied in the present paper, three types of mouthparts are found: relatively simple mouthparts (without lateral lips) in Arachnida s. str.; a rostrosoma (with lateral lips) in Apatellata; and a myliosoma is Scorpionida and Xiphosura. It may be added here that the most simplified type of mouthparts (consisting of labrum and labium) is found in Palpigradi; Actinotrichida and Cryptognomae are characterized by the presence of a gnathosoma, Opilionida by the presence of a myliosoma.

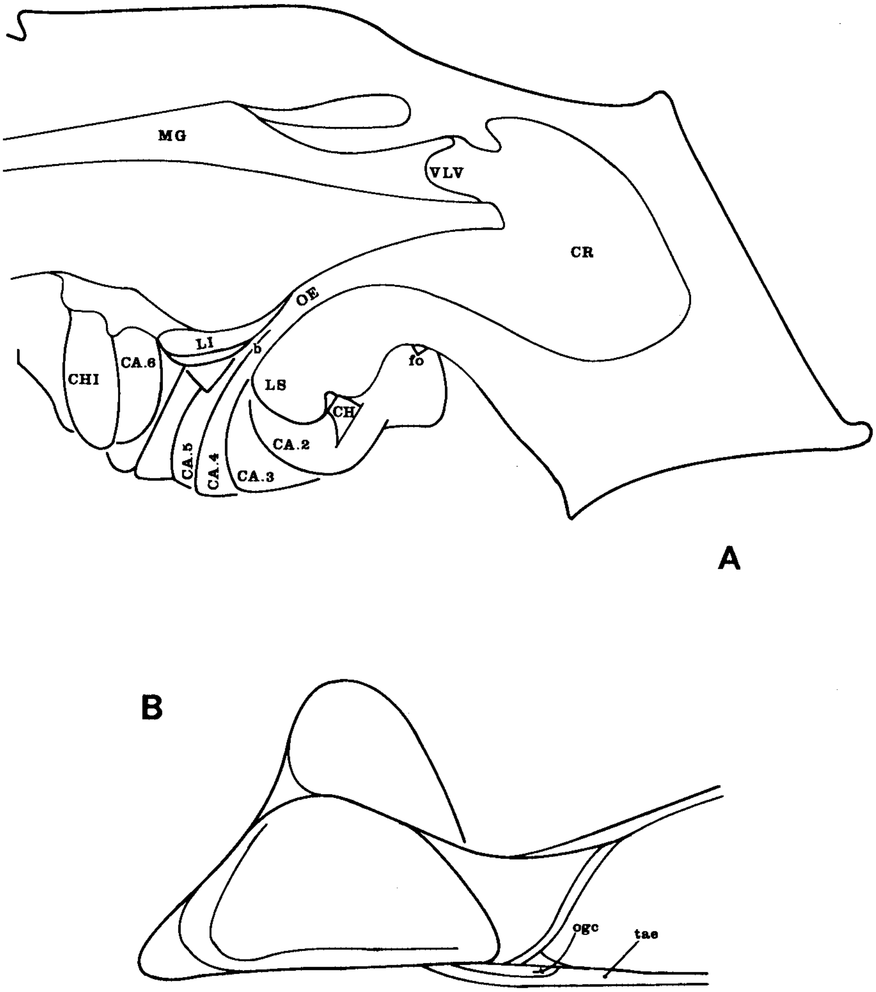

Fig. 14. *Limulus polyphemus* (Linnaeus), juvenile specimen; A, longitudinal (nearly sagittal) section of prosoma; B, posteroventral view of the coxal base of right limb 5, with the orifice of the coxal glands; A, × 5.1; B, × 20.3.

V. APPENDAGES

I have dealt with the segmentation and articulation of the chelicerate appendages in two previous papers (Van der Hammen, 1977a and 1985b). In both papers mention is made of chelicera, palp and legs. In the present section, the discussion is mainly restricted to the legs. Generally, one leg (leg IV) is studied as an example, whilst other legs are studied in the case of important differences only. In Xiphosura, limb 2 (homologous with the palp of other Chelicerata) is also studied, because it functions as a leg. For data pertaining to chelicera and palp of the groups dealt with in the present paper, I refer to the above-mentioned two papers.

The Solifugid legs consist of coxa, trochanter 1, trochanter 2 (not present in legs I and II), femur 1, femur 2, tibia, basitarsus, telotarsus and apotele (sometimes reduced or lacking in leg I). Leg IV of a species of Solifugae is represented in fig. 15A, leg II in fig. 15B. The coxae occupy the ventral surface of the prosoma, and present relatively large internal apodemes; they are not movable. They stand, in fact, midway between epimera and free coxae, and are here regarded as coxae in the course (at the beginning) of evolutionary development (not as free coxae which have become fixed). There is a sejugal interval between coxae II and III, which permits of prosomatic articulation. The promotor-remotor movements take place at the coxa-trochanter (legs I-II) or coxa-trochanter 1 (legs III and IV) articulation; it constitutes a pivot joint. The articulation between trochanter 1 and trochanter 2 is a pivot joint with levator and depressor muscles. In the trochanter-femur 1 (legs I-II) or trochanter 2-femur 1 (legs III-IV) articulation, the axis of movement is nearly longitudinal (because of the advanced position of one of the condyles) and permits of leg rocking. The articulation between femur 1 and femur 2 is constituted by a hinge joint with flexor muscles. The hinge joint between femur 2 and tibia (there is no patella) permits of considerable flexion. A hinge joint with flexor muscles is also present between tibia and basitarsus. The adesmatic articulation between basi- and telotarsus is operated by the tendons of the apotele. The telotarsus-apotele articulation is constituted by the usual bicondylar articulation with levator and depressor muscles. The telotarsus can be subdivided into a variable number of eudesmatic segments (leg IV of *Pseudocleobis andinus* presents four eudesmatic segments: the telotarsi 1-4).

The Pseudoscorpionid legs (see Chamberlin, 1931: 146-165, figs. 40-44) consist of eight eudesmatic and adesmatic segments at the most, viz., coxa, trochanter, femur 1, femur 2, tibia, basitarsus, telotarsus and apotele. In several groups there is, however, only one femur in the two anterior or in all four legs; the same applies to the tarsus. In *Chthonius (Chthonius) tenuis*, leg

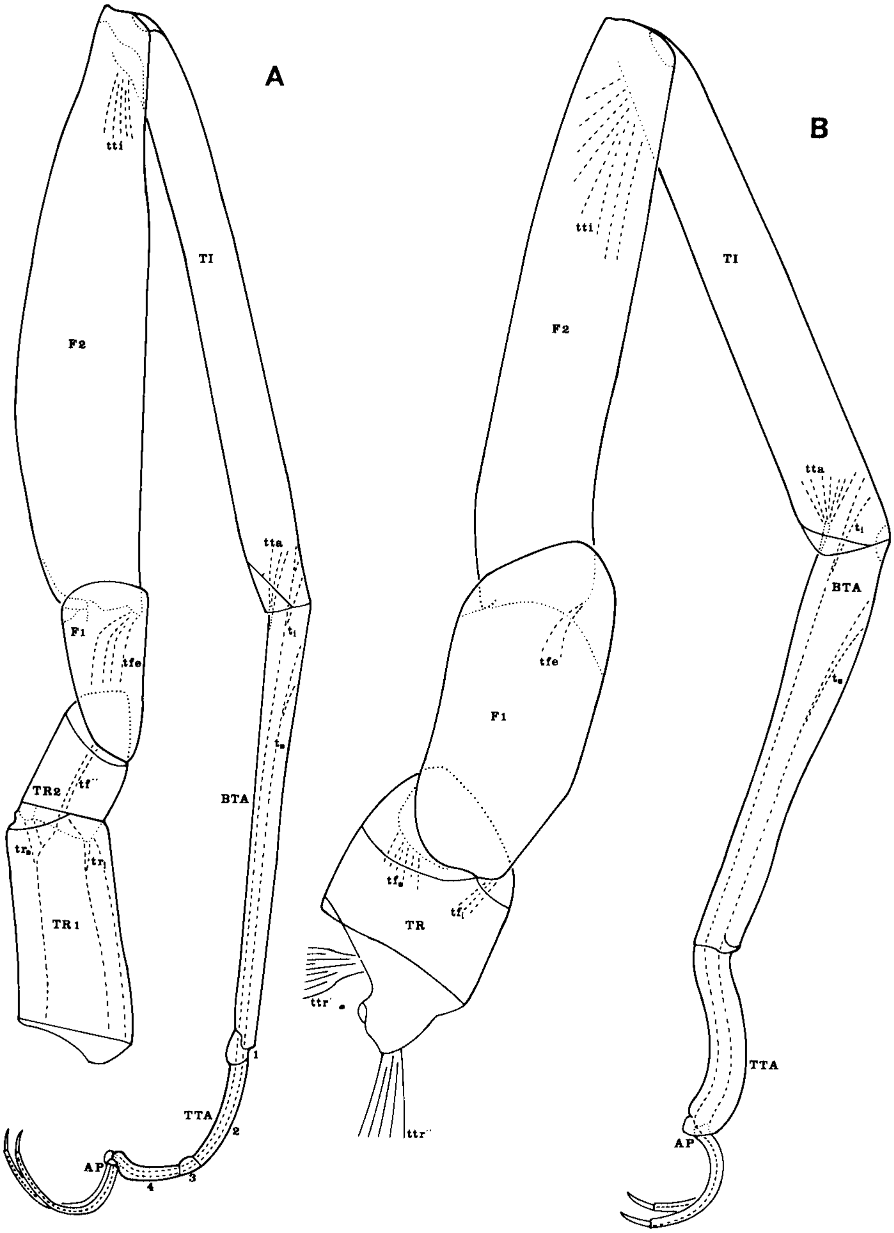

Fig. 15. *Pseudocleobis andinus* (Pocock); A, lateral (posterior) view of right leg IV; B, lateral (posterior) view of right leg II; A, × 17.4; B, × 36.6.

I (fig. 16B) consists of coxa, trochanter, femur, tibia, basitarsus, telotarsus and apotele; leg IV of the same species (fig. 16A) consists of coxa, trochanter, femur 1, femur 2, tibia, basitarsus, telotarsus and apotele. The Pseudoscorpionid coxae are similar to those of the Solifugae (with the exception of the large apodemes); they are here also regarded as coxae in the course of evolutionary development, and as standing midway between epimera and free coxae. The promotor-remotor movements take place at the coxa-trochanter articulation. The articulation between trochanter and femur (or femur 1) is constituted by a bicondylar, bidesmatic pivot joint. In leg IV of *Chthonius* the axis of movement of this joint is more or less longitudinal (as in Solifugae), for which reason it could be associated with leg rocking. The separation of femur 1 and femur 2 in leg IV of *Chthonius* is incomplete; the articulation is adesmatic and probably permits of little movement. The articulation between femur and tibia (or between femur 2 and tibia) is constituted by a hinge joint with two superior condyles and several inferior muscles. The tibia-basitarsus articulation is also constituted by a hinge joint; it is operated by inferior muscles, whilst the inferior tendon of the apotele passes the articulation (because it has its base in the tibia). The articulation between basi- and telotarsus is adesmatic; it is operated by the two tendons of the apotele. The telotarsus-apotele articulation is bicondylar and bidesmatic. It may be remarked here that, in several species of Pseudoscorpionida, the femur 1-femur 2 articulation is constituted by a monodesmatic hinge joint, representing the ancestral condition of this joint (similar to that in Epimerata); the type of regression of the joint (disappearance of the muscles, followed by gradual disappearance of the separation of the joints) is also similar to that in Epimerata. Weygoldt & Paulus (1979: 95-96) homologized femur 2 with a patella. The above-mentioned similarities with Epimerata, and the general pattern of the evolutionary development of the chelicerate appendages (see Van der Hammen, 1985a: 50-51) do not support this hypothesis, although the problem is certainly not yet sufficiently studied.

The Uropygid legs are studied here in both groups (Schizomida and Holopeltida). Leg IV of a *Trithyreus* species (Schizomida) is represented in fig. 17. The Schizomid legs consist of coxa, trochanter, femur, patella, tibia (patella and tibia have fused in leg I, as in the case of the palp), basitarsus, telotarsus (subdivided into several adesmatic segments) and apotele (absent in leg I). Leg I consists (in *Trithyreus*) of coxa, trochanter, femur, patellotibia, basitarsus and telotarsi 1-7. Legs II-IV consist (in *Trithyreus*) of coxa, trochanter, femur, patella, tibia, basitarsus, telotarsi 1-3 and apotele. The coxae of the legs occupy the ventral surface of the prosoma; they are regarded here as coxae at an advanced stage of evolutionary development (not as coxae which

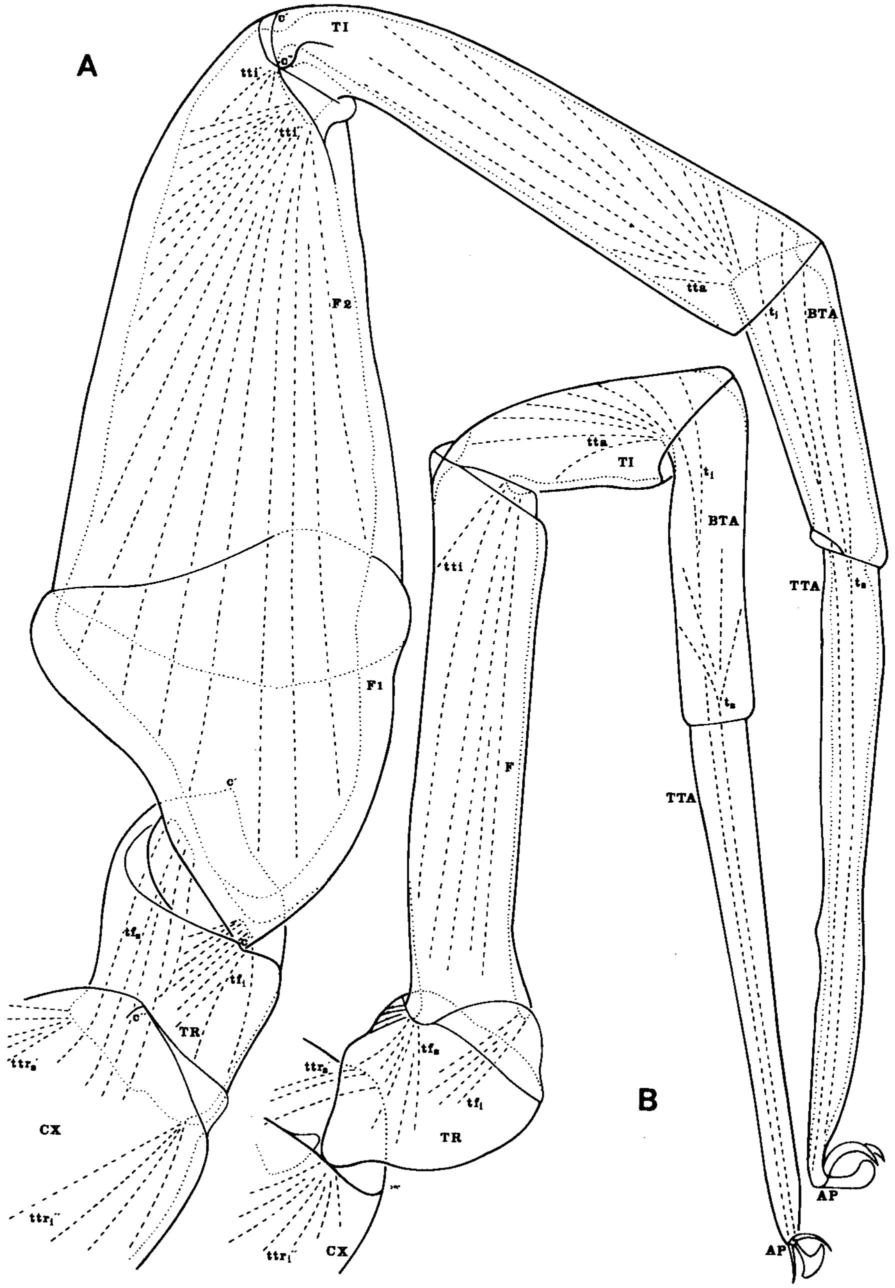

Fig. 16. *Chthonius (Chthonius) tenuis* L. Koch; A, lateral (posterior) view of right leg IV; B, lateral (posterior) view of right leg I; A, B, × 169.

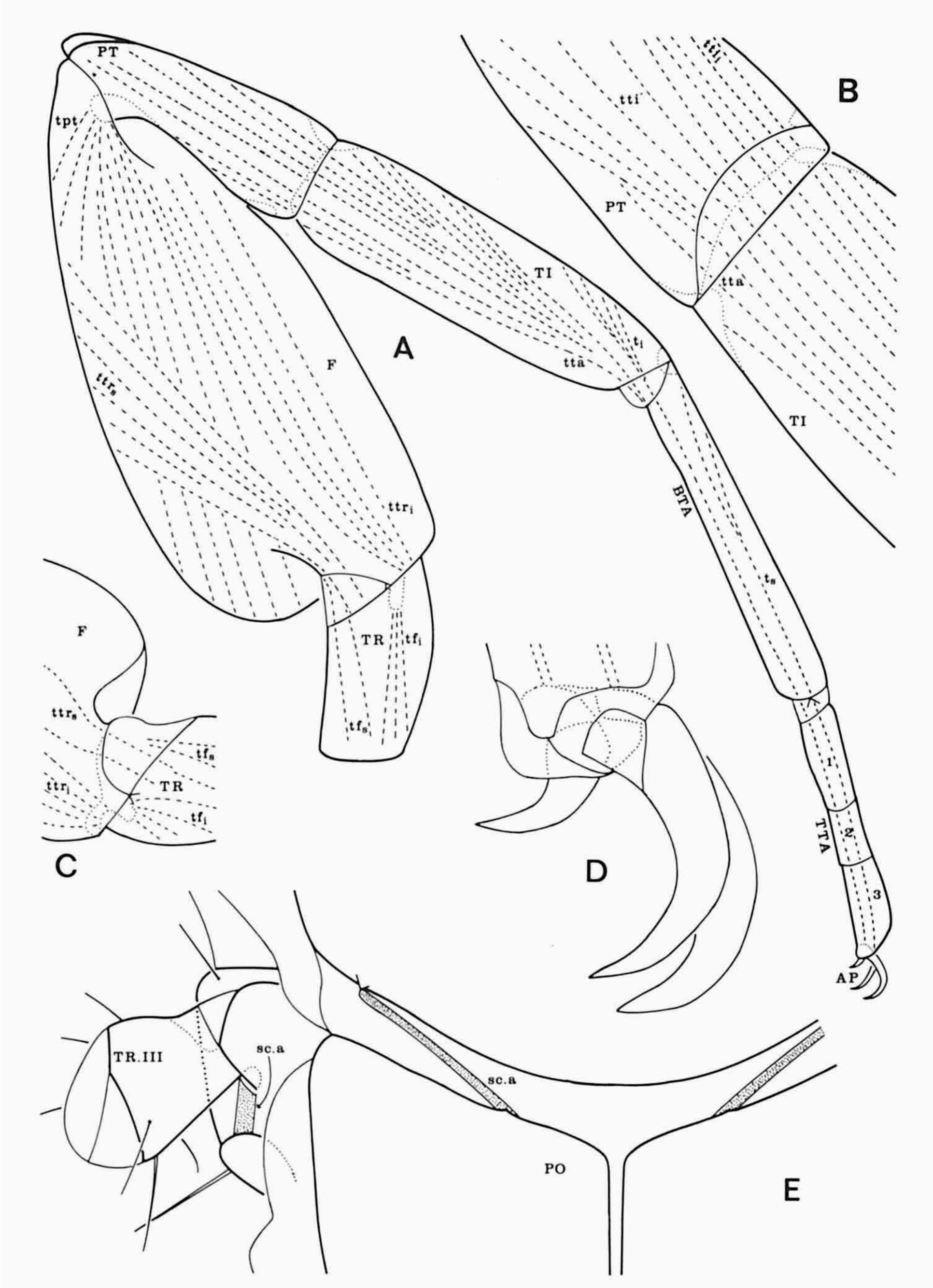

Fig. 17. *Trithyreus* spec., right leg IV of adult female; A, lateral (posterior) view of trochanter, femur, patella, tibia, basitarsus, telotarsi 1-3 and apotele; B, lateral (anterior) view of patella (distal part) and tibia (proximal part) (the lower part of the figure is dorsal); C, lateral (anterior) view of trochanter (distal part) and femur (proximal part); D, lateral (posterior) view of distal part of telotarsus 3 and apotele; E, dorsal view of part of prosoma (with arthrodial sclerites between pro- and postpeltidium) and coxa and trochanter of right leg III; A, C, × 88; B, × 186; D, × 550; E, × 141.2.

secondarily have become fixed). The coxa-trochanter articulation (fig. 17E) presents an anterior condyle and a posterior arthrodial sclerite; the arthrodial sclerite is movably connected with the coxa by a relatively broad hinge, and with the trochanter by an articulation point. This complicated joint (similar joints are present in other Arachnida s. str.) permits of promotor-remotor movements associated with leg rocking. The trochanter-femur articulation is constituted by a bicondylar pivot joint with superior and inferior muscles. The muscles of the trochanter are in the femur (as in other Arachnida s. str.). The femur-patella articulation is constituted by a bicondylar hinge joint with inferior muscles. The patella-tibia articulation (fig. 17A, B) is constituted by a particular type of hinge joint (similar types are found in the other groups of Arachnida s. str.); it is characterized by the presence of a dorsal condyle, whilst the entire posterior part of the joint can function as a hinge (flexion is in anterior direction); there are anterolateral and antero-inferior muscles, whilst the flexor muscles of the tarsus extend into the patella. The tibia-basitarsus articulation is represented by a hinge joint which is operated by the flexor muscles of the tarsus (the inferior tendon of the apotele extends into the tibia). The adesmatic basitarsus-telotarsus articulation and the adesmatic articulations in the telotarsus are operated by the tendons of the apotele. The tarsus-apotele articulation is bicondylar; it is operated by the usual two tendons (superior and inferior). The apotele of legs II-IV (fig. 17D) is characterized by the presence of two claws and a so-called pseudonychium (an apophysis of the apotele, not a true unguis).

Leg IV of a *Tetrabalius* species (Holopeltida) is represented in fig. 18. Holopeltid legs generally consist of coxa, trochanter, femur, patella, tibia (patella and tibia have fused in the case of leg I, as in the palp), basitarsus, telotarsus (subdivided into several adesmatic segments) and apotele (absent in leg I). In *Tetrabalius*, leg I consists of coxa, trochanter, femur, patellotibia, basitarsus and telotarsi 1-9; legs II-IV consist of coxa, trochanter, femur, patella, tibia, basitarsus, telotarsi 1-3 and apotele. The coxae of the Holopeltid legs occupy the ventral surface of the prosoma and are regarded (as in the case of Schizomida) as coxae at an advanced stage of evolutionary development. An internal apodeme (fig. 18C) is present at the anterior side of the coxae (as in other groups of Arachnida s. str.); it is probably homologous with the apodeme which is usually associated with an epimeron. The coxa-trochanter articulation (fig. 18C-E) presents an anterior condyle, distal to the coxal apodeme, and a posterior arthrodial sclerite (broad hinge with the trochanter, articulation point with the coxa). This joint permits of promotor-remotor movements associated with leg rocking. The other joints in the legs of *Tetrabalius* (fig. 18A) resemble those of Schizomida. The patella-

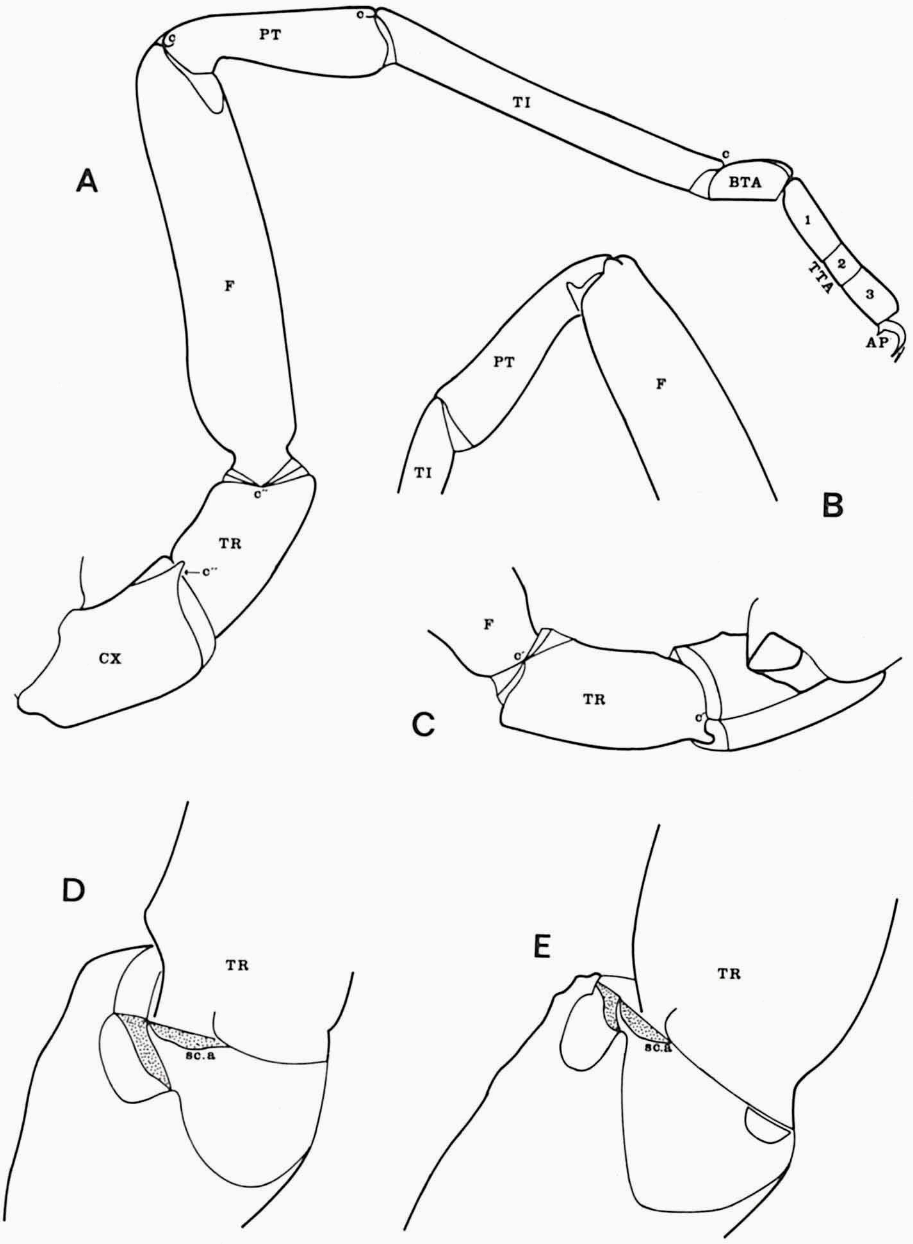

Fig. 18. *Tetrabalius seticauda* (Doleschall), right leg IV of adult male; A, lateral (posterior) view; B, lateral (anterior) view of distal part of femur, patella and proximal part of tibia; C, lateral (anterior) view of coxa, trochanter and proximal part of femur; D, E, articulation between coxa and trochanter, lateral (posterior) face; D, oblique view in the direction of the base of the leg (laterodorsal orientation); E, oblique view in the direction of the base of the leg (lateral orientation); A-C, × 8.3; D-E, × 20.3.

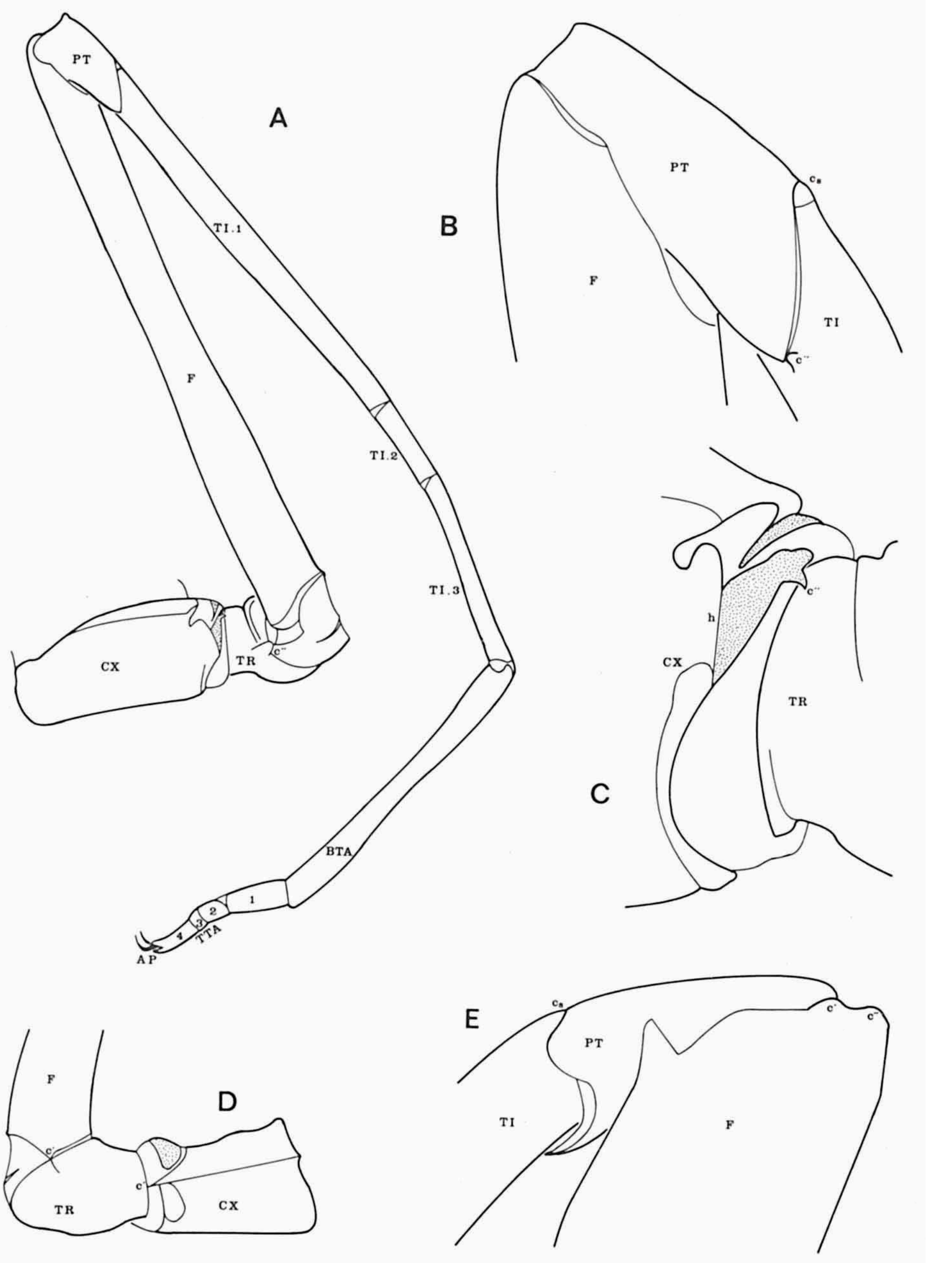

Fig. 19. *Heterophrynus alces* Pocock, right leg IV of adult; A, lateral (posterior) view; B, lateral (posterior) view of distal part of femur, patella and proximal part of tibia; C, lateral (posterior) view of articulation between coxa and trochanter; D, lateral (anterior) view of coxa, trochanter and proximal part of femur; E, lateral (anterior) view of distal part of femur, patella and proximal part of tibia; A, D, × 4.2; B, C, E, × 16.9.

tibia joint (fig. 18A, B) presents a superior condyle, whilst the posterior part of the joint can function as a broad hinge; the joint permits also of leg rocking.

The legs of *Heterophrynus alces* are studied here as an example of the Amblypygi; leg IV of this species is represented in fig. 19. In my specimen leg I consists of coxa, trochanter, femur, patella, tibia 1-31 (in the palp, patella and tibia have fused), tarsus 1-71 (basitarsus and telotarsus are indistinguishable) and a reduced apotele (of which the ungues have fused at the base); the numbers of tibial and tarsal segments are certainly variable in this species. Legs II-IV consist of coxa, trochanter, femur, patella, tibia (tibiae 1-3 in the case of leg IV), basitarsus, telotarsus 1-4, and apotele. The coxae of palp and legs are arranged around a sternum; they are boat-shaped and present an anterior apodeme (fig. 19D). The coxa-trochanter joint presents an anterior condyle, distal to the coxal apodeme, and a posterior arthrodial sclerite (broad hinge articulation with the coxa, articulation point with the trochanter; see fig. 19C); the muscles of the trochanter are in the femur. The coxa-trochanter joint permits of promotor-remotor movements and is associated with leg rocking. The trochanter-femur articulation is constituted by a bicondylar pivot joint, associated with levator and depressor movements. The femur-patella articulation is constituted by a hinge joint which permits of considerable flexion. The patella-tibia articulation (fig. 19B, F) is constituted, in legs II-IV, by a bicondylar hinge joint of which the hinge is posterolateral (there is a superior and a posterolateral condyle); in leg I there is only a superior condyle, but anterior flexion can occur because of the presence of a ventral sclerotized structure, by which ventral flexion is restricted. Adesmatic joints are present in tibia IV. The tibia-basitarsus articulation is constituted by a hinge joint. The basitarsus-telotarsus articulation and the adesmatic articulations in the telotarsus are operated by the tendons of the apotele. The telotarsus-apotele articulation is constituted by the usual bicondylar pivot joint with superior and inferior tendons. The apotele bears two ungues.

The Araneid legs are studied here in two species: *Liphistius desultor* (fig. 21) and *Segestria senoculata* (fig. 20). An important and detailed study of the legs of *Heteropoda venatoria* was recently published by Clarke (1984); in this paper, a discussion of previous literature can be found. The segments present in the Araneid legs are: coxa, trochanter, femur, patella, tibia, basitarsus, telotarsus and apotele. The coxae of *Liphistius* are large and boat-shaped (as in Amblypygi) and are arranged at both sides of a narrow sternum; they are surrounded by soft skin, by which they are movable. The coxae of *Segestria* (as in most other species of Araneida) are short and cylindrical; they have a much more lateral position, and have a loose articulation with the sternum.

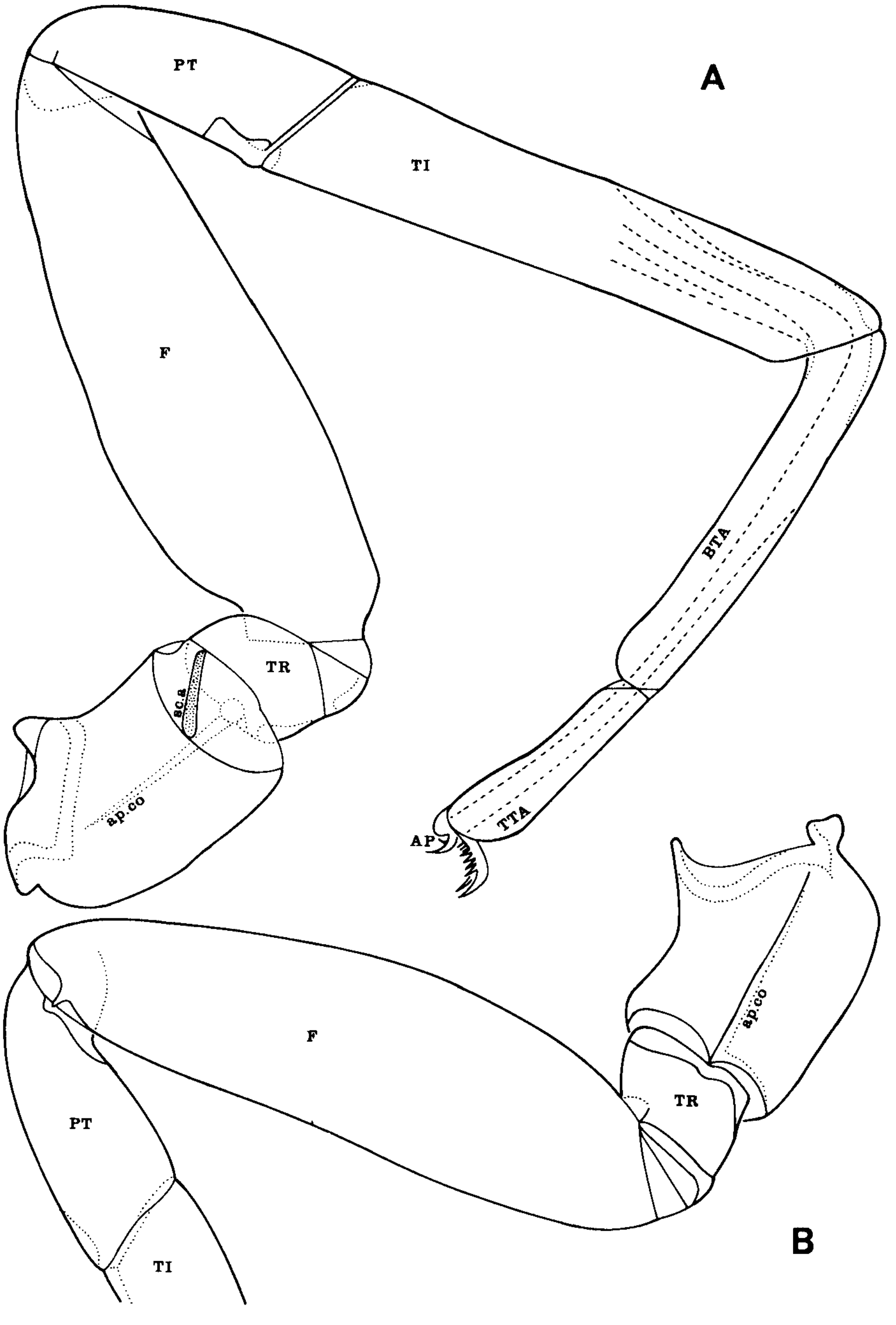

Fig. 20. *Segestria senoculata* (Linnaeus), right leg IV of adult female; A, lateral (posterior) view; B, lateral (anterior) view of coxa, trochanter, femur, patella and proximal part of tibia; A, B, × 46.8.

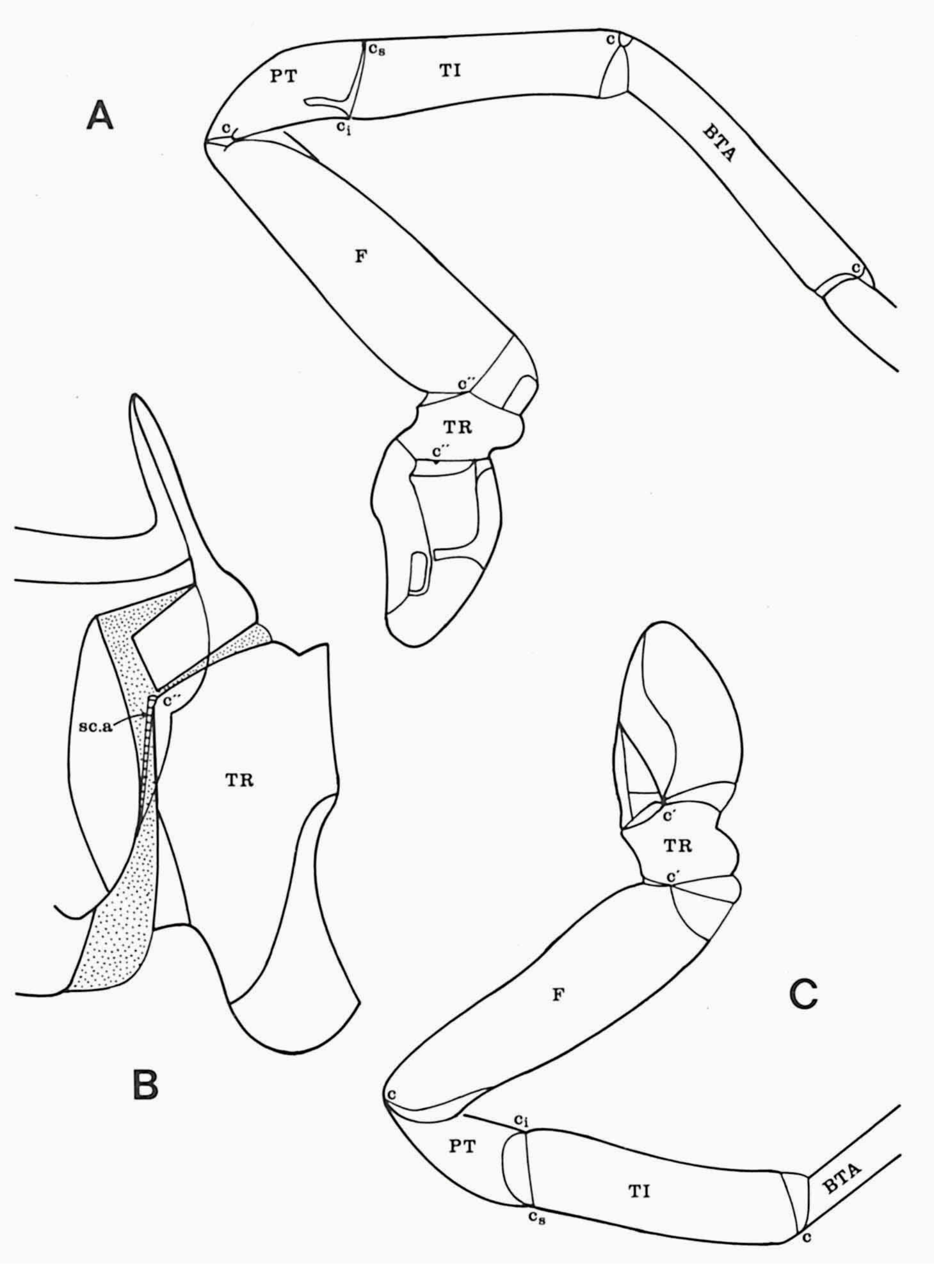

Fig. 21. *Liphistius desultor* Schiödte, adult female; A, B, right leg IV; A, lateral (posterior) view; B, lateral (anterior) view; C, coxa-trochanter articulation of right leg III, lateral (posterior) view (in C, the arthrodial sclerite is indicated by hatching, the desclerotized coxal tegument by stippling; A, B, × 4.3; C, × 16.9.

All coxae present an anterior apodeme (figs. 20B, 21C). The coxae in *Liphistius* are regarded here as an advanced stage in the evolutionary development of free coxae from epimera, the coxae in *Segestria* (and most other species of Araneida) as the final stage. The possibilities of movement at the coxa-body joint are restricted, particularly in *Liphistius*. The coxa-trochanter joint presents an anterior condyle, distal to the coxal apodeme, and a posterior arthrodial sclerite (fig. 20A, 21B). The last-mentioned sclerite (often hidden from view by a fold of the arthrodial menbrane) takes the place of the triangular sclerite of Uropygi and Amblypygi, but does not present the broad hinge at one of the ends; it is supposed here that movements at the coxa-trochanter joint are guided and restricted by the presence of this sclerite. The coxa-trochanter joint is associated with levator-depressor movements, and with some dorso-ventral movement and rocking. As in other Arachnida s. str., the muscles of the trochanter are in the femur. The trochanter-femur articulation is constituted by a bicondylar pivot joint associated with levator and depressor movements. The femur-patella articulation is constituted by a hinge joint (with two superior condyles) and inferior flexor muscles; this joint allows of considerable flexion. The Araneid patella-tibia articulation is very interesting from an evolutionary point of view. In *Liphistius* (fig. 21A, C), this joint is similar in all four legs (and in the palp); it is constituted by a main superior articulation point, and a very small inferior one. The main movements are antero-posterior, whilst dorso-ventral movements are restricted by the presence of the ventral articulation point (which functions when the joint is at its maximum flexion). In *Segestria* (fig. 20A, B), the patella-tibia joint of legs I-III is more or less similar to that in *Liphistius*, whilst in leg IV patella and tibia are in close permanent contact at the posterior side (constituting a posterior hinge, allowing of antero-posterior movements only). According to the data published by Clarke (1984: 184), legs I and II of *Heteropoda* are similar to legs I-IV of *Liphistius* and legs I-III of *Segestria*, whilst legs III and IV are similar to leg IV of *Segestria*. Evidently, the evolution of the patella-tibia joint, in the direction of a structure allowing of antero-posterior movements only, is still in progress in Araneida (where it has started with leg IV); because it is found in the three groups of Arachnida s. str., it must be an example of parallel evolution attributable to similarities in the evolutionary potentialities of these groups. The Araneid tibia-basitarsus articulation is constituted by a hinge joint with superior articulation; it is associated with flexion. The adesmatic basitarsus-telotarsus articulation is operated by the tendons of the apotele. The telotarsus-apotele articulation is constituted by a bicondylar pivot joint with the usual two tendons (superior and inferior). The apotele bears two ungues, whilst a pseudonychium is

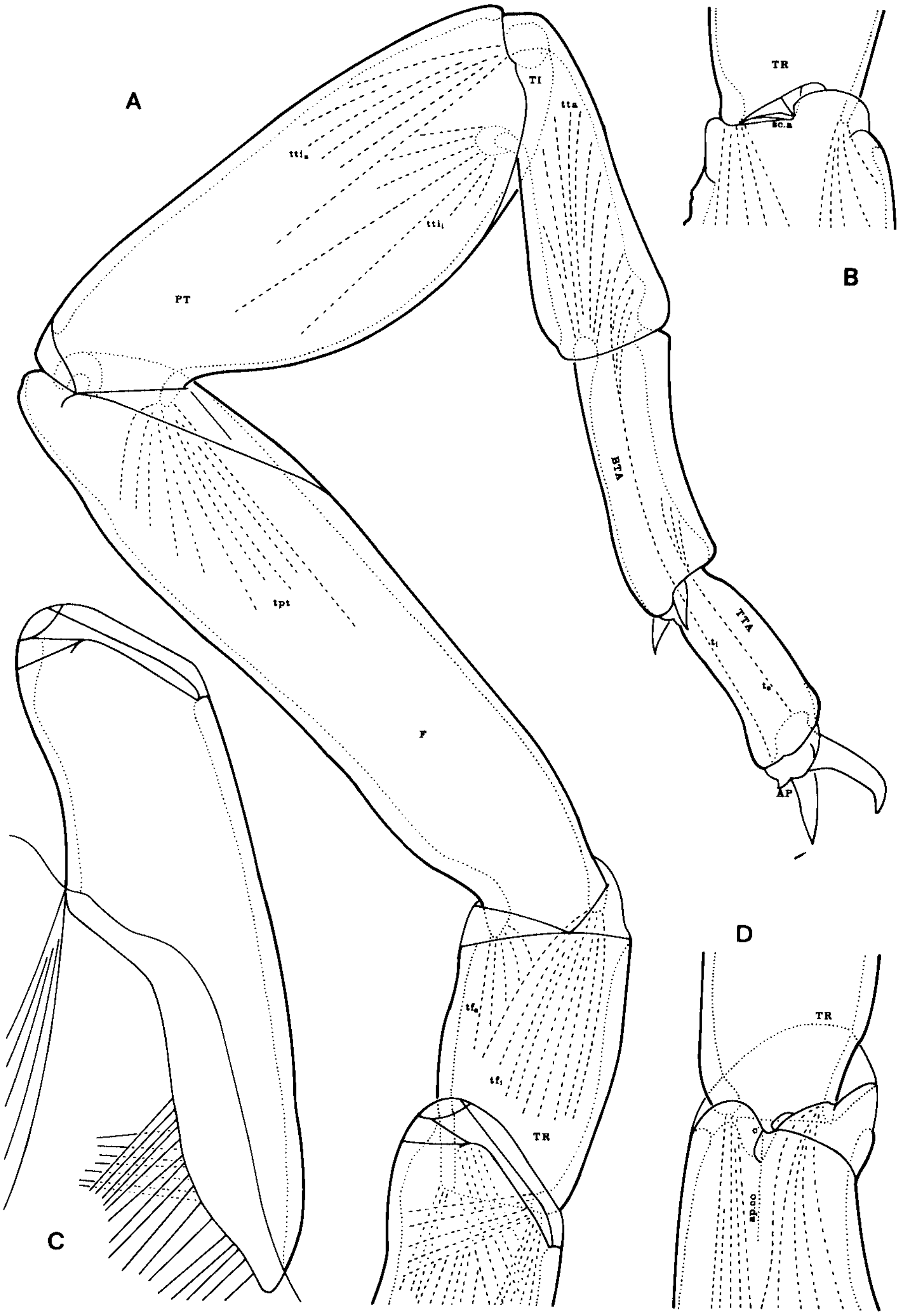

Fig. 22. *Euscorpius carpathicus* (Linnaeus), right leg IV of adult male; A, lateral (posterior) view of distal part of coxa, trochanter, femur, patella, tibia, basitarsus, telotarsus and apotele; B, posterodorsal view of the coxa-trochanter articulation; C, lateral (posterior) view of coxa; D, lateral (anterior) view of the coxa-trochanter articulation; A-D, × 31.4.

present in many groups of Araneida.

In all three groups of Arachnida s. str., the legs present some fundamental characteristics which point to a close relationship; this pertains, in particular, to the coxa-trochanter joint (with arthrodial sclerite), and the patella-tibia joint (associated with antero-posterior movements).

The legs of *Euscorpius carpathicus* are studied here as an example of the Scorpionida. A detailed study of the functional morphology of the Scorpionid legs was published by Couzijn (1976). In this group, the legs consist of coxa, trochanter, femur, patella, tibia, basitarsus, telotarsus and apotele. Leg IV of *Euscorpius carpathicus* is represented in fig. 22. With the exception of leg I, the Scorpionid coxae (fig. 22C) are not movably connected with the body (coxa I is movable because its coxapophysis is associated with food-intake); the coxae occupy the ventral surface of the prosoma, and extend laterally beyond the outline of the prosoma. The coxa-trochanter joint presents an anterior condyle (distal to the coxal apodeme) and, in the case of leg IV, also a posterodorsal arthrodial sclerite (fig. 22A, B, D); it allows of rocking movements. The trochanter-femur articulation is constituted by a bicondylar pivot joint with levator and depressor muscles. The femur-patella articulation is constituted by a bicondylar hinge-joint with inferior muscles. The patella-tibia articulation is a pivot joint with two superior condyles and flexor and extensor muscles. The tibia-basitarsus articulation is constituted by a hinge joint with two superior condyles and an inferior flexor; the inferior tendon of the apotele passes into the tibia. The articulation between basi- and telotarsus is constituted by an adesmatic joint operated by the tendons of the apotele. The articulation between telotarsus and apotele is constituted by a bicondylar pivot joint with the usual two tendons (superior and inferior). The apotele bears two ungues and a pseudonychium.

In Xiphosura limbs 2-6 function as ambulatory appendages (limb 1 is the chelicera; limb 2 is homologous with the palp of other Chelicerata). Limbs 2 and 6 of *Limulus polyphemus* are represented in fig. 23. Xiphosurid limbs 2-5 (see fig. 23C) consist of coxa, trochanter, femur, patella, tibiotarsus and apotele; limb 6 (see fig. 23A, B) consists of coxa, trochanter, femur, patella, tibia, tarsus and apotele. The coxae are extended in antiaxial (laterodorsal) direction and include pleural sclerites (an evolutionary development not known from other Chelicerata); they are also extended in paraxial direction (well-developed coxapophyses). The coxa of limb 6 presents an exite (the so-called flabellum). The body-coxa articulation is associated with promotor-remotor movements (see Manton, 1977: 450, figs. 10.2a, 10.4f); this is not known from other Chelicerata. The coxa-trochanter articulation is constituted by a bicondylar pivot joint with levator and depressor muscles. The

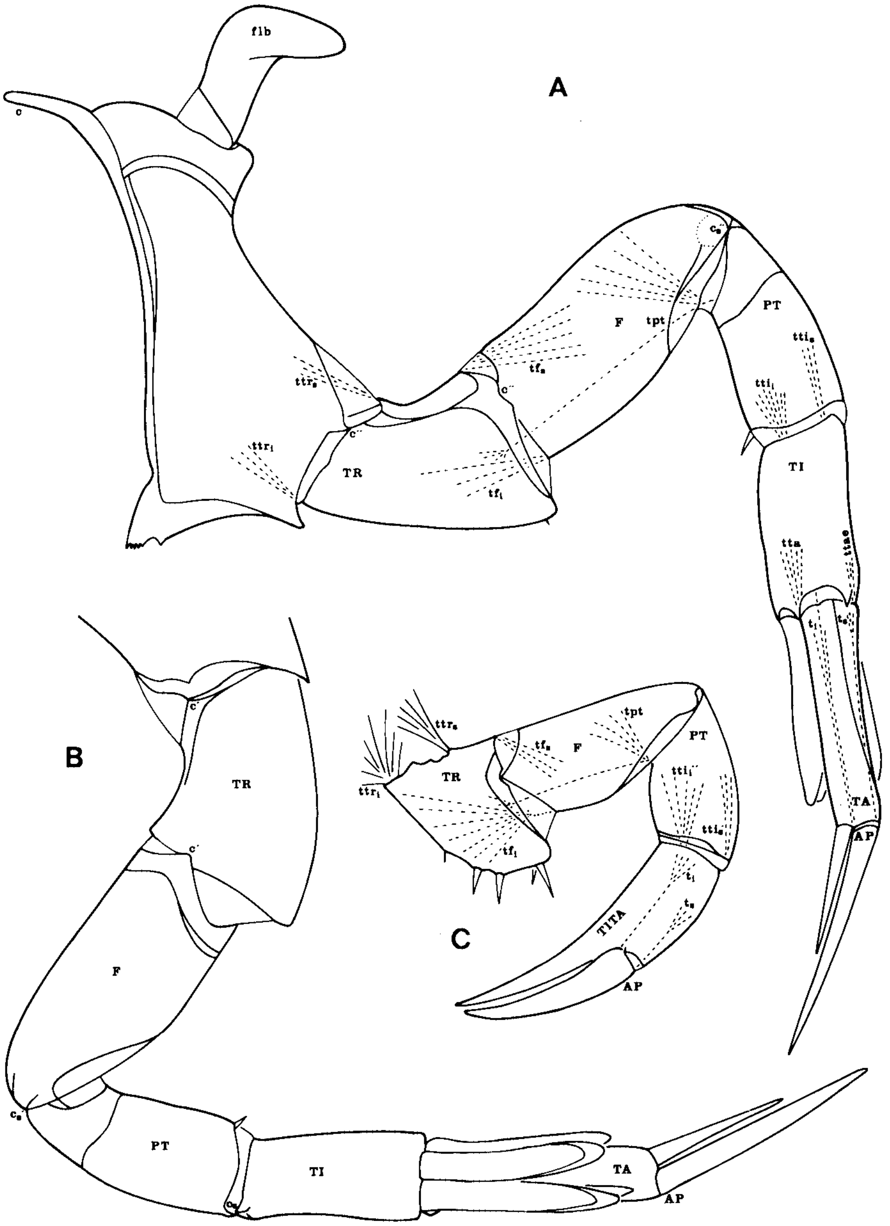

Fig. 23. *Limulus polyphemus* (Linnaeus), juvenile specimen; A, B, limb 6; A, lateral (posterior) view of entire limb; B, lateral (anterior) view of distal part of coxa, trochanter, femur, patella, tibia, tarsus and apotele; C, lateral (posterior) view of trochanter, femur, patella, tibiotarsus and apotele of limb 2; A-C, × 7.

trochanter-femur articulation is also constituted by a bicondylar pivot joint with levator and depressor muscles; it is remarkable because the superior muscle is in the femur (its direction is opposite to the normal one). The femur-patella articulation is constituted by a hinge joint with two superior condyles and inferior flexors. In limbs 2-5 the patella-tibiotarsus articulation is constituted by a hinge joint with superior articulation, an inferior flexor and a superior extensor muscle. In limb 6 the patella-tibia articulation is similar to that of the patella-tibiotarsus articulation in limbs 2-5. The tibia-tarsus articulation of limb 6 is also characterized by the presence of flexor and extensor muscles. The tibiotarsus (or tarsus)-apotele articulation presents the usual two tendons (superior and inferior). It may be remarked here that, in literature, the patella is generally regarded as a patellotibia (because of the presence of a suture in limbs 3-6). As a consequence of this, tibia and tarsus of limb 6 must be interpreted as basi- and telotarsus; this is evidently erroneous because of the presence of a eudesmatic joint between these segments.

The data collected in the present section shed a new light on the evolution of the coxa in Chelicerata. All Chelicerata, with the exception of Xiphosura, differ from other Arthropoda by the fact that the main promotor-remotor movement is not at the body-coxa, but at the coxa-trochanter joint. This has led to the conclusion that the evolutionary development of the chelicerate coxa took place after the development of the other segments (see Van der Hammen, 1985a: 50-51). Up to now, however, the chelicerate fixed coxae have been regarded as originating from free coxae. It has now become evident that coxae originate from epimera, and that the condition in Apatellata stands midway between epimera and free coxae (Solifugid coxae are still characterized by the presence of well-developed apodemes; a sternum is not yet present). In the more primitive groups of Arachnida s. str., such as Liphistiidae, the boat-shaped coxae have a ventral position and the sternum is still narrow. It is in the higher Araneida that the coxae have become cylindrical, with lateral position, and the sternum (a new structure) relatively large. In all Arachnid coxae, anterior apodemes (homologous with the apodemes associated with epimera) are distinctly present. According to this view, free coxae with lateral position (known from higher Araneida and Anactinotrichida) represent the final stage in the evolution of chelicerate coxae (it is evident that pleural regions must have been included in this evolution; see Van der Hammen, 1977b); it is interesting that these free coxae are found in two of the most successful groups of Chelicerata.

VIII. THE RELATIONSHIPS OF THE CHELICERATE CLASSES AND SUBCLASSES

The results of the present study confirm the general lines of my 1977 classification, whilst additional characters of some of the classes have come to light. Although the relationships between the classes have now become more clear, it is perhaps too early for the introduction of new superclass names.

The two groups of Apatellata (Solifugae and Pseudoscorpionida) present similar types of segmentation, whilst the main difference is constituted by the presence of a regressive segment XVIII (the anal segment) in Pseudoscorpionida. It is demonstrated that the coxae stand midway between epimera and true coxae in both Apatellate groups. Both groups present also great similarities in the structure of the mouthparts: there is a rostrosoma, characterized by the presence of lateral lips. An important difference between Solifugae and Pseudoscorpionida is constituted by the presence of a second trochanter in legs III and IV of Solifugae, although an explanation of this difference (trochanter 2 arises by repetition of information, and disappears by suppression) is given in my general model of the evolution of the chelicerate appendages (Van der Hammen, 1985a: 50-51). Another important difference is constituted by the position of the orifice of the coxal gland: in Pseudoscorpionida it is associated with coxa III, in Solifugae the orifice is at the base of the palp (probably secondarily; the gland could belong to the segment of leg I).

The three groups of Arachnida s. str. (Uropygi, Amblypygi and Araneida) are characterized, among others, by the same number of body segments, by great similarities in the segmentation and articulation of the legs and in the structure of the respiratory organs, and by the absence of lateral lips (important similarities are found in the mouthparts of Schizomida and Holopeltida). Differences are found in the position of the orifices of the coxal glands (which can be associated with sternapophyses). Judging from the condition in Amblypygi (where three sternapophyses are still present), three pairs of orifices must originally have been present; of these, all Arachnida s. str. have preserved the anterior pair (associated with coxa I), whilst some Amblypygi and Araneida have also preserved the posterior pair (associated with coxa III). In Uropygi and Amblypygi, the orifice near coxa I is associated with a taenidium and a coxapophysis.

A remote relationship apparently exists between Epimerata and Apatellata (particularly Solifugae). The segmentation of the Apatellate body (apart from the regressive segment XVIII of Pseudoscorpionida) presents a great similarity to the segmentation of the Epimerate plesiotype (see Van der Hammen, 1982: 49-51, fig. 26A, B). In Epimerata and Apatellata, the fundamental leg type is characterized by the presence of two femora. The duct of the Solifugid coxal gland, and the advanced position of the orifice, resemble the Actinotrichid podocephalic canal in groups where it is internal. The Apatellate mouthparts present lateral lips as in Actinotrichida, whilst the Apatellate coxae still resemble epimera.

Among the most important affinities between Arachnida s. str. and Cryptognomae, mention must be made of the ventral position of the orifice of the coxal gland, near coxa I, associated with a taenidium and a sternapophysis, and of the great similarity between the Cryptognomic subcapitular gutter and the Uropygid intercoxal gutter (this does not imply that the Cryptognomic gnathosoma can be derived from the Uropygid mouthparts). Important similarities exist also between the structure of sternum and coxae in many Araneida and Anactinotrichida.

It may be remarked here that, according to my views (see Van der Hammen, 1981a, 1981b, and in press 1), the relationships between the classes (probably separated since the Palaeozoic) is more evident from similarities in evolutionary potentialities and evolutionary programs (and the manifestations in parallel evolution), than from the presence of shared derived characters.

IX. LIST OF NOTATIONS

an, anal opening.
AP, apotele.
ap.ce, apodeme of cervix.
ap.co, coxal apodeme.
ap.pa, apodeme of palp.
ap.ro, rostrosomatic apodeme.
at, line of attachment of cheliceral frame.

b, mouth.
bch, base of chelicera.
br, brush of palpal coxapophysis.
BTA, basitarsus.

c, c', c'', condyles.
c_i, inferior condyle.
c_s, c_s', c_s'', superior condyles.
CA.P, coxapophysis of palp.

CA.I, coxapophysis of leg I.
CA.II, coxapophysis of leg II.
CA.2-6, coxapophyses of limbs 2-6.
CE, cervix.
CHI, chilarium.
CR, crop.
CX, coxa.
CX.P, coxa of palp.
CX.III, coxa of leg III.
CX.IV, coxa of leg IV.

fla, flagellum.
flb, flabellum.
fo, frontal organ.
F1, femur 1.
F2, femur 2.

h, hinge.

ICG, intercoxal gutter.

Js, superior commissure of the mouth.

LI, labium.
LL, lateral lip.
LL_i, inferior lobe of lateral lip.
LL_s, superior lobe of lateral lip.
LS, labrum.
L2-6, limbs 2-6.

MG, midgut.

OA.IX-XIII, opisthosomatic appendages of segments IX-XIII.
OC, eye.
OCU, ocularium.
OE, oesophagus.
og, orifice of labial gland.
ogc, orifice of coxal gland.

PA, palp.

PD, prodorsum.
pe, comb (pecten).
PH, pharynx.
PO, postpeltidium.
PR, propeltidium.
PT, patella.
P.I, leg I.
P.II, leg II.
P.III, leg III.
P.IV, leg IV.

SA, sternapophysis.
SA.I-III, sternapophyses of the segments III-V (the segments of legs I-III).
sc.a, arthrodial sclerite.
ST, sternum.
st, *st.1-4*, stigmata.

t_{i}, inferior tendon of apotele.
t_{s}, superior tendon of apotele.
TA, tarsus.
tae, taenidium.
TE, telson.
tf, tendons and muscles of femur.
tf_{i}, inferior tendons and muscles of femur.
tf_{s}, superior tendons and muscles of femur.
tfe, tendons and muscles of femur 2.
TI, tibia.
TITA, tibiotarsus.
TI.1-3, tibiae 1-3.
tpt, tendons and muscles of patella.
tr_{i}, inferior tendons and muscles of trochanter 2.
tr_{s}, superior tendons and muscles of trochanter 2.
TR, trochanter.
TR.P, trochanter of palp.
TR.III, trochanter of leg III.
TR1, trochanter 1.
TR2, trochanter 2.
TTA, telotarsus.
TTA1-4, telotarsus 1-4.
tta, tendons and muscles of tarsus.

ttae, extensor muscles of tarsus.
tti, tendons and muscles of tibia.
tti_{i}, inferior tendons and muscles of tibia.
tti_{s}, superior tendons and muscles of tibia.
ttr, tendons and muscles of trochanter.
ttr_{i}, inferior tendons and muscles of trochanter.
ttr_{s}, superior tendons and muscles of trochanter.

VLV, valve (entrance to midgut).

VII-XIX, segments VII-XIX.

′ (prime), anterior (pertaining to the anterior face of an appendage).
′ ′ (double prime), posterior (pertaining to the posterior face of an appendage).

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