COMPARATIVE STUDIES IN CHELICERATA III. OPILIONIDA

by

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A comparative study is made of the three groups (Cyphophthalmi, Laniatores and Palpatores) into which Opilionida are currently subdivided. Methods, principles and terminology, adopted in this paper, correspond with those of parts I and II of the present series of studies in Chelicerata. Special attention is paid to mouthparts and appendages, to opilionid relationships, and to the evolution of chelicerate characters. It is demonstrated that Cyphophthalmi present all the essential opilionid characters, and evidently do not constitute a separate group. It is also demonstrated that Opilionida are not closely related to Actinotrichid or Anactinotrichid mites, but to other groups with a so-called myliosoma (mouthparts associated with coxisternal feeding); these groups constitute the new superclass Myliosomata. The phylogenetic relationships of Epimerata (Palpigradi and Actinotrichid mites) and Cryptognomae (Anactinotrichid mites and Ricinulei) are discussed, and these groups are regarded as representatives of a new superclass Acaromorpha. As a result of these conclusions, a new diagram is prepared of the phylogenetic relationships of all extant groups of Chelicerata.

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CONTENTS

I. INTRODUCTION

In continuation of the previous papers in the present series (Van der Hammen, 1979, 1982), a detailed comparative study is made of representatives of the three orders (Cyphophthalmi, Laniatores, Palpatores) into which Opilionida are currently subdivided. As mentioned before, it is the purpose of the series to prepare an introduction to comparative arachnology, and to study the phylogenetic relationships, the evolution and the classification of chelicerate groups. 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), in which encyclopedic work several general conventions are also mentioned. Some of my theoretical views, which influenced my approach in the study of evolution and classification, are expounded in separate studies (Van der Hammen, 1981, 1981a, 1983); other papers in this field are, moreover, in course of preparation. Special attention is paid to mouthparts and appendages, and to the evolution of these structures. Opilionid (and other chelicerate) relationships are reconsidered. It is demonstrated that Cyphophthalmi present all the essential opilionid characters, and evidently do not constitute a separate chelicerate group.

II. MATERIAL

The original part of the present paper is based on the study of three species, representing the three groups into which Opilionida are currently subdivided, viz., *Siro rubens* Latreille (Cyphophthalmi), *Scotolemon lespesi* Lucas (Laniatores), and *Paroligolophus agrestis* (Meade) (Palpatores). The material of *Siro rubens* was collected on 21 September 1960 at Mongaillard, Coulounieux (Dordogne), France. The specimens of *Scotolemon lespesi* originate from Moulis, near St. Girons (Arriège), France, and were collected on 29 April 1951. The material of *Paroligolophus agrestis* was collected, in the period September 1953 – January 1954, in catch-boxes in the sand-dunes, Meijendel, Wassenaar, The Netherlands. The specimens were studied in cavity slides, in diluted lactic acid; in the course of the investigations, several specimens have been completely dissected.

III. DESCRIPTIVE PART

Habitus. — Opilionida are small to medium-sized Chelicerata, with rounded or oval body, more or less distinct segmentation, and inconspicuous separation of prosoma and opisthosoma. The condition of the cuticle varies from soft and thin to heavily sclerotized; in many cases the cuticle of body and legs is characterized by the presence of more or less heavy spines. The legs can be comparatively short, but are more often very, sometimes even extremely, long (the characteristic habitus of a "harvestman" being that of an Opilionid with small, rounded body and very long legs).

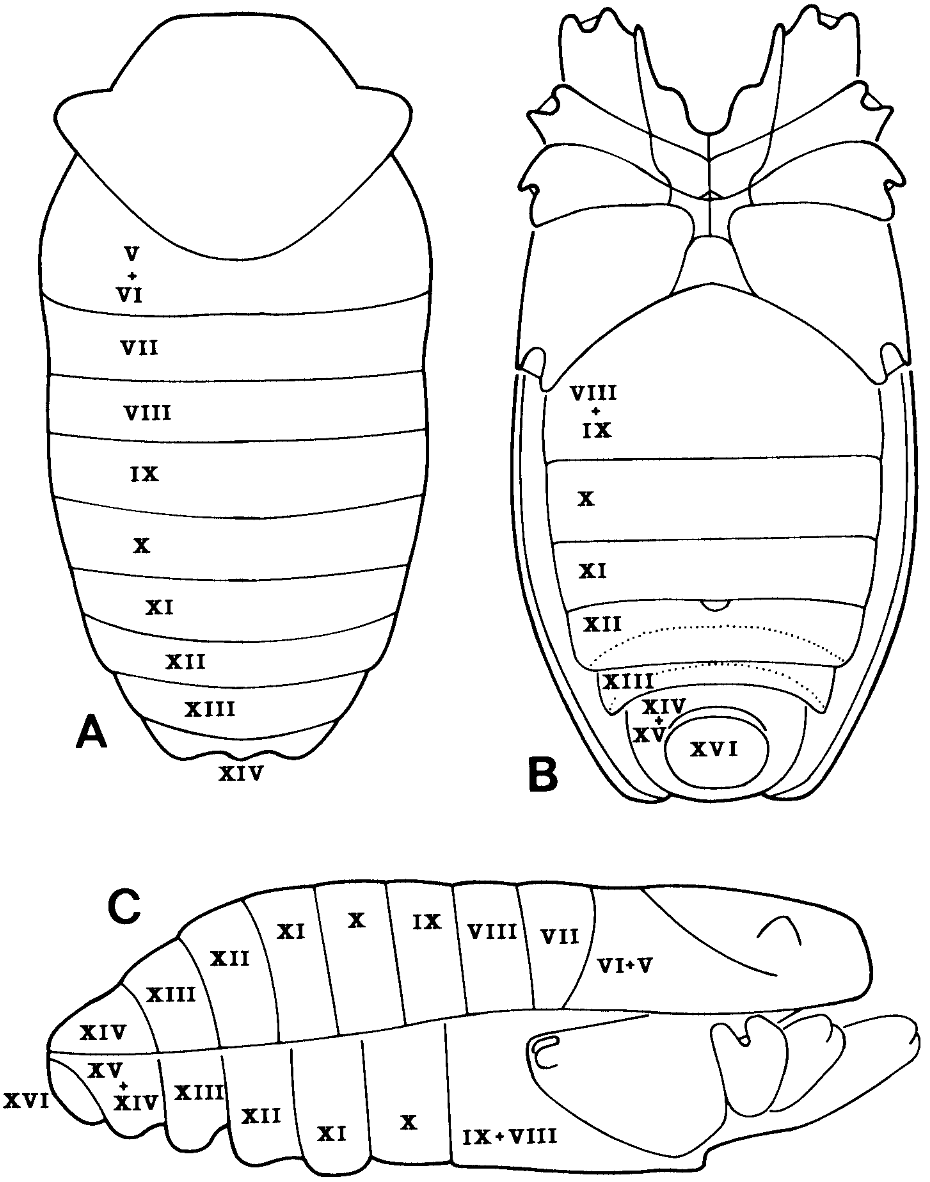

Fig. 1. *Siro rubens* Latreille, adult (chelicerae and palps removed); A, B, male; A, dorsal view; B, ventral view; C, lateral view of female (posterior segments extended); A-C, × 63.

Divisions of the body and segmentation. — The opilionid body consists, as in other Chelicerata, of prosoma and opisthosoma; these two tagmata are broadly joined (the body is latigastric). Opilionida generally present a more or less distinct external segmentation of the body. As a result of the study of the embryonic and postembryonic development of the body in the family Phalangiidae, by Winkler (1957), the numbering of the segments is now known with more or less certainty. Winkler discovered that, in Phalangiidae, segment VII (the first opisthosomatic segment, reduced in several other groups of Chelicerata) is normally developed in the case of the dorsal part (the tergite), reduced in the case of the ventral part (the sternite). The prosoma consists of an unknown number of precheliceral metameres and the segments I-VI. The tergites of the prosoma constitute the prodorsum; most of these tergites have fused, but tergites V and VI are often more or less distinctly separated. The labium (if present) represents, according to Winkler, the sternite of segment III. As mentioned below (in the section on the mouthparts), chelicerae and palps, and the coxal and sternal regions of the segments bearing the anterior legs, constitute a separate myliosoma (a pseudotagma) which can be movably attached to the main part of the body.

The opisthosoma consists of the segments VII-XVI. Ventrally, the genital region occupies an advanced position between the coxae of the legs. The operculum genitale of the Phalangiidae consists, according to Winkler, of part of segment VIII and probably sternite VI (sternite VII being reduced). The posterior segments of the opisthosoma are subject to regression. In Cyphophthalmi (fig. 1) the position of the anal opening is more ventral than in other groups of Opilionida; this certainly represents a secondary translocation (the ancestral position of the chelicerate anal opening is terminal). The cyphophthalmic anal cover (operculum anale) represents segment XVI; the surrounding plate represents a fusion of tergite XV and sternites XIV and XV (according to Juberthie, 1970, sternite XIV has a separate position in some Cyphophthalmi; in all Cyphophthalmi, tergite XIV has a separate dorsal position). In Laniatores (figs. 2, 11E), tergite XIV has a separate dorsal position, whilst sternites XIV and XV have fused; the anal cover articulates with the tergite of segment XIV, and could represent a fusion of tergite XV and segment XVI (this notation is added to fig. 11E). In Palpatores (figs. 3, 4) the posterior segments have fused in various degrees. In *Paroligolophus agrestis* (Meade), tergites XIV and XV have apparently fused, sternite XIV has fused with sternite XIII, and sternite XV is no more recognizable, whilst the anal cover represents segment XVI. It is interesting that in all Opilionida segments XIV and XV (and not XVI) are subject to a regression which is associated with fusion, whilst in Actinotrichida (see Van der Hammen, 1963: 445-447;

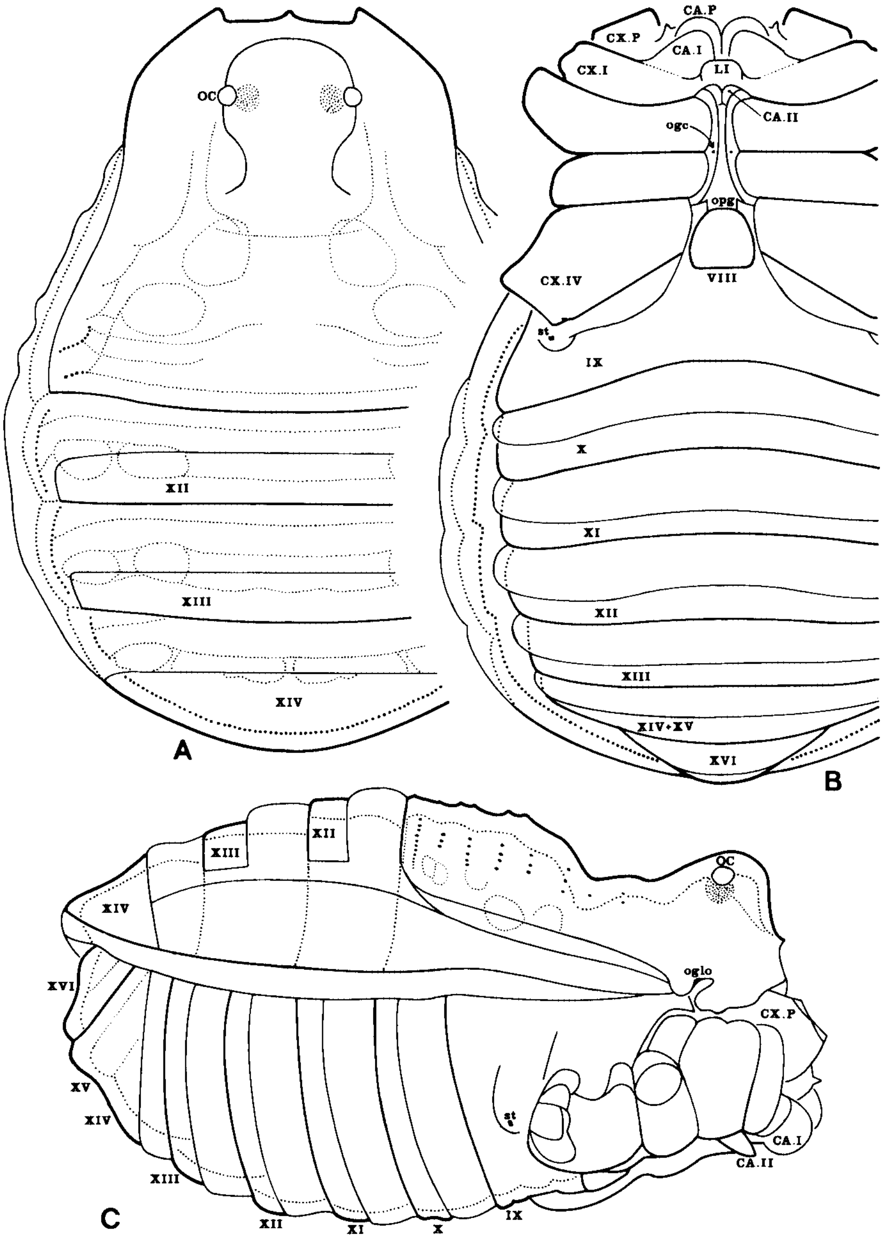

Fig. 2. *Scotolemon lespesi* Lucas, adult male; A, dorsal view; B, ventral view; C, lateral view; A-C, × 37.

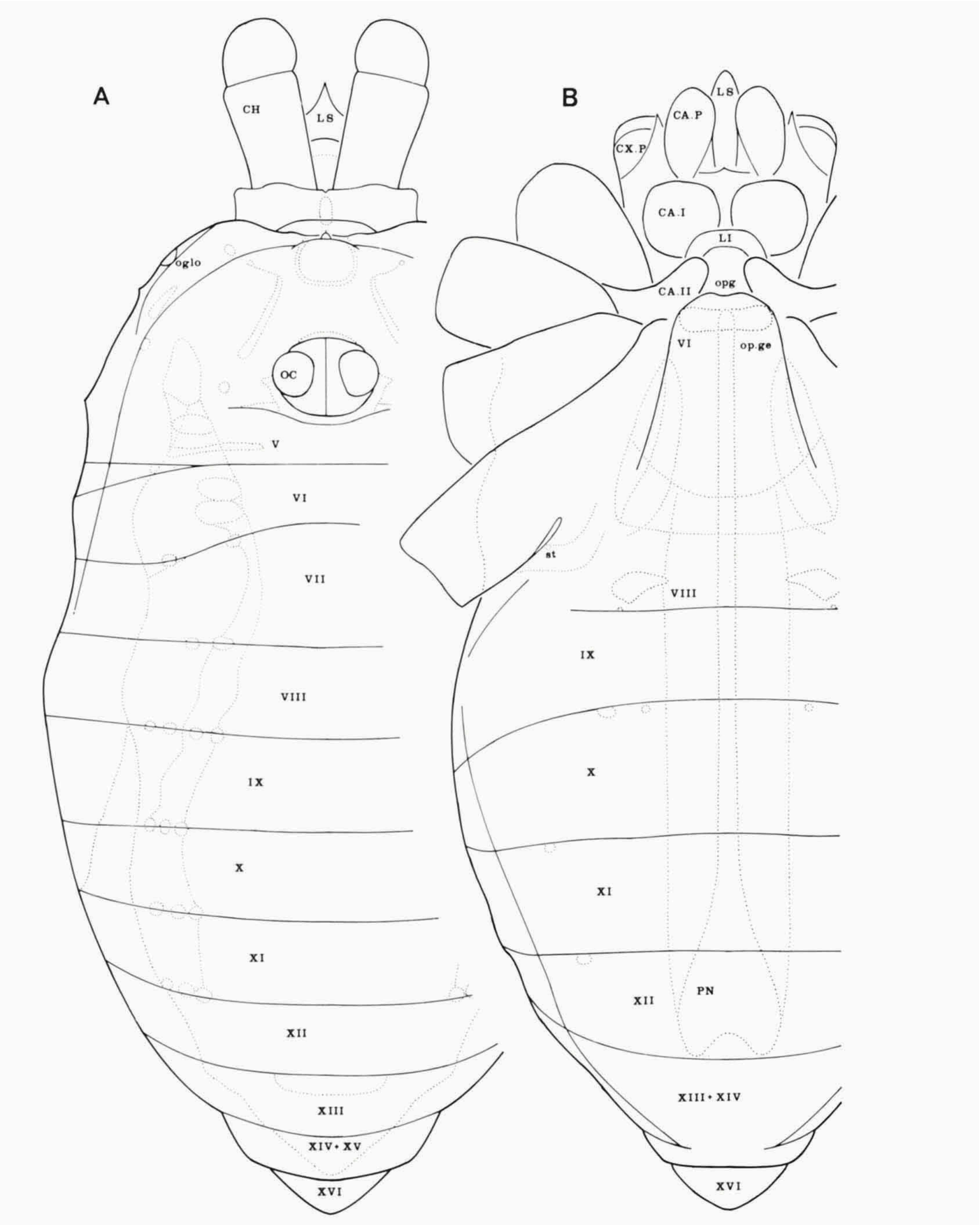

Fig. 3. *Paroligolophus agrestis* (Meade), adult male (anal cover extended); A, dorsal view; B, ventral view; A, B, × 37.

1970: 9; 1982: 27-29, figs. 11-12) the regression, which is associated with suppression, started with the posterior segment (which is in accordance with Lankester's laws). The opisthosomatic segments, particularly the tergites, can fuse in various ways (with each other, as well as with the prodorsum), constituting various types of shields (see: Martens, 1978: 16-17, figs. 2-5). In *Scotolemon lespesi* Lucas (fig. 2), tergites VII-XI have fused with the prodorsum; tergites XII-XIV and sternites X-XIV are partly covered by membraneous tegument.

Tegument. — The cuticle varies from more or less heavily sclerotized (Cyphophthalmi, Laniatores, Trogulidae, Nemastomatidae) to soft (Phalangiidae). It presents a variety of phaneres, such as spines, tubercles (often with apical spine or seta; see fig. 23B), papillae, various types of setae, and solenidia (fig. 28A, F). The cuticle can present various types of microsculpture, among which an aciculate ornamentation which resembles a dense arrangement of small setae (figs. 28E, 30B, 33E); the aciculate ornamentation can be associated with a reticulate microsculpture. Lyrifissures can occur as single slits, or arranged in groups, rings or lyriform organs; they are regularly found on the appendages (chelicera, palp, legs), often associated with the articulations, but they can also occur on the coxapophyses (see figs. 12A, B, 18, 21C, 23B, 24, 30A, C, 31A, B, C, 32A, C-E, G, 33F).

Prodorsum (figs. 1A, C, 2A, C, 3A, 4, 13A). — The prodorsum, or dorsal shield of the prosoma, includes the tergites of the segments I-VI; it includes also material of precheliceral origin (such as the eyes). All or most of the tergites can have fused, but tergites V and VI often constitute separate sclerites. The prodorsum can also be integrated in a larger dorsal shield which includes a number of opisthosomatic tergites (up to eight). The lateral border of the prodorsum is above the coxae of the legs. Generally, there are two eyes, situated on an ocular tubercle or ocularium; the ocularium can be lacking, or the eyes can be situated on separate tubercles. In some cases (e.g. *Siro*) there are no eyes. The orifices of the odoriferous glands (one on either side) are situated in the lateral part of the prodorsum, or just below its lateral border (figs. 11A, 12A, 13E); they can each be associated with a taenidium (see: Van der Hammen, 1980: 154; Juberthie, 1961), an external, narrow gutter or canal, of a ribbon-like shape, running at the surface of the tegument. In Cyphophthalmi, the orifices are near the apex of a lateral tubercle. Various more or less distinct sigilla are also present in the prodorsal region, among which the sigilla of the dorsal suspensor muscles of the endosternite, and the sigilla of the large depressor muscles of the chelicerae.

Dorsal and laterodorsal region of opisthosoma. — This region (which includes the tergites VII-XV) consists of a variable number of separate sclerites, ranging from a single dorsal shield (fused with the prodorsum) to eight

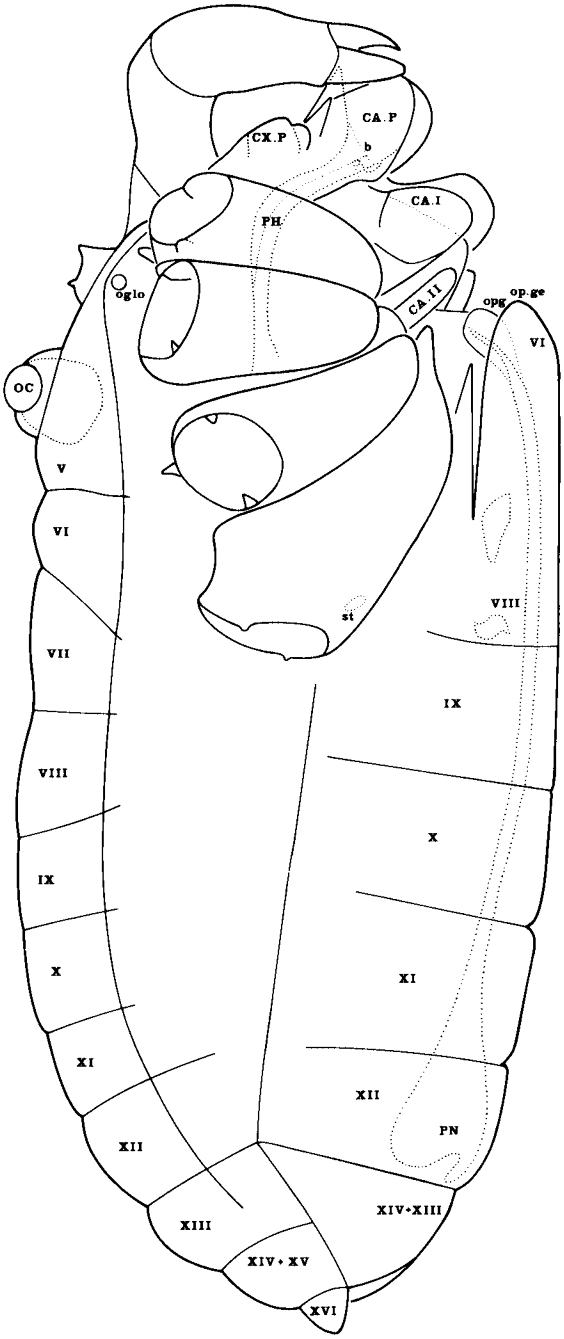

Fig. 4. *Paroligolophus agrestis* (Meade), adult male (anal cover extended), lateral view; × 37.

free sclerites. Tergite XIV of the male of *Siro* (fig. 13C, D) contains the orifices of the male postero-opisthosomatic glands (see: Juberthie, 1967, 1967a; Rafalski, 1958, regarded them as respiratory organs).

Ventral and lateroventral region of opisthosoma. — In the discussion of this region, anal and genital regions are not included (they are discussed in separate sections). The ventral region of the opisthosoma is influenced by a posterior shortening of the body, and a forward translocation of sternites. Sternite VIII and IX have fused; and, in the case of the Phalangiidae, a forward projection of sternite VIII has probably fused with the prosomatic sternite VI, constituting the genital cover (operculum genitale). The stigma (figs. 11B, 12B, 13A) is situated in sternite VIII, either free on the surface of the sternite (Sironidae, many Laniatores), or hidden in a fold posteriorly of coxa IV (Phalangiidae, Trogulidae). In *Siro rubens* and *Scotolemon lespesi*, sternites XIII and XIV + XV are movable, and can be retracted and extended.

Anal region (figs. 1B, C, 2B, C, 3B, 4). — The anal cover (operculum anale) presents a dorsal hinge; it is opened by pressure and closed by muscles inserted ventral to (and close to) the hinge (fig. 11C). The anal cover is generally regarded as representing segment XVI. In several cases, particularly when the anal cover is movably attached to the dorsal shield, it could perhaps also include the tergite of segment XV; this hypothesis is introduced in one of the figures of *Scotolemon* (fig. 11C). In Cyphophthalmi (fig. 13F), the anal opening has a less terminal and more ventral position than in other groups of Opilionida; it is surrounded by a sclerite representing a fusion of tergite XV and sternites XIV and XV (as mentioned above, sternite XV has, in some cases, a separate position). Fig. 1C demonstrates that, in *Siro*, tergite XV separates the anal cover and the dorsal shield; a comparison of figs. 1C and 2C supports the hypothesis of an inclusion of tergite XV in the anal cover of *Scotolemon.*

Genital region (figs. 1B, 2B, 3B). — The opilionid genital opening is at the anterior border of segment VIII (Winkler, 1957: 365-367). It has an advanced position, between the coxae of the legs, probably because of the special type of Opilionid sperm transfer, which is associated with copulation (not known from Cyphophthalmi). Female Opilionida are characterized by the presence of an ovipositor, male Opilionida by the presence of a penis (or, in Cyphophtalmi, a spermatopositor; it is probably associated with the transfer of a spermatophore). Ovipositor and penis (and spermatopositor) originate from extensions (prolongations) of the internal reproductive system; consequently, the eugenital opening (the ancestral opening), which has the shape of a fissure, is now in the distal part of ovipositor and penis (its current name is secondary genital opening). The genital opening (it is currently named primary

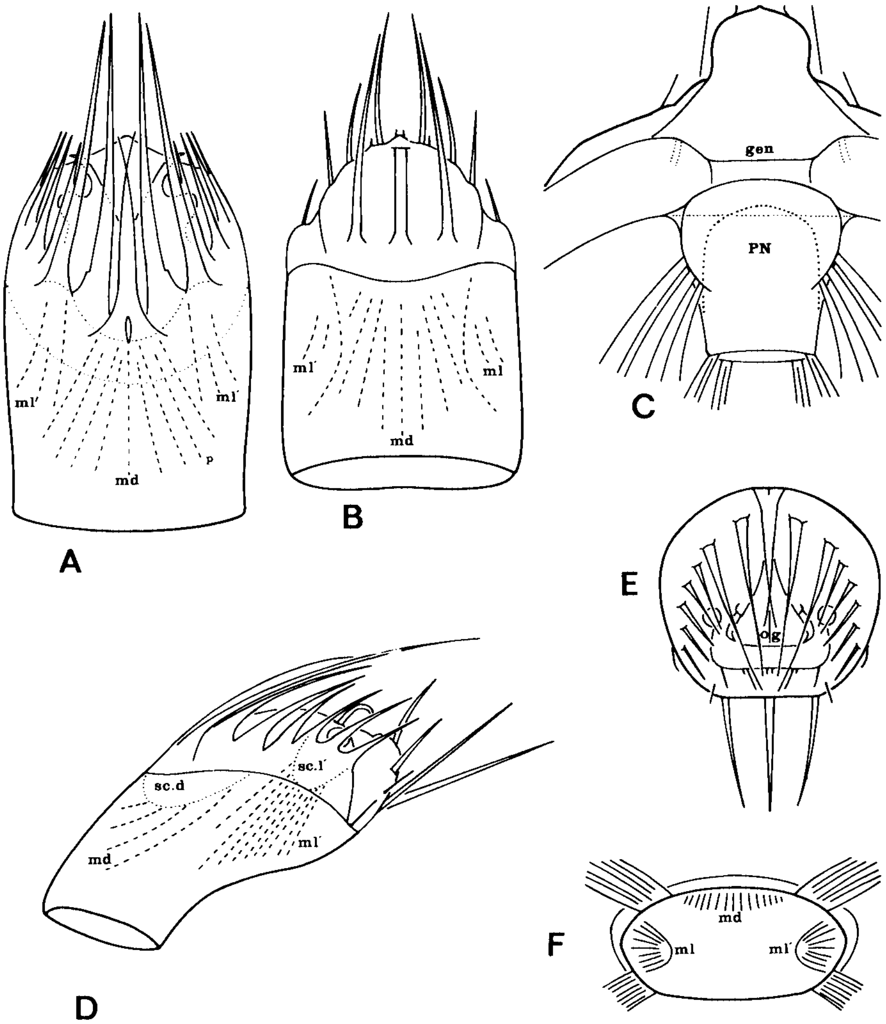

Fig. 5. *Siro rubens* Latreille, invaginated penis (spermatopositor) of adult male (in all drawings, except C and F, the sheath of the invaginated part is omitted); A, dorsal view; B, ventral view; C, ventral view of invaginated penis (spermatopositor) (after removal of opisthosomatic sternites), with sheath, retractor muscles, and genital opening; D, lateral view (the left upper part of the figure is dorsal); E, apical view (the upper part of the figure is dorsal); F, basal view, with proximal retractor muscles and internal muscles *md*, *ml*, and *ml'* (the upper part of the figure is dorsal); A-B, D-F, × 295; C, × 141.

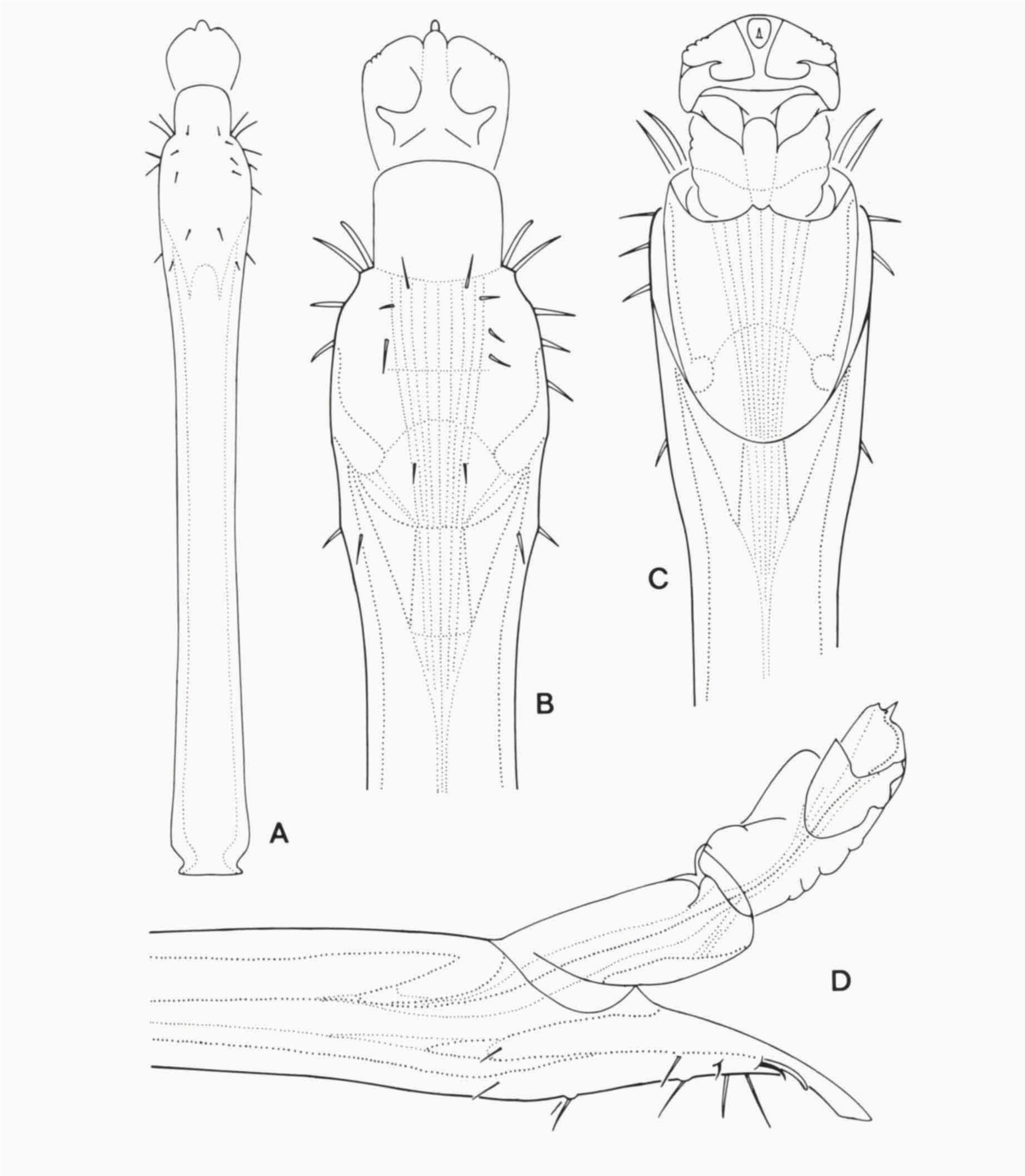

Fig. 6. *Scotolemon lespesi* Lucas, penis of adult male; A, ventral view; B-D, distal part; B, ventral view; C, dorsal view; D, lateral view; A, × 141; B-D, × 295.

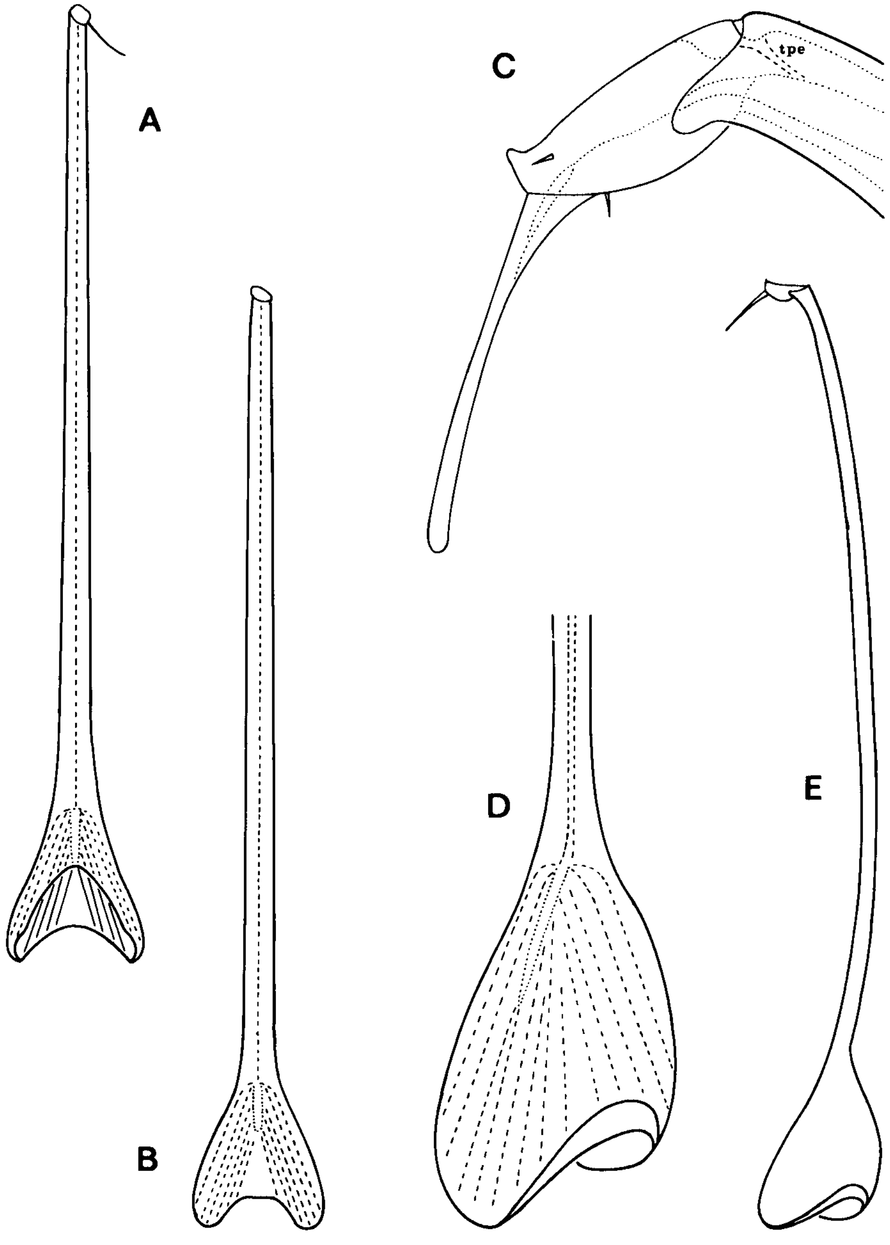

Fig. 7. *Paroligolophus agrestis* (Meade), penis of adult male; A, dorsal view; B, ventral view; C, lateral view of apical part; D, lateral view of basal part; E, lateral view; A, B, E, × 44; C, × 295; D, × 92.

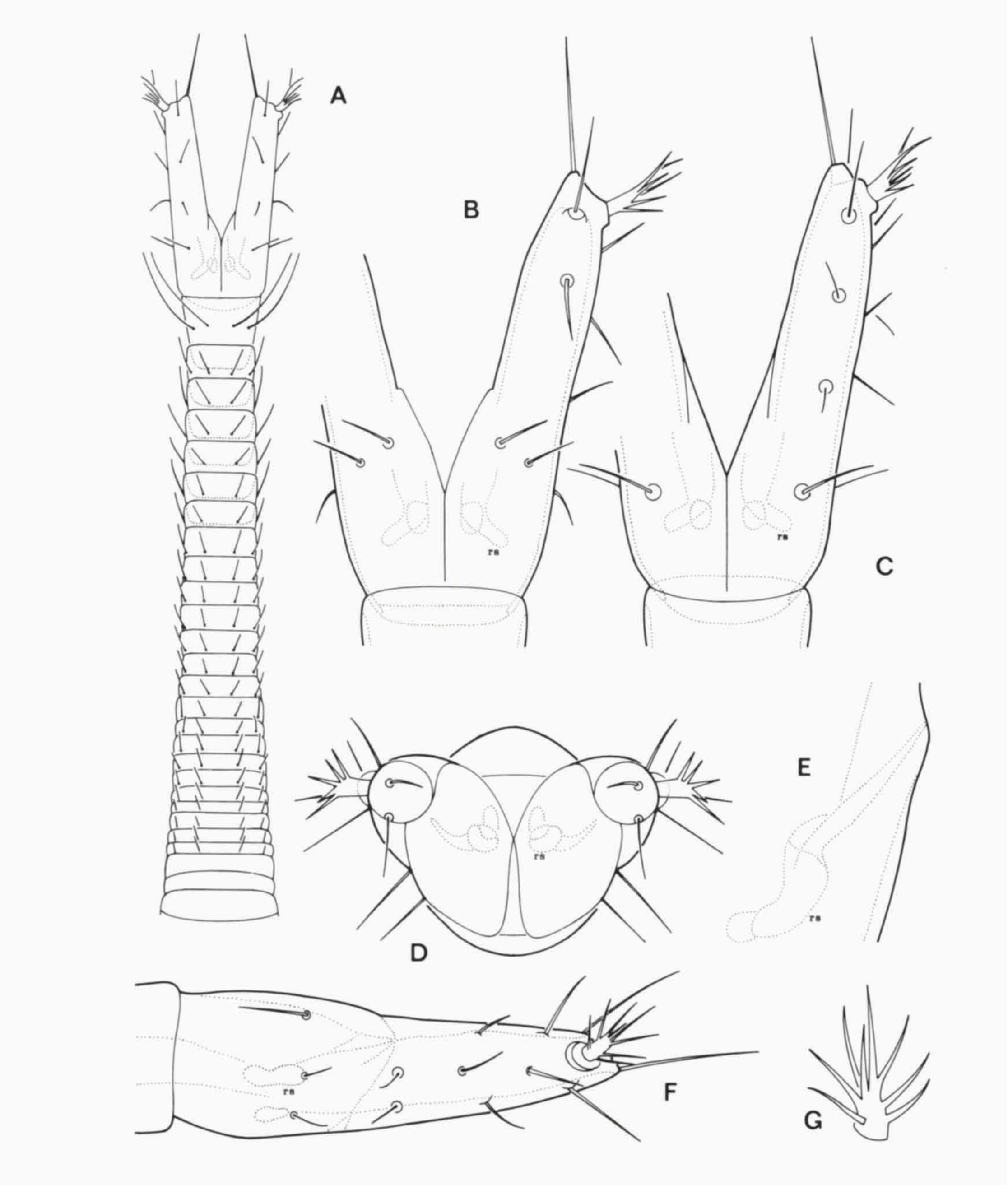

Fig. 8. *Siro rubens* Latreille, ovipositor of adult female; A, ventral view of invaginated ovipositor (after removal of opisthosomatic sternites); B, C, apical part; B, dorsal view; C, ventral view; D, apical view; E, paralateral (oblique) view of part of one of the apical lobes (with the receptaculum seminis); F, antilateral view of apical part; G, antilateral view of ramified apical seta; A, × 118; B-D, F, × 246; E, G, × 458.

genital opening), i.e. the opening at the anterior border of segment VIII, through which ovipositor and penis are evaginated (fig. 11D), is unprotected (Cyphophthalmi) or protected by a genital cover (operculum genitale) which originates from a forward projection (a fold) of segment VIII. In Phalangiidae, it can be relatively long, and probably includes the sternite of segment VI (Winkler, 1957: 370). The opening between genital cover and prosomatic sternites is here named progenital opening (it is currently named tertiary genital opening). Originally (in the ancestors), eugenital and genital opening must have coincided. Penis and ovipositor can be very long; in invaginated position they can extend as far as the posterior border of segment XII (fig. 4).

There are various types of penis (spermatopositor) and ovipositor (see: Dumitrescu, 1970; Martens, 1976, 1978; Martens, Hoheisel & Götze, 1981). The spermatopositor of *Siro* (fig. 5; see also: Janczyck, 1956: 516-518, figs. 25-26; Rafalski, 1958: 539-550, figs. 15-18; Juberthie, 1967: 166, fig. 8A) is very short and flattened, and not distinctly subdivided into a so-called truncus and a so-called glans. The apical part is surrounded by a verticil of some 22 setae. The eugenital opening (a fissure) is bordered, on either side, by a lobe bearing a claw-shaped clutch and a rounded tubercle. There are three muscle bundles (a dorsal one and two laterals), inserted on internal sclerites.

The penis of *Scotolemon lespesi* (fig. 6) is large and presents two apical lobes, a dorsal and a ventral, which are not operated by muscle bundles, but by hydrostatic pressure. Setae are present in the ventral and lateral regions of the ventral apical lobe; the sperm duct is in the dorsal lobe. The ventral lobe is flattened, and apically truncate; the dorsal lobe is membraneous, and consists of various movable parts.

The penis of *Paroligolophus agrestis* (fig. 7) is large; it distinctly consists of a truncus and a distal glans. A long tendon is inserted on the base of the glans. In the genus *Paroligolophus*, the penis is characterized by a very narrow truncus and a very large base; the muscle bundle, operating the tendon of the glans, is concentrated here in the large base. In rest the glans is at an oblique angle with the truncus; it terminates in a long stylus.

The ovipositor of *Siro rubens* (fig. 8; see also: Janczyck, 1956: 518-520, fig. 28; Rafalski, 1958: 550-552, figs. 19-20; Juberthie, 1967: 166, fig. 8B) is long and annulated. There are some 27 rings and a distal furca. With the exception of the basal ones, the rings present rows of setae. The furca consists of a pair of externally unsegmented lobes, each characterized by the presence of simple setae and a subapical ramified seta (on a low antilateral process). Each of the two lobes presents moreover, near its base, an internal receptaculum seminis.

The ovipositor of *Scotolemon lespesi* (fig. 9) is short, not annulated, with two low terminal lobes. The eugenital opening (a fissure) is between the base

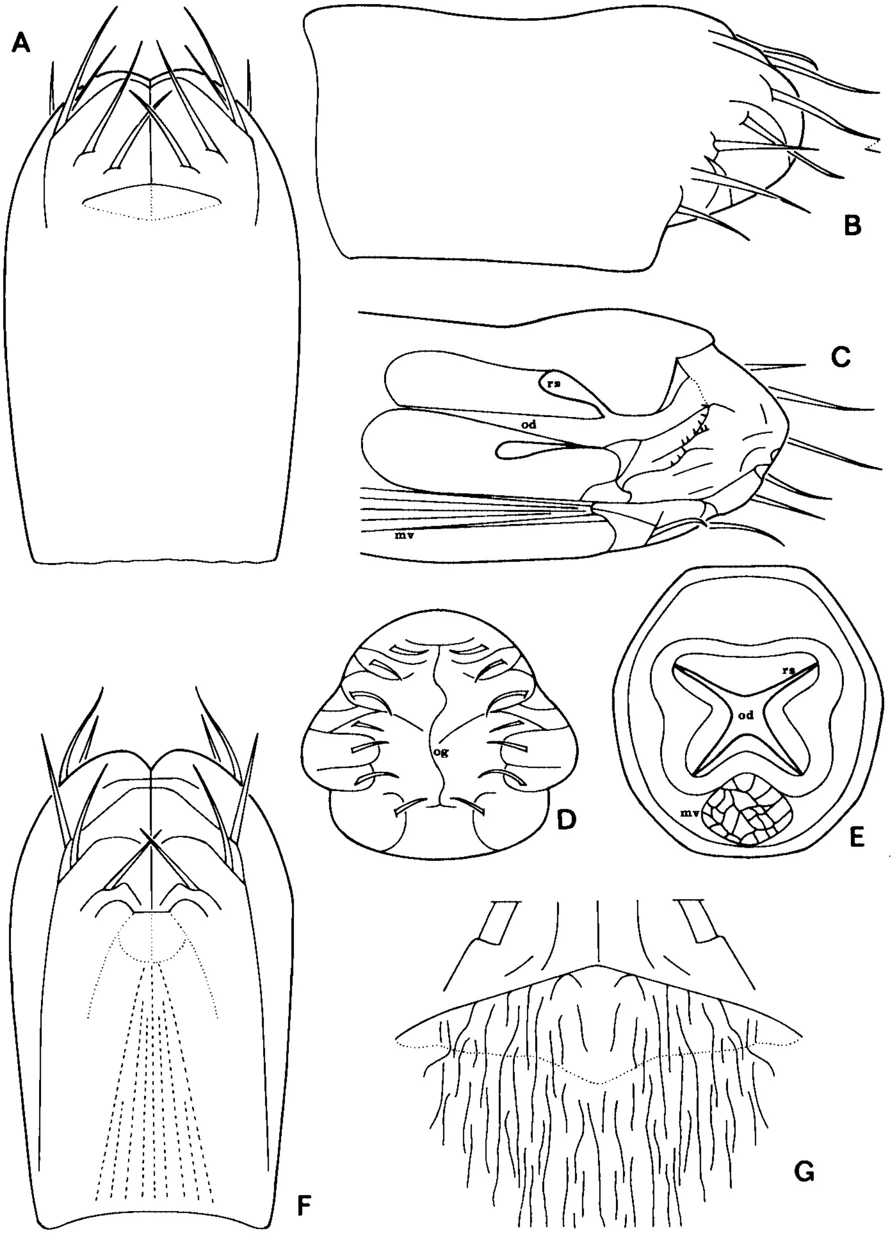

Fig. 9. *Scotolemon lespesi* Lucas, ovipositor of adult female; A, dorsal view; B, lateral view; C, longitudinal (sagittal) section, lateral view; D, apical view; E, transverse section; F, ventral view; G, dorsal view of microsculpture posteriorly of the two lobes; A-F, × 155; G, × 458.

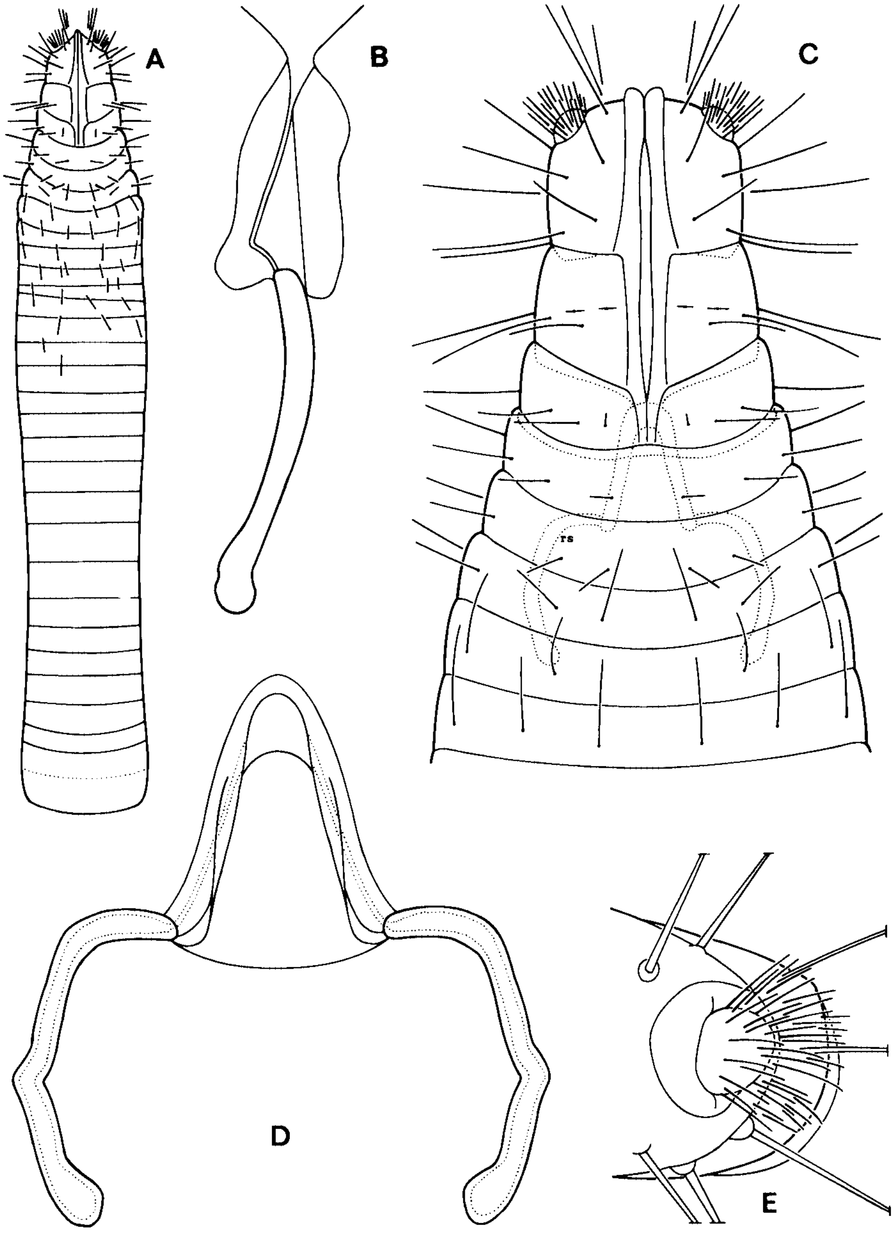

Fig. 10. *Paroligolophus agrestis* (Meade), ovipositor of adult female; A, dorsal view; B, lateral (antiaxial) view of right receptaculum seminis; C, dorsal view of distal part; D, dorsal view of receptaculum seminis; E, lateral view of distal part of right furca; A, × 37; B, D, E, × 246; C, × 118.

of the lobes; it is surrounded by a verticil of some seven pairs of setae. There is a ventral muscle bundle, inserted on the base of the lobes, by which these are probably slightly retractable. There are four receptacula seminis, radially arranged around the distal part of the oviduct (see also: Martens, Hoheisel & Götze, 1981: 47-49, figs. 30B, 33, 43B).

The ovipositor of *Paroligolophus agrestis* (fig. 10) is long and annulated. There are some thirty rings (the three rings of the elements of the furca included). The paired receptacula seminis extend from segment 3 (the basal segment of the furca) to segment (ring) 7. The furca consists of two three-segmented lobes. The terminal part of each of the two lobes presents a rounded protuberance with numerous short setae.

In all these ovipositors, the eugenital opening is represented by a fissure between the base of the lobes. The lobes probably represent the opisthosomatic appendages of segment VIII. In the penis of *Siro rubens*, the apical part presents also two lobes, one on either side of the eugenital opening; these could also represent the opisthosomatic appendages of segment VIII. In the penis of *Scotolemon lespesi* and *Paroligolophus agrestis*, the ancestral paired lobes (i.e. the supposed opisthosomatic appendages) have apparently fused.

Ventral aspect of prosoma. — The coxal and sternal regions of palp and legs (segments II-VI) are represented in figs. 1B, 2B, 3D and, in more detail, in figs. 11D, 12C, 13A, B. The coxae of the legs are enlarged and immovably integrated in the ventral surface of the prosoma, with the exception of the anterior coxae which, when they participate in feeding, are able to perform adductor-abductor movements (see the section on the mouthparts). The coxae of palp and several legs are associated with coxapophyses, or coxal lobes, which are regarded as endites (paraxial branches of the appendages); they are supposed to be homologous with the sternapophyses of other groups of Chelicerata (see: Van der Hammen, 1980: 149-150). The occurrence of enlarged coxae is associated with a reduction in size of the sternal area. The last-mentioned area is also reduced in size because of the advanced position of the genital opening. The orifice of the coxal gland is in the sternal area, close to the paraxial border of coxa III.

In *Siro rubens* (figs. 1B, 13A, B), the coxa of the palp, and coxae I and II present large coxapophyses which are completely fused with the coxae. They are separated from each other, and from coxae III, by an area of soft skin, which can be extended (fig. 13B). There is no labium. It is difficult to decide whether the area between coxae III and IV consists of the sternites of segments V and VI, or of the coxapophyses III and IV. In the last-mentioned case, the coxapophyses must be completely integrated in the sternal area, because the orifice of the coxal gland is at the surface, at the border of segments V and VI (fig. 13A).

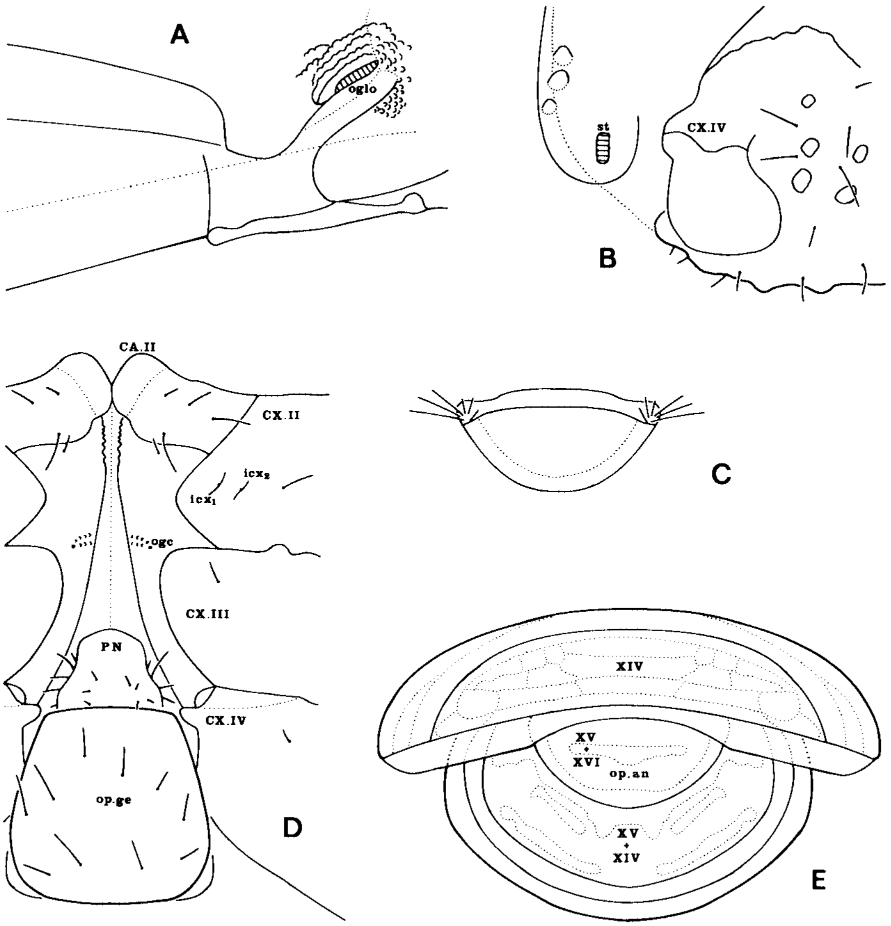

Fig. 11. *Scotolemon lespesi* Lucas, adult male; A, part of lateral region of prosoma, dorsal to coxa II, with orifice of odoriferous gland, lateral view; B, lateral view of right coxa IV and stigma; C, anal cover, separated from opisthosoma, viewed from inside; D, sternal and genital region (penis partly evaginated), ventral view; E, posterior part of opisthosoma, posterior view; A, × 147; B, D, × 118; C, E, × 37.

In *Scotolemon lespesi* (figs. 2B, 11D), the coxae of palp and legs I and II present large coxapophyses which are fused with the coxae. The presence of the lyrifissures *icx*$_1$ and *icx*$_2$ is certainly associated with the adductor-abductor movements of coxa II. Although a labium is sometimes supposed to be absent in Laniatores, it is here supposed to be represented by the membraneous pro-

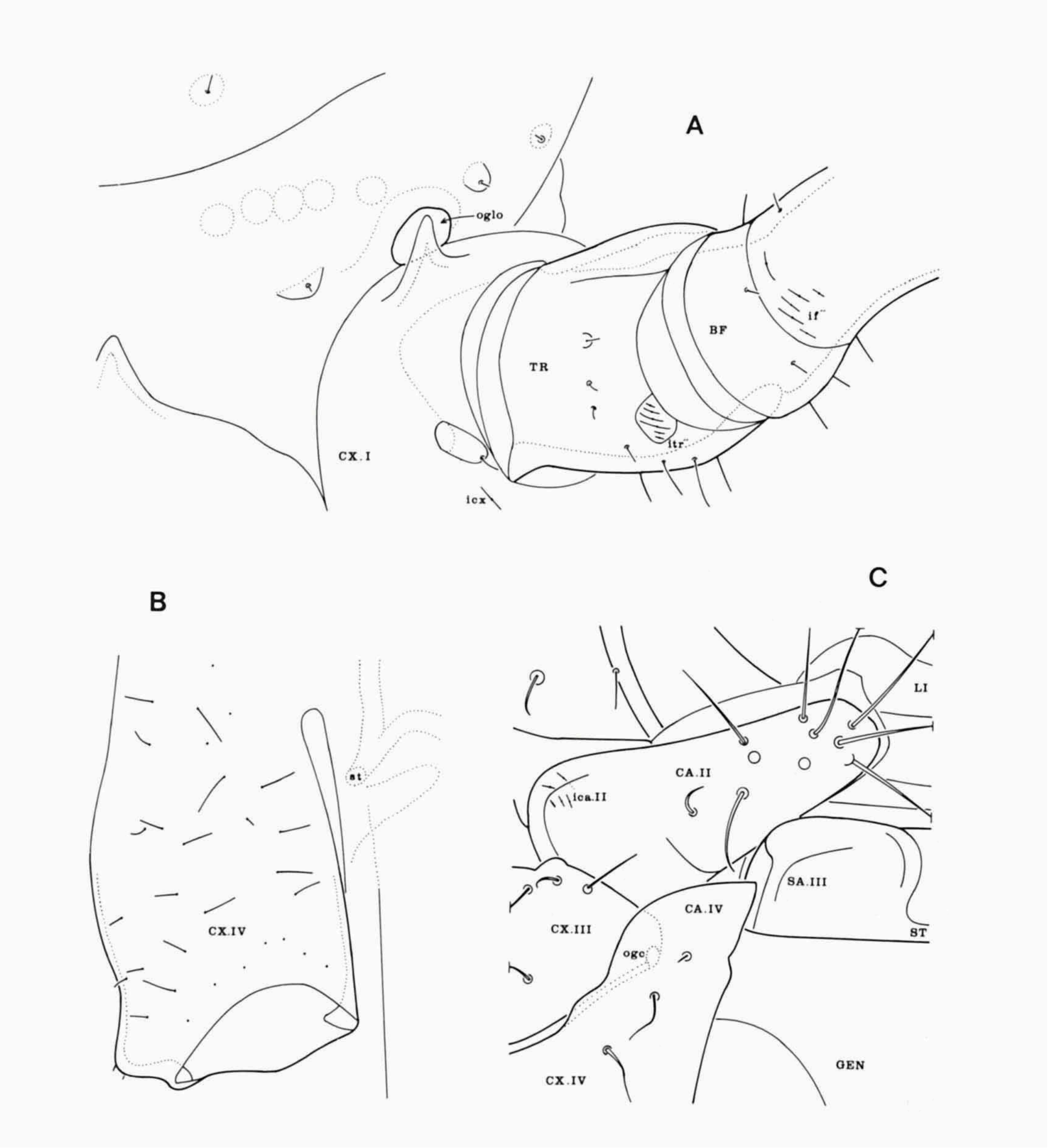

Fig. 12. *Paroligolophus agrestis* (Meade), adult female; A, lateral view of part of prosoma, with orifice of odoriferous gland, and base of leg I; B, ventral view of coxa IV and stigma; C, ventral view of coxal and sternal region, with orifice of coxal gland; A, C, × 118; B, × 73.

jection between coxapophyses I and II (in this case it could be homologous with the sternite of segment III). The remaining part of the sternal area is constituted by a narrow plate, fused with the coxae (and coxapophyses II). The orifice of the coxal gland is near the paraxial border of coxa III (more advanced than in *Siro* or *Paroligolophus*); it is connected with the median part of the sternum by two rows of very small tubercles (fig. 11D).

In *Paroligolophus agrestis* (figs. 3B, 12C), the coxae of palp and legs I, II and IV are associated with coxapophyses. These apophyses are more or less flexibly attached to the coxae. The presence of lyrifissures at the base of coxapophyses II (fig. 12C: *ica. II*) is evidently associated with this movability. The sternite of segment III is represented by the labium. The sternite of segment V is probably represented by the transverse sclerite between legs III; it presents, on either side, a rounded prominence which could represent the sternapophyses of segment V (there are no coxapophyses in this segment). According to Winkler (1957: 370), the anterior part of the genital cover, which overlaps the greater part of the sternal area, could represent the sternite of segment VI. The remaining part of the sternal area, which partly consists of soft skin, certainly includes the sternal part of other prosomatic segments. The orifices of the coxal glands are at the paraxial border of coxa III, covered by coxapophyses IV (fig. 12C).

Lateral aspect of prosoma. — A study of the prosoma in lateral view (figs. 1C, 2C, 4) demonstrates the more or less upward direction of the coxae. Different aspects of shape and size of the coxapophyses are visible in this orientation. The orifice of the odoriferous gland is best visible in lateral view. In *Siro rubens* (fig. 1C), the orifice is near the apex of a cone-shaped tubercle, in the lateral part of the prodorsum. In *Scotolemon lespesi* (figs. 2B, 11A), it is situated at the border of the prodorsum; it is associated with a taenidium (see: Juberthie, 1961). In *Paroligolophus agrestis* (figs. 4, 12A), it is ventral to the lateral border of the prodorsum.

Mouthparts. — The opilionid mouthparts (see: Snodgrass, 1948: 43-51, figs. 15-17) include: the chelicerae (see following section) and the cheliceral frame (i.e. the part of the tegument to which the chelicerae are attached); labrum, cervix (generally named epistome or clypeus; see Van der Hammen, 1980: 28-29) and apodeme (here named myliosomatic apodeme); labium, mouth and pharynx; palp (dealt with in a separate section), and the coxa-

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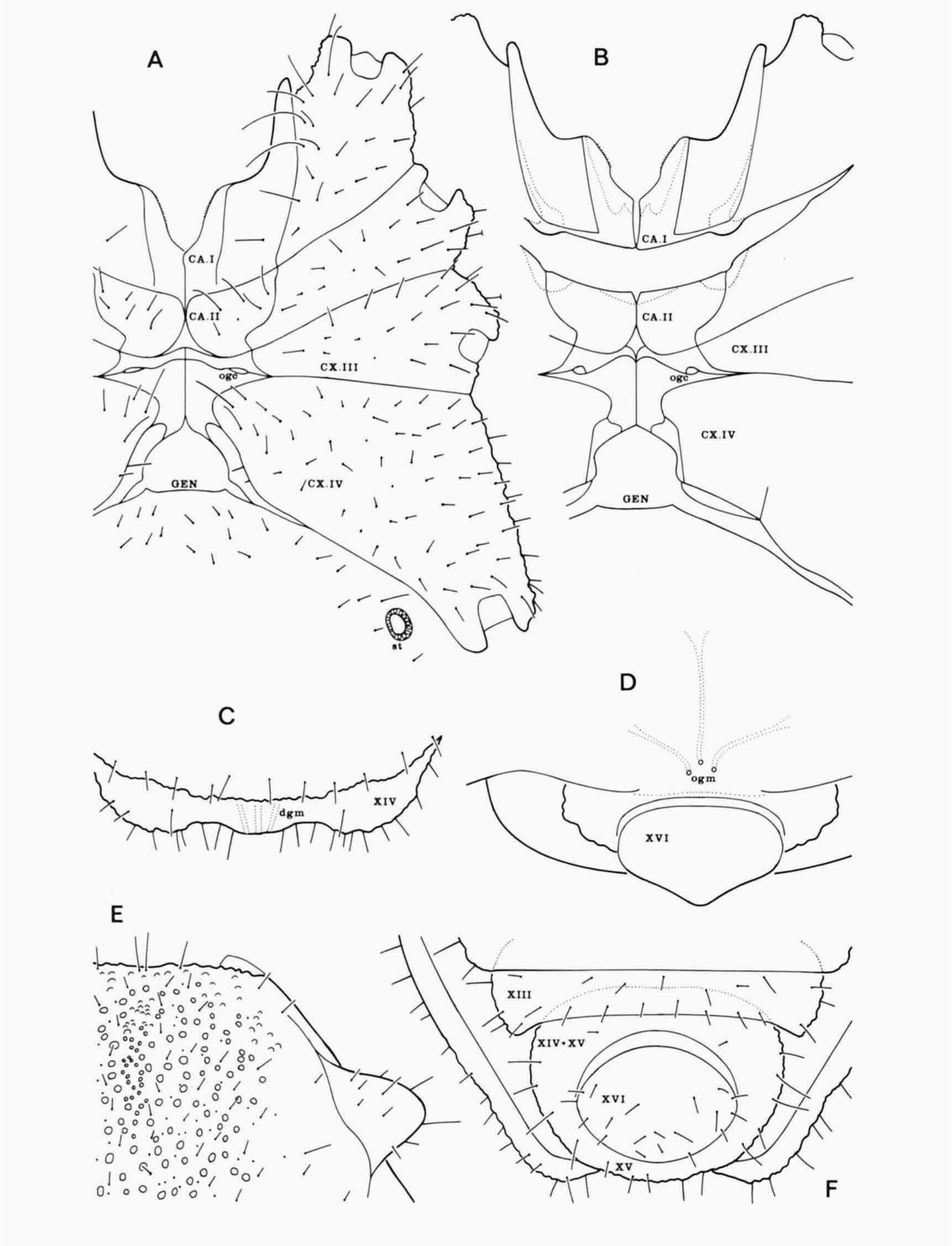
Fig. 13. *Siro rubens* Latreille, adult male; A, B, ventral view of coxisternal region (chelicerae and palps removed); A, coxae contiguous; B, coxae I uncoupled and separated from coxae II by soft skin; C, dorsal view of posterior border of opisthosoma; D, posterior view of opisthosoma; E, dorsal view of rostral region; F, ventral view of anal region; A-F, × 118.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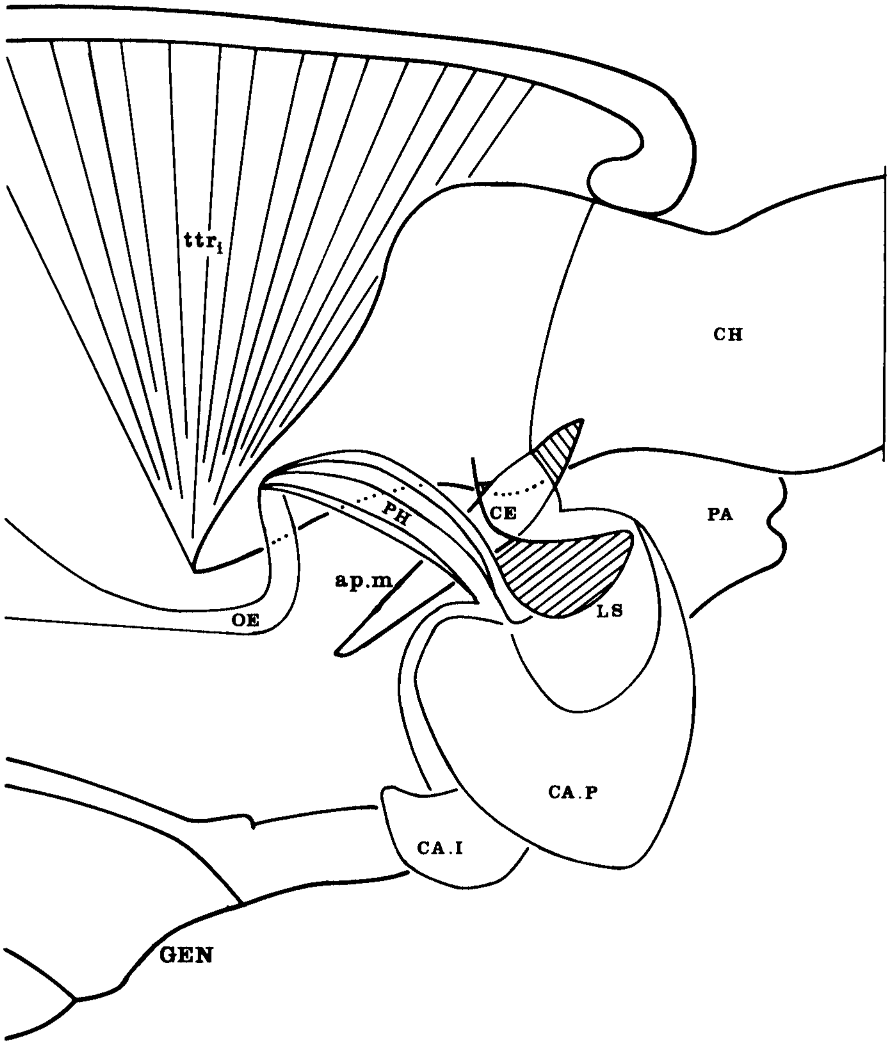


Fig. 14. *Siro rubens* Latreille, adult female, longitudinal (sagittal) section of anterior region of body with mouthparts; × 212.

pophyses of palp and anterior legs. The mouthparts are particularly characterized by the more or less ventral position of the mouth, the curved pharynx and the participation of the coxapophyses of palp and anterior legs in food-intake (see fig. 4). The type of ingestion associated with these mouthparts (it is also found in Xiphosura and Scorpionida) is here named coxisternal feeding.

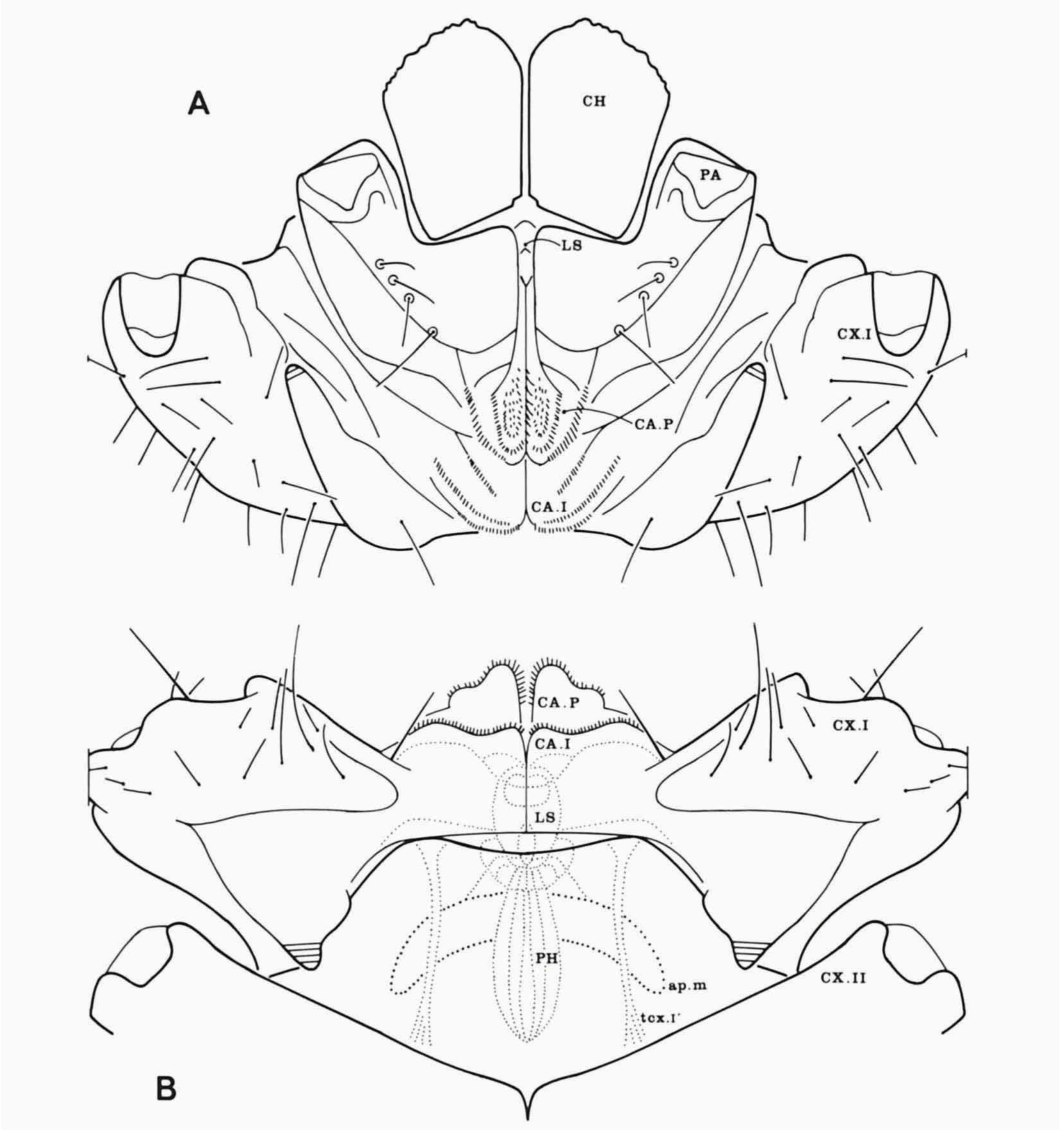


Fig. 15. *Siro rubens* Latreille, mouthparts of adult female; A, frontal view (chelicerae partly cut off, and represented by a transverse section of the trochanter); B, ventral view (coxae I and II widely separated by extension of the area of soft skin); A, B, × 141.

The compound structure made up of the elements involved in coxisternal food-intake is here named myliosoma. Among the groups with coxisternal feeding, Opilionida and Xiphosura are characterized by the ingestion of solid food and internal digestion, Scorpionida by the ingestion of fluid food and external digestion.

A myliosoma is a more or less cone-shaped subdivision of the body. It has a complicated structure, which is studied here in various orientations, and in sections. Dorsal view generally refers here to the dorso-frontal view, frontal view to the ventro-frontal view, posterior view to the dorso-posterior view (the ancestral position of the mouthparts has considerably changed, in connection with the ventral translocation of the mouth, and its association with the coxapophyses of the legs).

The cheliceral frame, which is relatively small, extends from the cervix (to which it is attached according to the line *at*, see fig. 16C) to the rostral border of the prodorsum. Part of the articulation point of a chelicera is constituted by a condyle near the line *at* (figs. 14, 18); the greater part of the arthrodial membrane is dorsal. The chelicerae are operated by a large inferior depressor muscle (ttr_i), attached to the prodorsum, and a smaller superior levator muscle (ttr_s). The cervix (*CE*) extends from the base of the labrum to the myliosomatic apodeme (*ap.m*) (see: figs. 14, 17A, C, 18, 19A, F); generally, it is rather heavily sclerotized. Near the labral base, the cervix presents a distinct median convexity. The myliosomatic apodeme constitutes the internal continuation of the cervix; a strong median tendon (*tm*) and paired lateral tendons can be inserted on it (figs. 16A, C, 17A-C, 19A, B, E, F). The labrum (*LS*) constitutes the anterior prolongation of the cervix (figs. 14, 15, 16C, 17A, C, 18, 19A, C, E, F). It is partly attached to the coxapophyses of the palp, and can present a pointed terminal part, which is directed downwards. The labium (*LI*), if present, is situated between coxapophyses I and II (it overlaps coxapophyses I); as mentioned above, it is homologous with the sternal region of segment III. It is distinctly sclerotized in Palpatores (fig. 3B). The mouth (*b*) has a ventral position, and is bordered (figs.14, 18, 19F) by labrum, coxapophyses of palp and leg I, and labium (if present). The pharynx (*PH*) has a hexagonal transverse section (fig. 16A); it is curved downwards in the anterior part (figs. 4, 14, 18, 19F). The coxapophyses of palp and legs I and II (figs. 14-19) are constituted by paraxial lobes of the appendages; generally, these lobes are named endites, which collective noun must be regarded as a "neutral" descriptive term indicating structures which are, as yet, not completely understood. According to Dumitrescu (1975), salivary glands are present in the coxapophyses of palp and leg I. The palpal coxae participate in the general movements of the palp; the coxapophyses are operated by the adductor and abductor muscles *tcx'*, *tcx''* and tcx_i (figs. 22, 23A, 24A). The coxae of the legs do not participate in the walking movements of these appendages; adduction of the coxae (and the coxapophyses) of legs I and II, during ingestion, is operated by the adductors

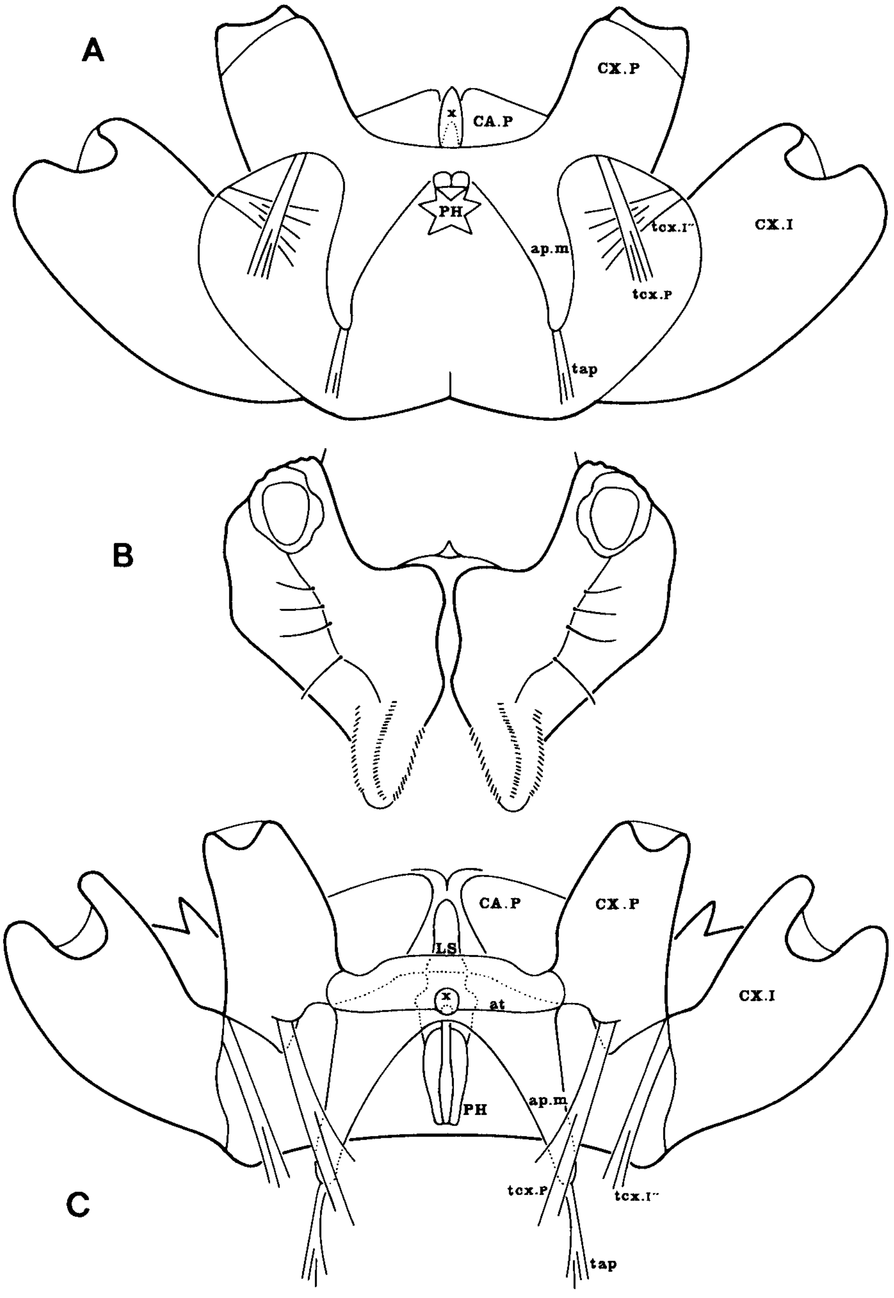


Fig. 16. *Siro rubens* Latreille, mouthparts of adult (A, C, female; B, male); A, posterior view; B, frontal view of (widely separated) palpal coxae; C, dorsal view; A-C, × 141.

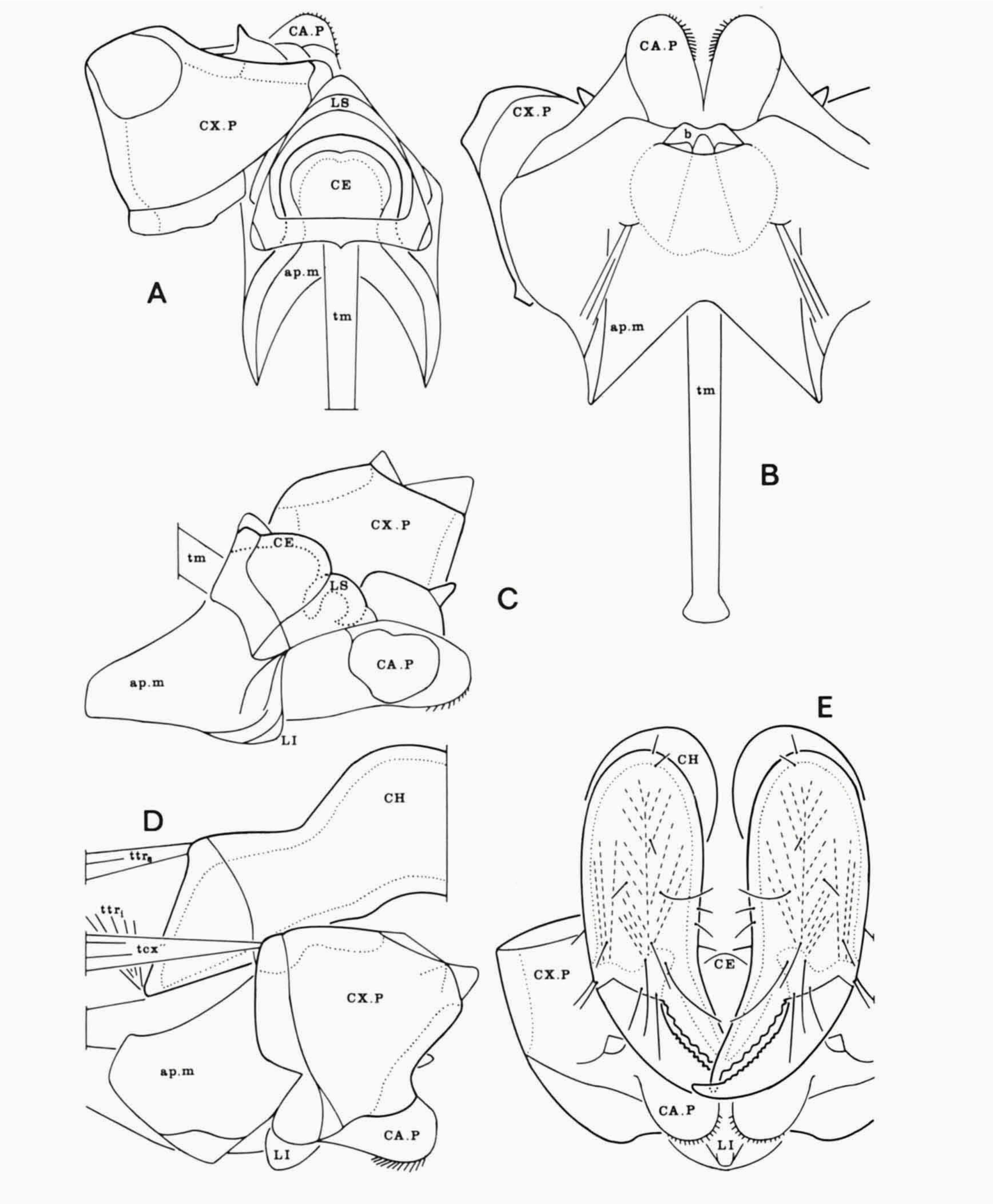


Fig. 17. *Scotolemon lespesi* Lucas, mouthparts of adult female; A, dorsal view (chelicerae and right palpal coxa removed); B, ventral view; C, lateral view (chelicerae and right palpal coxa removed); D, lateral view; E, frontal view; A-E, × 88.

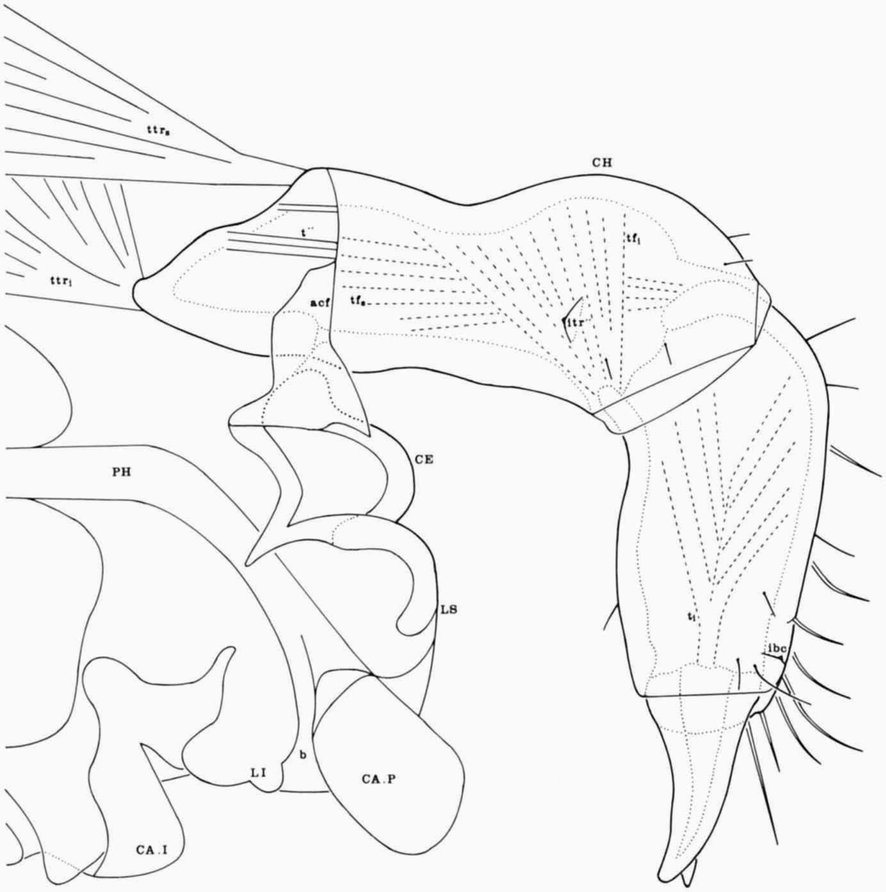


Fig. 18. *Scotolemon lespesi* Lucas, adult male; longitudinal section of anterior prosomatic region (with mouthparts), antiaxial to right chelicera; × 118.

tcx (figs. 29B, C, 30A, 32F); abduction probably takes place by hydrostatic pressure. As mentioned above, in the section on the ventral aspect of the prosoma, the coxae of palp and legs I and II can be separated by soft skin. In these cases, the soft skin can be extended (fig. 13B) by hydrostatic pressure, whilst the myliosoma turns around an articulation point at the laterofrontal border of the prodorsum. Retraction apparently takes place by the retractor muscles tcx_r (fig. 29C).

The mouthparts of *Siro rubens* (see figs. 13A, B, 14-16, 22A, 29B, C) are particularly characterized by the absence of a labium, and by the possibility of coxisternal extension and retraction (associated with myliosomatic articulation). The cuticle of the palpal coxapophyses is rather soft, particularly in the distal part. The concavity, laterally bordered by the coxae of leg I, which contains the coxapophyses of palp and leg I, is generally named stomotheca; its occurrence is probably related to the extension and retraction of these coxapophyses. The labrum has probably completely fused with the coxapophyses of the palp; it has apparently no free distal part.

The mouthparts of *Scotolemon lespesi* (see figs. 17, 18, 23A, 30A) are particularly characterized by: the membraneous labium; the large coxapophyses I and II, which are immovably connected with the coxae; and the labrum which has fused with the coxapophyses of the palp, and has no free distal part. The mouthparts of *Paroligolophus agrestis* (see figs. 3B, 4, 19, 24A, 32F) are particularly characterized by: the sclerotized labium; the large coxapophyses which can be rather soft and individually movable; and the superficial taenidia (named pseudotracheae by Kästner, 1933), associated with the salivary glands in the palpal coxapophyses, which run up into the mouth.

Chelicera (figs. 18, 20, 21). — The opilionid chelicera consists of three segments which are named trochanter, body of the chelicera (including the fixed jaw of the chela), and apotele (the movable jaw of the chela). The basal part of the trochanter is internal: the cheliceral frame and the arthrodial membrane are attached to the trochanter according to the line *acf*. The basal articulation-point of the chelicera is constituted by a condyle (close to the line of attachment of the cheliceral frame to the cervix) and the antilateroventral part of the trochanter (close to the line *acf*). As mentioned above, in the section on the mouthparts, the chelicerae are operated by a large inferior depressor muscle (ttr_i) and a smaller superior levator muscle (ttr_s); there can also be additional muscles. The articulation between the trochanter and the body of the chelicera is constituted by a pivot joint with one or more superior levator muscles (tf_s, tf_s'') and one or more inferior depressor muscles (tf_i, tf_i', tf_i''). The joint between the body of the chelicera and the apotele is operated by the usual tendons of the claw segment (t_s and t_i). Owing to torsion, the articulation axis of the joint between the body of the chelicera and the apotele can have become more or less parallel to the sagittal plane of the body, instead of perpendicular to it; in these cases (*Scotolemon lespesi, Paroligolophus agrestis*; much less in *Siro rubens*), the position of the apotele is antiaxial instead of ventral.

The trochanter and the body of the chelicera present setae, especially in the dorsal regions. In *Scotolemon lespesi* and *Paroligolophus agrestis*, the setae are most numerous on the body of the chelicera. Lyrifissures can be present in the trochanter (*Scotolemon lespesi*, fig. 18: *itr''*) and in the body of the chelicera

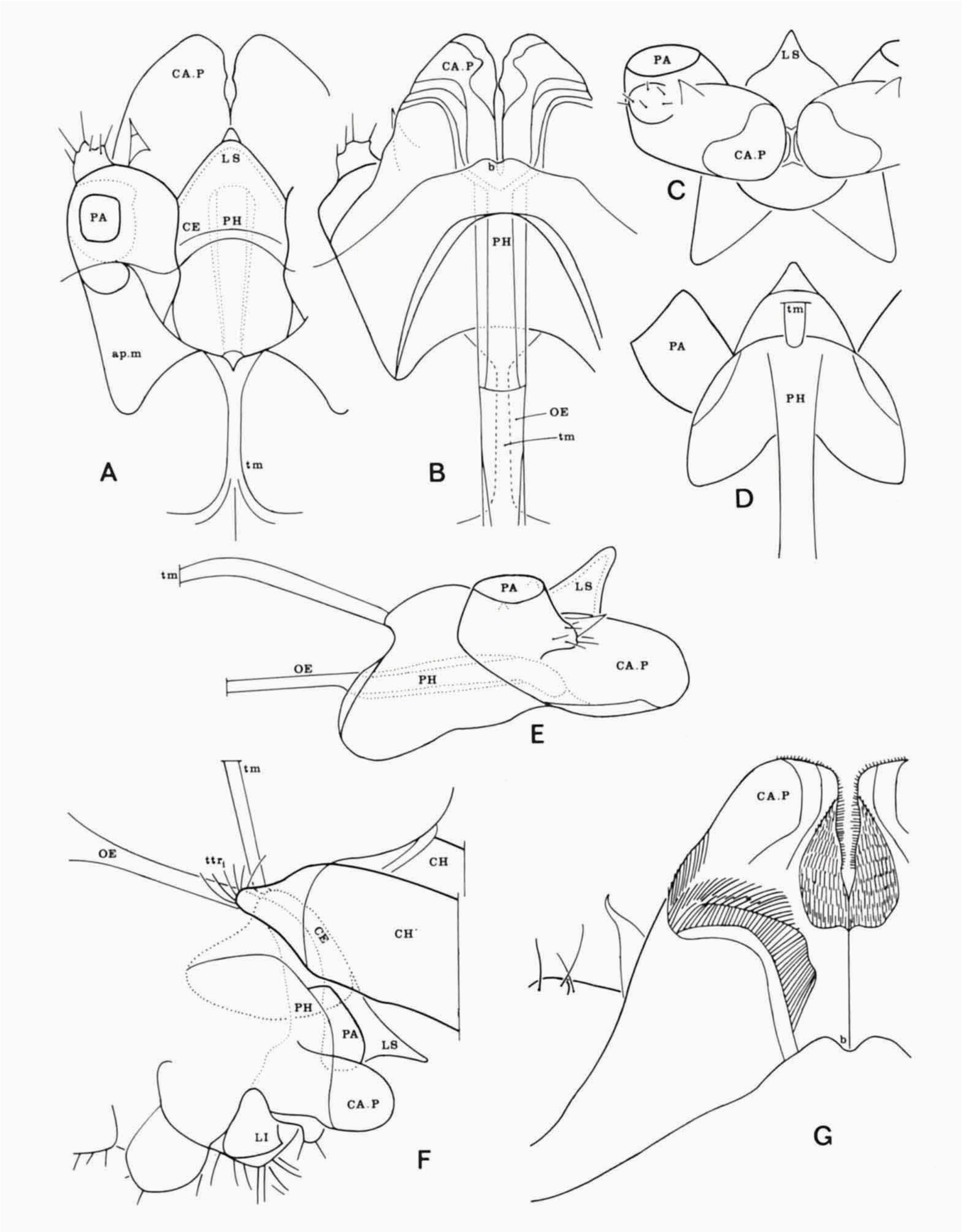


Fig. 19. *Paroligolophus agrestis* (Meade), mouthparts of adult male (chelicerae removed, except in the case of F); A, dorsal view; B, ventral view; C, frontal view; D, posterior view; E, lateral view, F, longitudinal section (antiaxial to right chelicera); G, ventral view of mouth and coxapophyses of the palps; A-F, × 118.

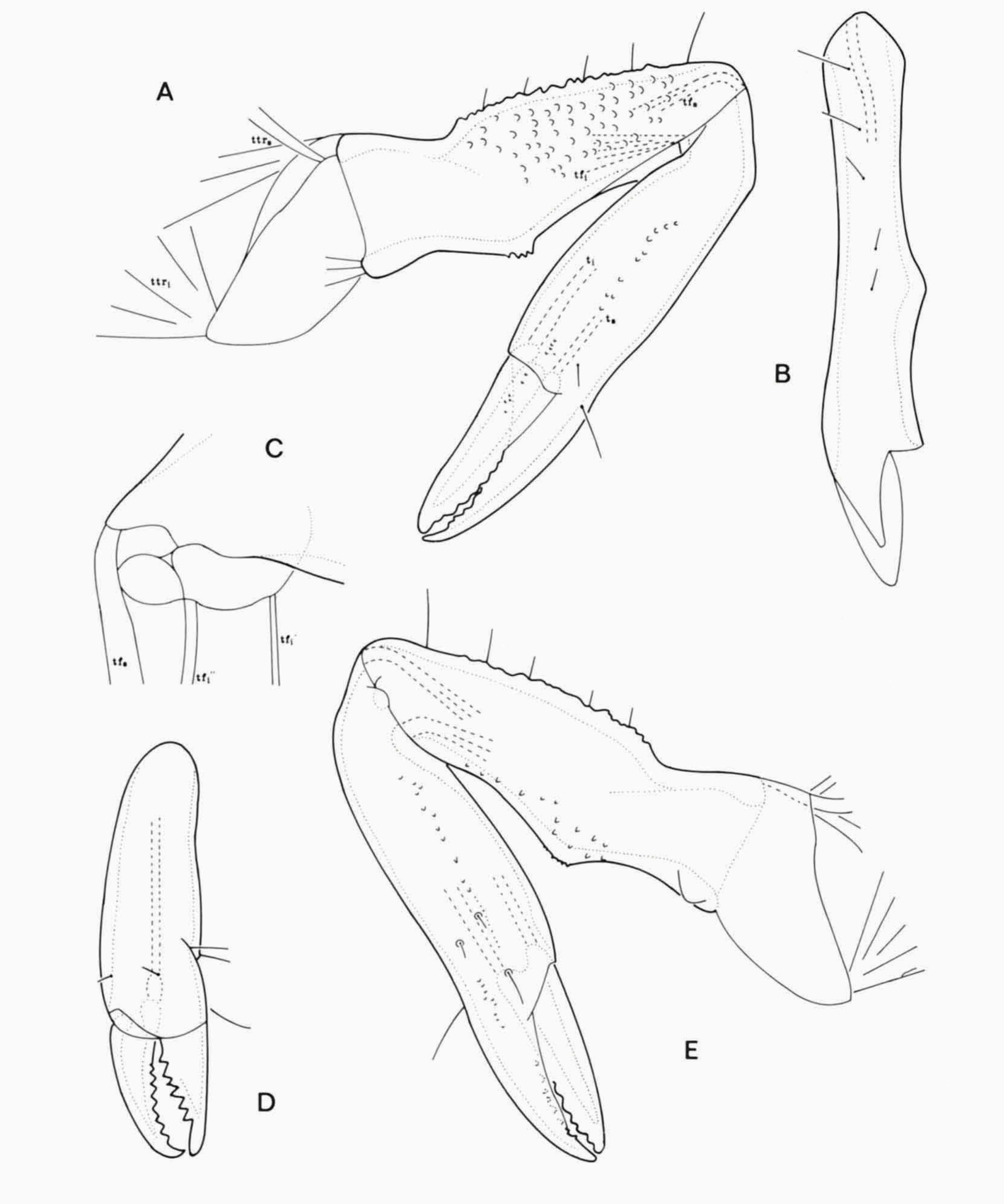


Fig. 20. *Siro rubens* Latreille, right chelicera of adult male; A, lateral (antiaxial) view; B, dorsal view of trochanter; C, lateral (antiaxial) view of proximal region of body of chelicera (separated from trochanter); D, ventral (oblique) view of body of chelicera and apotele; E, lateral (paraxial) view; A-B, D-E, × 118; C, × 246.

near the chela (in *Scotolemon lespesi*, see fig. 18, a single lyrifissure *ibc*; in *Paroligolophus agrestis*, see fig. 21C, a group of lyrifissures *ibc*). Cheliceral glands in the anterior prosomatic region, with an orifice in the dorsodistal part of the cheliceral trochanter, were described by Dumitrescu (1974).

Palp (figs. 22-24). — The opilionid palp consists of coxa, trochanter, femur, patella, tibia, tarsus and apotele (or claw segment; it is absent in many cases); there is no separate basitarsus, and there are no other tarsal subdivisions. The coxa presents a coxapophysis associated with ingestion (the coxa-body articulation is dealt with in the section on the mouthparts). The coxa-trochanter articulation is a pivot joint with superior levator and inferior depressor muscles. The trochanter-femur articulation is a rocking joint with ventral condyle and laterally inserted promotor and remotor muscles (*tf'*, *tf''*). The femur-patella articulation is a hinge joint with dorsal condyle and ventral flexor muscle (*tpt*). The patella-tibia articulation is a rocking joint with one condyle (originally dorsal) and two lateral muscles (*tti'* and *tti''*). The tibia-tarsus articulation is a hinge joint with dorsal condyle and ventral muscle (*tta*). The tarsus-apotele articulation, if present, is a pivot joint with lateral condyles, and two tendons, viz., the superior tendon t_s, and the inferior tendon t_i.

All palpal segments present setae (the seta of the apotele is the unguis); the setae can be inserted on large tubercles or apophyses (as in *Scotolemon lespesi*; see fig. 23). Solenidia can be present on the tarsus (in *Siro rubens* in the distal part, see fig. 22B; in *Paroligolophus agrestis* on the dorsal surface, see fig. 24A). Lyrifissures can be present in various segments; in *Scotolemon lespesi* (fig. 23B), the femur presents two dorsal lyrifissures, if_1 and if_2; in *Paroligolophus agrestis* (fig. 24A), the trochanter presents a group of three lateral (antiaxial) lyrifissures *itr''*.

Apart from the coxapophysis (which is associated with ingestion), the function of the palp is probably either predominantly sensory, or predominantly prehensile (as in *Scotolemon lespesi*).

Legs (figs. 25-33). — The opilionid legs consist of seven eudesmatic segments: coxa, trochanter, femur, patella, tibia, tarsus and apotele. The femur can be incompletely subdivided, by a basifemoral ring (figs. 30A, 32A), into two adesmatic segments, viz., basi- and telofemur. The tarsus is always subdivided into two adesmatic segments, viz., basi- and telotarsus, which can both present further subdivisions (basitarsus 1, 2, etc.; telotarsus 1, 2, etc.; see figs. 30A, 31E-F, 33A-C).

The coxae of the anterior legs are movable (abduction and adduction) in connection with ingestion, but not in connection with locomotion; the other coxae are fixed. The coxa-trochanter articulation is a bicondylar pivot joint with superior levator (ttr_s) and inferior depressor (ttr_i) muscles. The trochan-

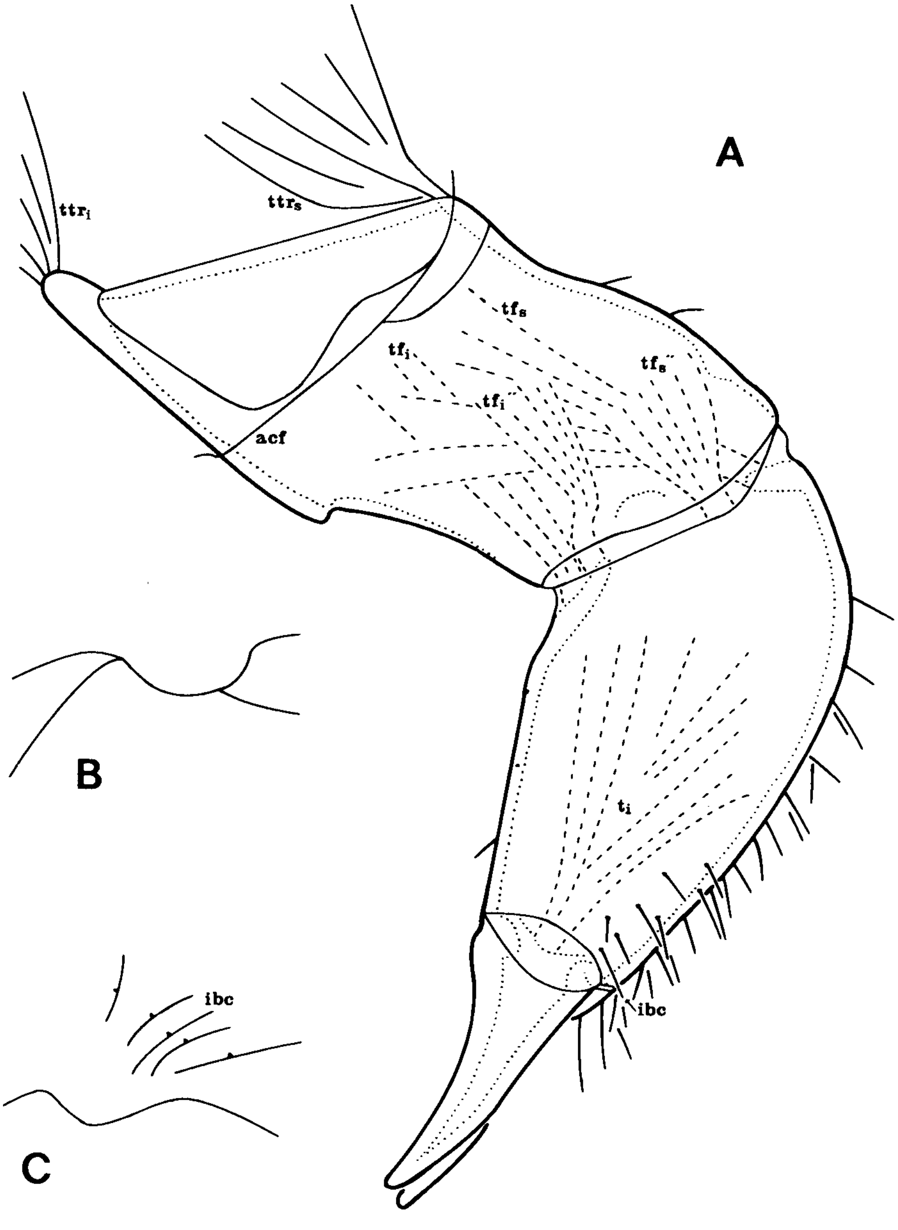


Fig. 21. *Paroligolophus agrestis* (Meade), right chelicera of adult male; A, lateral (antiaxial) view; B, C, articulation between body of chelicera and apotele; B, ventral view; C, dorsal view; A, × 110; B, C, × 368.

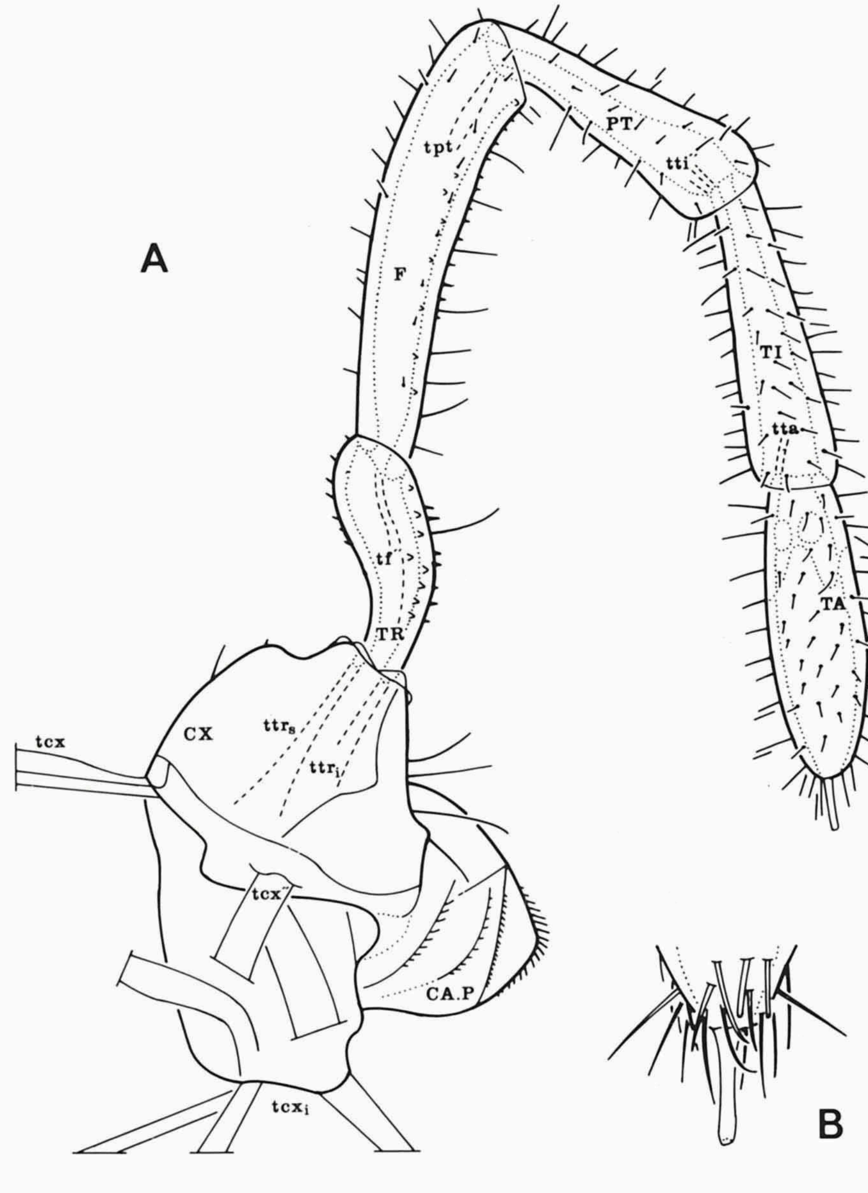


Fig. 22. *Siro rubens* Latreille, lateral (antiaxial) view of right palp of adult male; A, coxa, trochanter, femur, patella, tibia, tarsus and apotele (phanerotaxy of terminal part schematized); B, distal part of tarsus and apotele; A, × 176; B, × 368.

Fig. 23. *Scotolemon lespesi* Lucas, right palp of adult male, lateral (antiaxial) view; A, coxa and proximal part of trochanter; B, distal part of coxa, trochanter, femur, patella, tibia, tarsus and apotele; A, B, × 118.

ter-femur articulation is a rocking joint with inferior condyle and laterally inserted muscles *tf′* and *tf″*. The femur-patella articulation is a hinge joint with superior condyle and inferior muscle *tpt*. The patella-tibia articulation is a rocking joint with superior condyle and laterally inserted muscles *tti′* and *tti″*. The tibia-tarsus articulation is a hinge joint with superior condyle and inferior muscle *tta*. The tarsus-apotele articulation is a pivot joint with lateral condyles and two tendons, viz., a superior tendon t_s and an inferior tendon t_i (which continues in the tibia). The adesmatic segments of basi- and telotarsus can move under the influence of t_s and t_i.

Setae can be present in all segments of the legs (the ungues of the apotele are homologous with setae); they can be inserted on tubercles or apophyses. Solenidia can be present on the tarsus only.

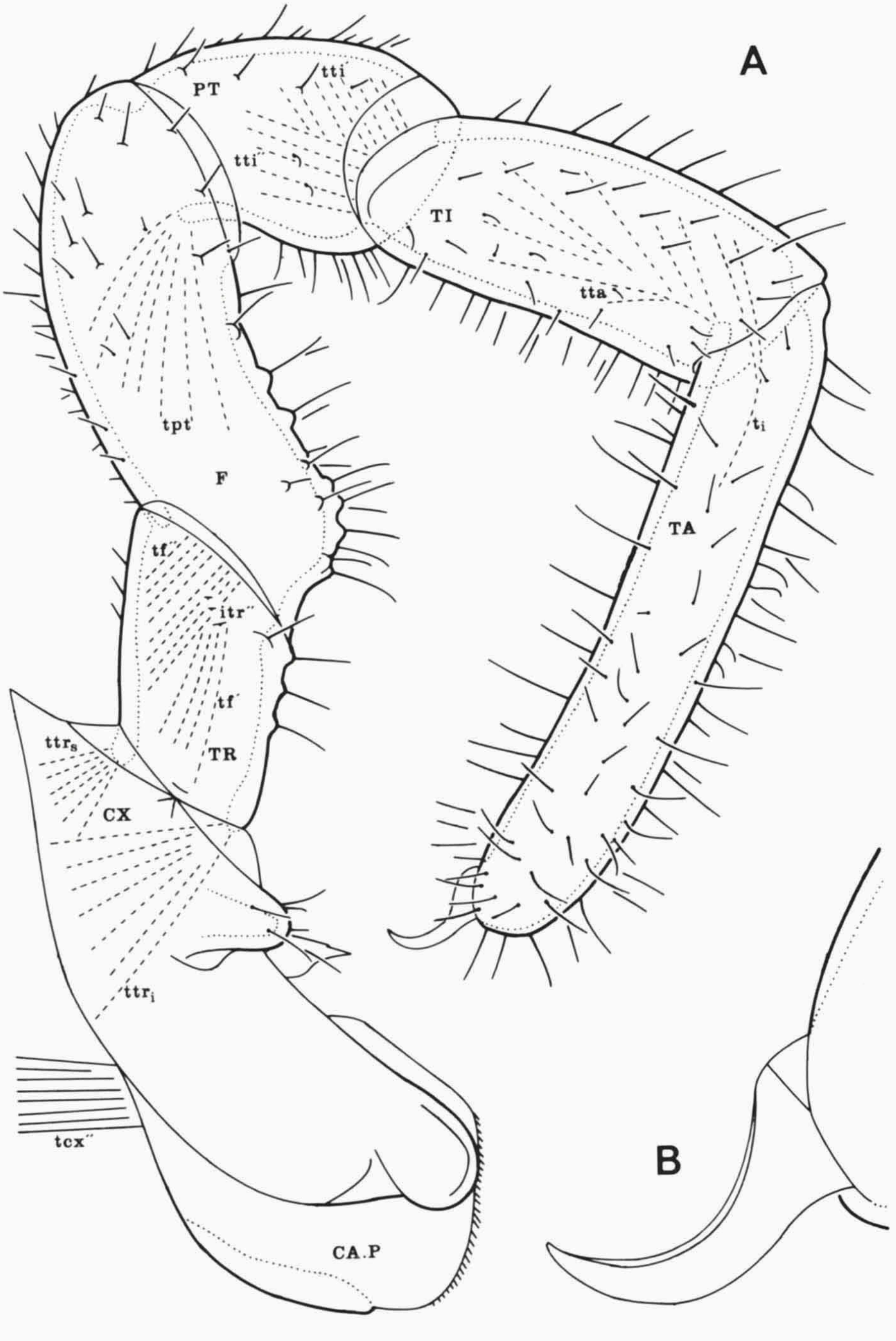
Lyrifissures (see: Barth & Stagl, 1976) are generally associated with articulations, particularly those of the proximal part of the legs (figs. 12A, 30A-C, 32A, C-F), but in Phalangiidae also associated with the basitarsus-telotarsus articulation (fig. 33A, F). They occur as solitary slits, or they are arranged in groups or lyriform organs.

Accessory stigmata and tracheae are present (proximally and distally) in the tibiae of the legs in Phalangiidae.

In *Siro rubens* (figs. 25-29), femur, basitarsus and telotarsus are not subdivided. Lyrifissures are not discernable (although this can be connected with the granulate microsculpture of the tegument). Telotarsus I presents, in my specimens, a dorsal row of eleven solenidia; solenidia are also present on telotarsus II (but not on telotarsus III and IV). All legs are monodactyl. Leg IV of the male presents a telotarsal organ, consisting of a dorsal apophysis which contains the orifice of the so-called tarsal gland (fig. 25; see also: Rafalski, 1958: 535-539, figs. 10-13; Juberthie, 1967: 162-163, fig. 6B).

In *Scotolemon lespesi* (figs. 30, 31), the femur of the legs is incompletely subdivided by a basifemoral ring (an arrangement of lyrifissures) into a small basifemur and a much larger telofemur. The telotarsi I-IV present three (leg I), four (leg III) or five (legs II, IV) adesmatic segments. Legs I and II are monodactyl, legs III and IV bidactyl. Lyrifissures are present in trochanter and femur of legs I-IV (figs. 30A, C, 31A-C).

In *Paroligolophus agrestis* (figs. 32, 33) the femur is subdivided, by a basifemoral ring (associated with lyrifissures), into a small basifemur and a much larger telofemur. The tarsus is subdivided into numerous adesmatic segments; in the case of leg I, the basitarsus presents an incomplete subdivision, whilst the telotarsus of the figured specimen consists of 26 adesmatic segments (telotarsi 1-26). The curved phaneres, in the distal part of the tarsus, apparently represent solenidia. Lyrifissures are present in coxa, trochanter, femur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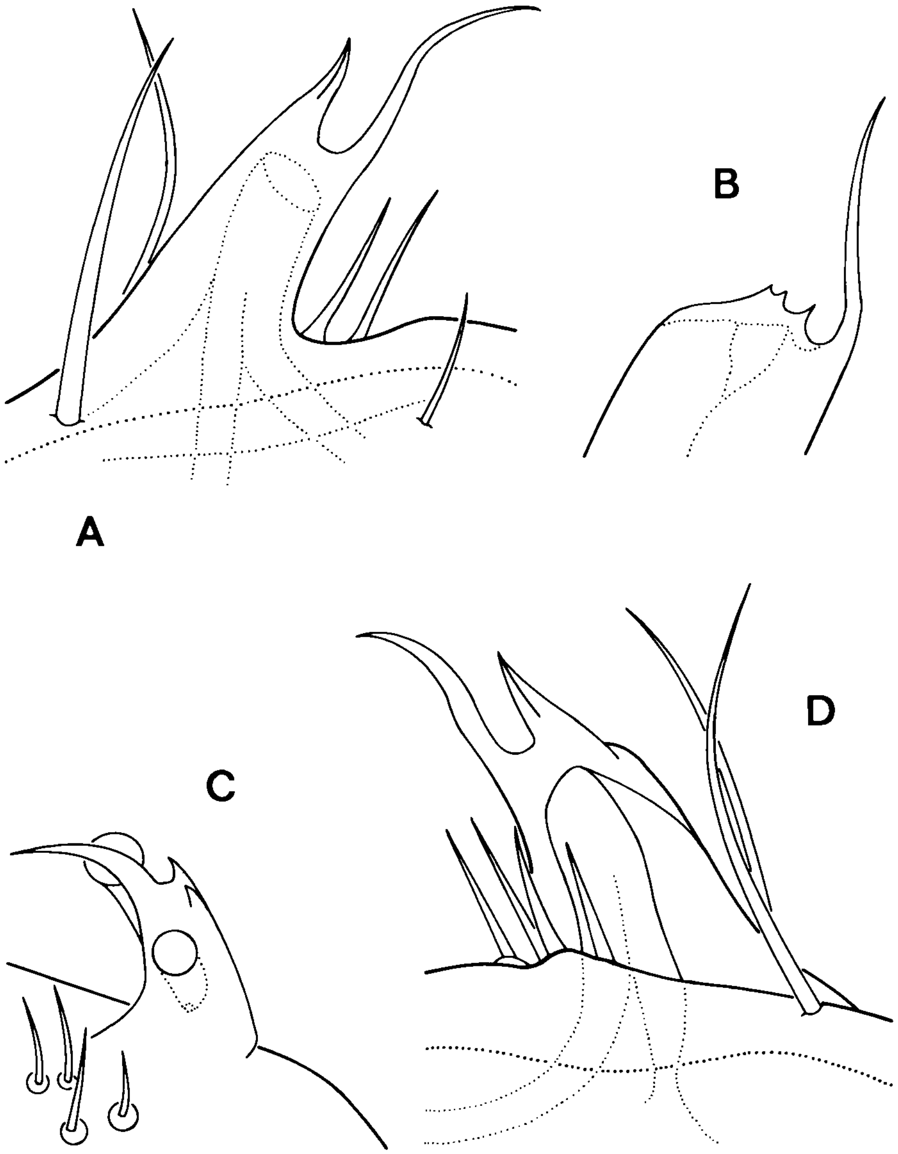

Fig. 25. *Siro rubens* Latreille, adult male, telotarsal organ of right leg IV; A, lateral (posterior) view; B, posterodorsal view; C, anterodorsal view; D, lateral (anterior) view; A-D, × 688.

Fig. 24. *Paroligolophus agrestis* (Meade), right palp of adult male, lateral (antiaxial) view; A, coxa, trochanter, femur, patella, tibia, tarsus and apotele; B, terminal part of tarsus and apotele (setae and aciculate microsculpture omitted; the secondary sexual characters are not visible in this orientation); A, × 110; B, × 368.

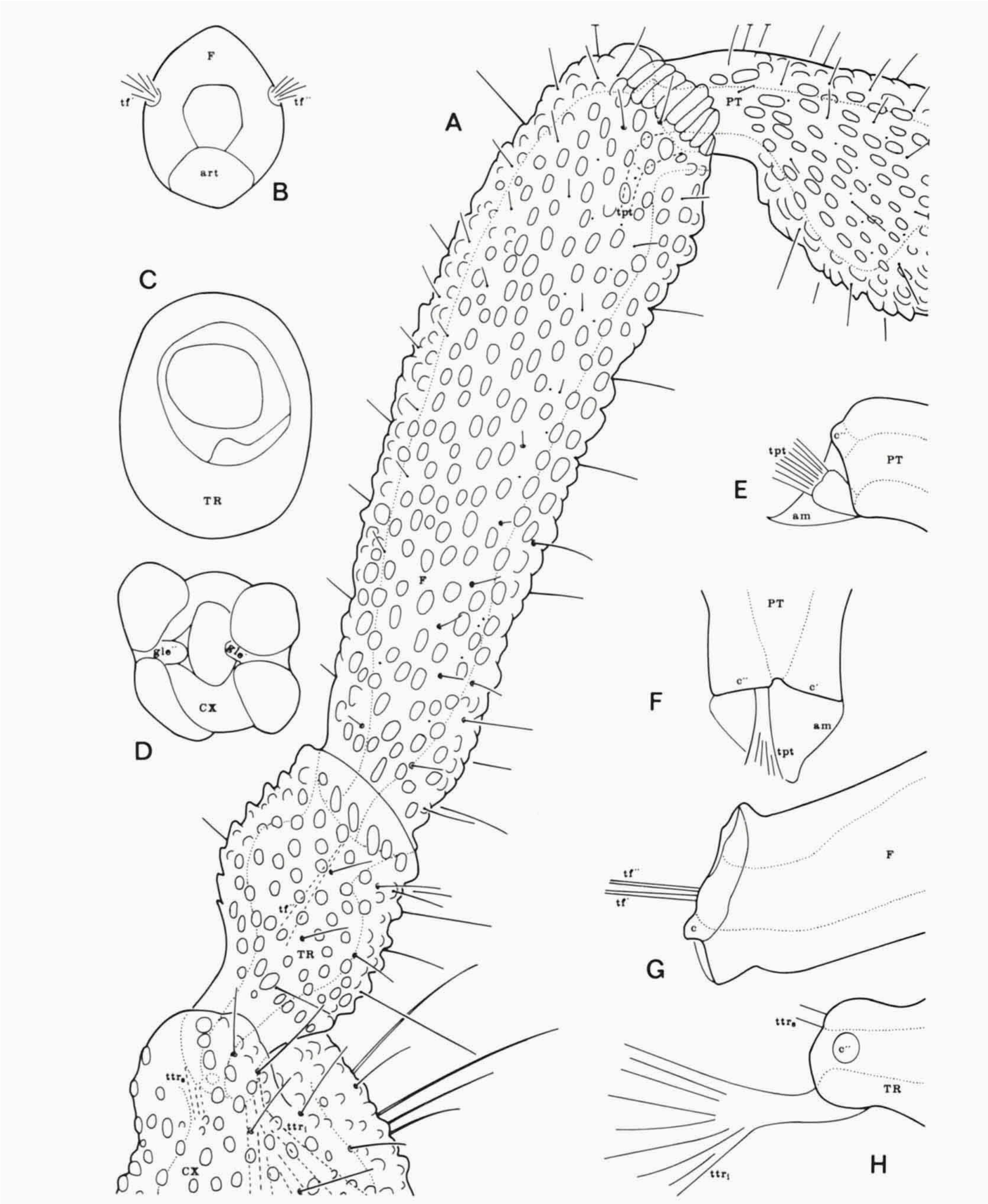

Fig. 26. *Siro rubens* Latreille, right leg I of adult male; A, distal part of coxa, trochanter, femur, and proximal part of patella, lateral (posterior) view; B, proximal view of femur; C, distal view of trochanter; D, distal view of coxa; E, lateral (posterior) view of patella; F, dorsal view of distal part of patella; G, lateral (posterior) view of proximal part of femur; H, lateral (posterior) view of proximal part of trochanter; A-C, E-H, × 246; D, × 187.

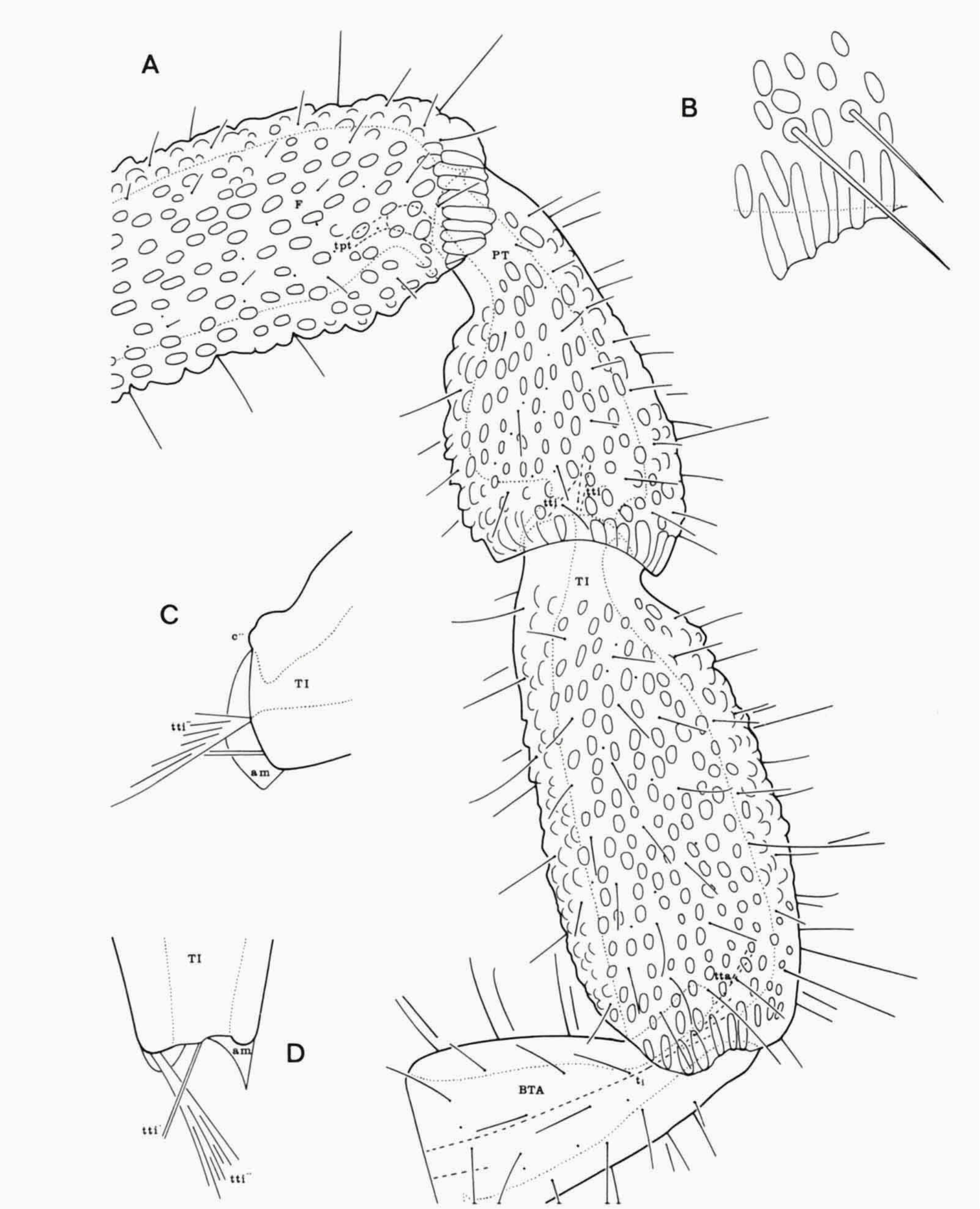

Fig. 27. *Siro rubens* Latreille, right leg I of adult male; A. lateral (posterior) view of distal part of femur, patella, tibia and basitarsus; B, tuberculate microsculpture of distal part of tibia, lateral (posterior) view; C, D, basal part of tibia (separated from patella); C, lateral (posterior) view; D, ventral view; A, C, D, × 246; B, × 458.

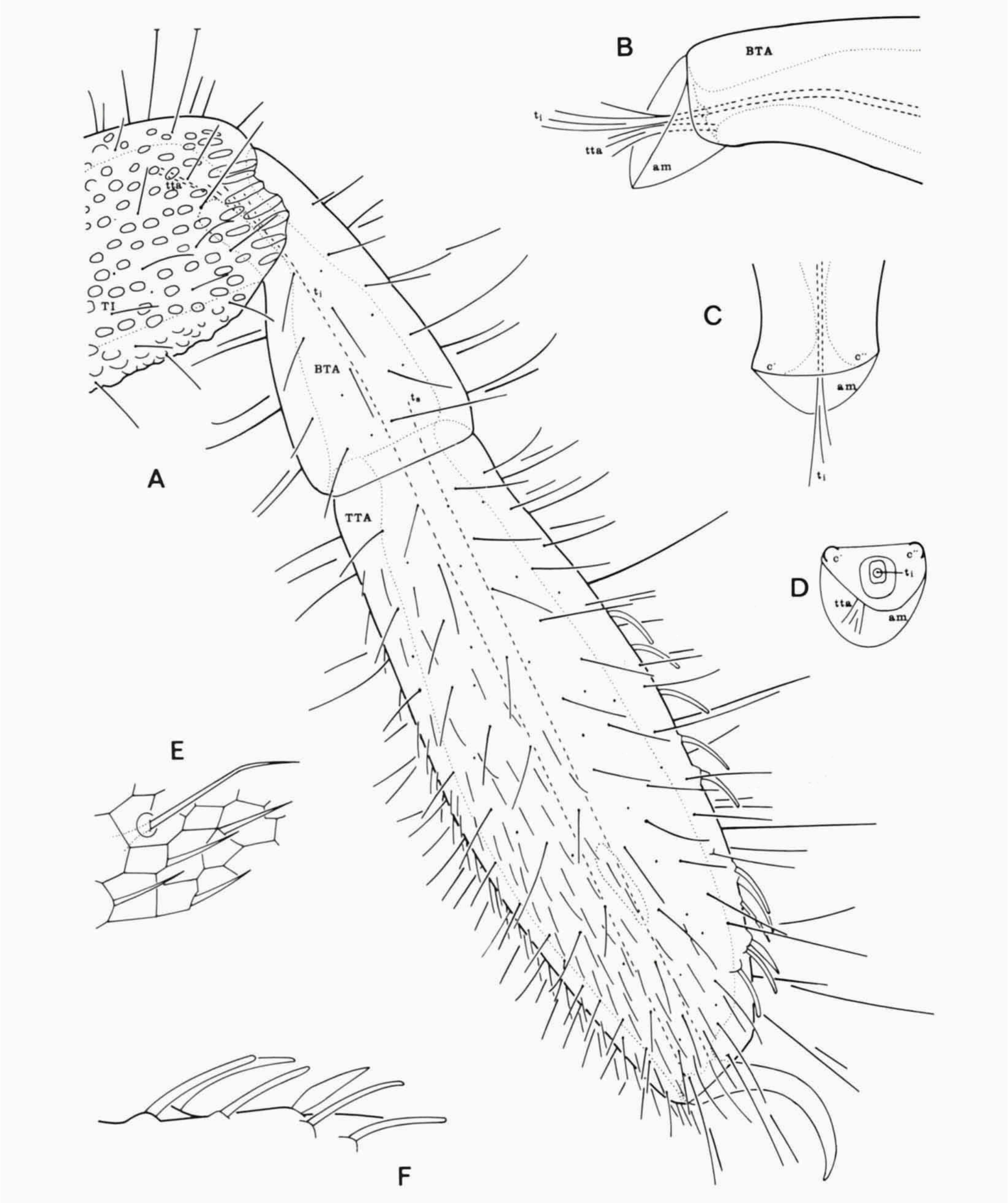

Fig. 28. *Siro rubens* Latreille, right leg I of adult male: A, lateral (posterior) view of distal part of tibia, basitarsus, telotarsus and apotele; B-D, basal part of basitarsus; B, lateral (posterior) view; C, dorsal view; D, proximal view; E, reticulate aciculate microsculpture of part of telotarsus, lateral (posterior) view; F, lateral (posterior) view of distal solenidia of telotarsus; A-D, × 246; E, F, × 458.

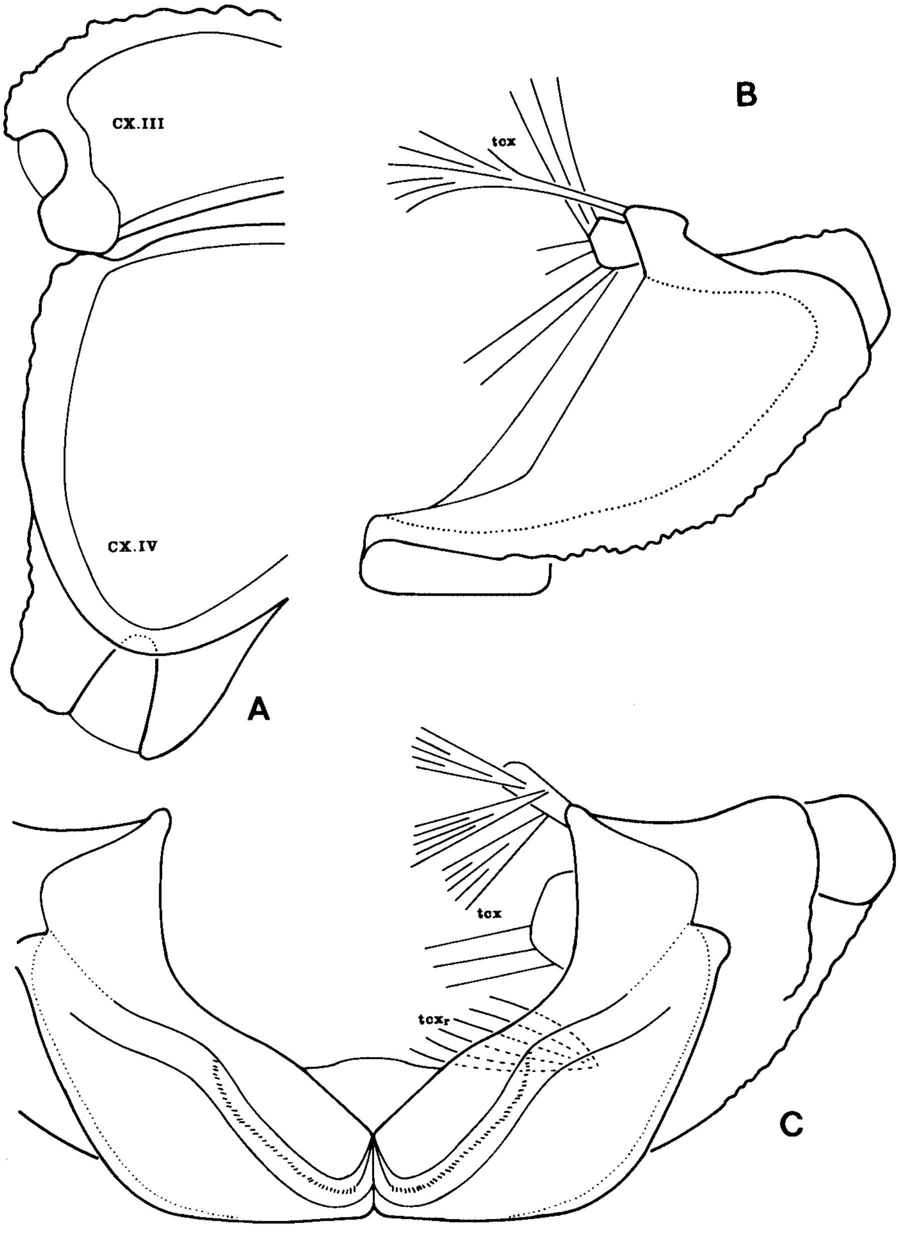

Fig. 29. *Siro rubens* Latreille, coxae of adult male; A, dorsal view of coxae III-IV, after removal of the dorsal body wall; B, anterior view of separated left coxa II; C, anterior view of separated coxae I; A-C, × 186.

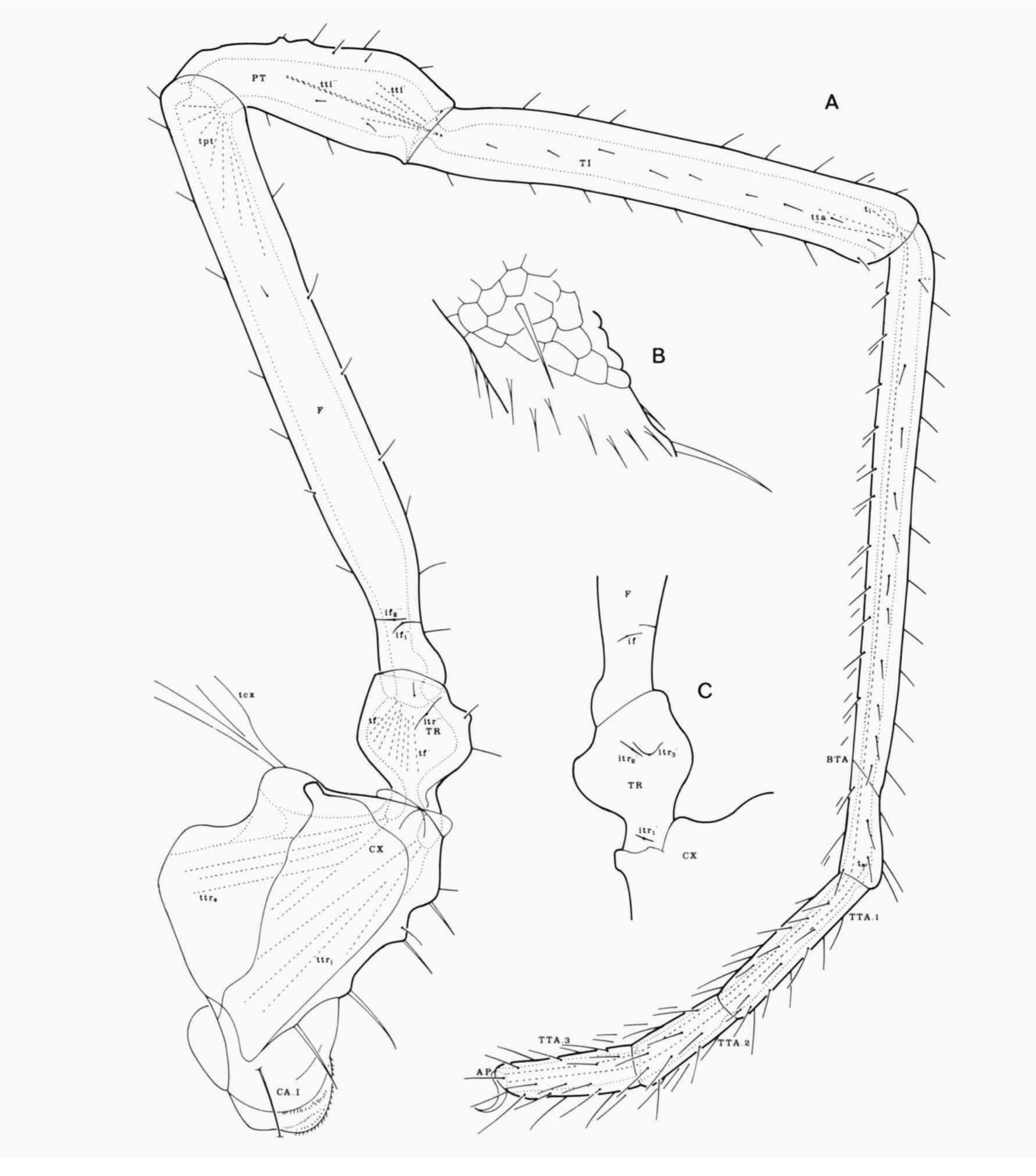

Fig. 30. *Scotolemon lespesi* Lucas, right leg I of adult male; A, lateral (posterior) view; B, transition from reticulate to aciculate microsculpture in the distal part of the basitarsus, lateral (posterior) view; C, lateral (anterior) view of distal part of coxa, trochanter, and proximal part of femur (setae omitted); A, C, × 99; B, × 385.

and basitarsus. The coxal lyrifissure *icx″* of leg I is close to the articulation-point of coxa and trochanter. The posterior lyrifissures of the trochanter of leg I constitute a lyriform organ *itr*, situated close to the laterodistal border of the segment. Femur I presents, posteriorly, a single distal lyrifissure if_a (close to the articulation with the patella), and a group of six lyrifissures *if″* (close to the basifemoral ring). The posterior lyrifissure of basitarsus I (*ita*) is close to the distal border of the basitarsus. The basal accessory stigma of tibia I is represented in fig. 32B.

Internal anatomy. — Important summaries of opilionid internal anatomy were published by Kästner (1935-1937) and Berland (1949); Janczyk (1956) studied the internal anatomy of *Siro duricorius* Joseph, in comparison with other Opilionida. The following section is nothing but a compendious survey.

The alimentary canal consists of mouth, pharynx (with six longitudinal folds), oesophagus, midgut and large caeca, hindgut and anus (see: Dumitrescu, 1974a, 1975a, 1975b, 1976, 1980). The excretory system comprises the coxal glands (orifice near coxa III; according to Moritz, 1959, the gland belongs embryologically to segment III), nephrocytes and perineural organs (for storage of waste products); there are no Malpighian tubes. The endosternite (Firstman, 1973: 8-15, figs. 5-8) presents two or four pairs of dorsal suspensor muscles and two pairs of ventrals (transverse suspensors are lacking); in Cyphophtalmi the endosternite is vestigial, with a single pair of dorsoventral suspensors. The circulatory system consists of a heart and an anterior aorta. The respiratory system consists of the pair of stigmata, posterior to coxae IV (in segment VIII), and tracheae; Phalangiidae present, moreover, tibial stigmata and pedal tracheae. The central nervous system consists of a supraoesophageal ganglion, a suboesophageal ganglion, and a small opisthosomatic ganglion (there is no true opisthosomatic nervecord). The sensory organs include, among others, one pair of eyes (absent in several cases), stress-sensitive organs (lyrifissures), and sensory phaneres (setae and solenidia; Opilionida have no trichobothria). The male reproductive system consists of testes, vasa deferentia, vesicula seminalis and penis (or spermatopositor); Opilionid sperm is completely aflagellate (with the exception of Cyphophtalmi, in which group a rudiment of a cilia is present during spermatogenesis; see Juberthie, Manier & Boissin, 1976). Opilionid sperm transfer is direct (by copulation; not known from Cyphophthalmi, where a "spermatophore" is produced which is transported to the female reproductive system in an unknown way). The female reproductive system consists of ovaria, oviducts, uterus and ovipositor (with receptacula seminis). The glandular system includes the prosomatic odoriferous glands (see Juberthie, 1961), salivary glands (see Dumitrescu, 1975), and cheliceral glands (see Dumitrescu, 1974).

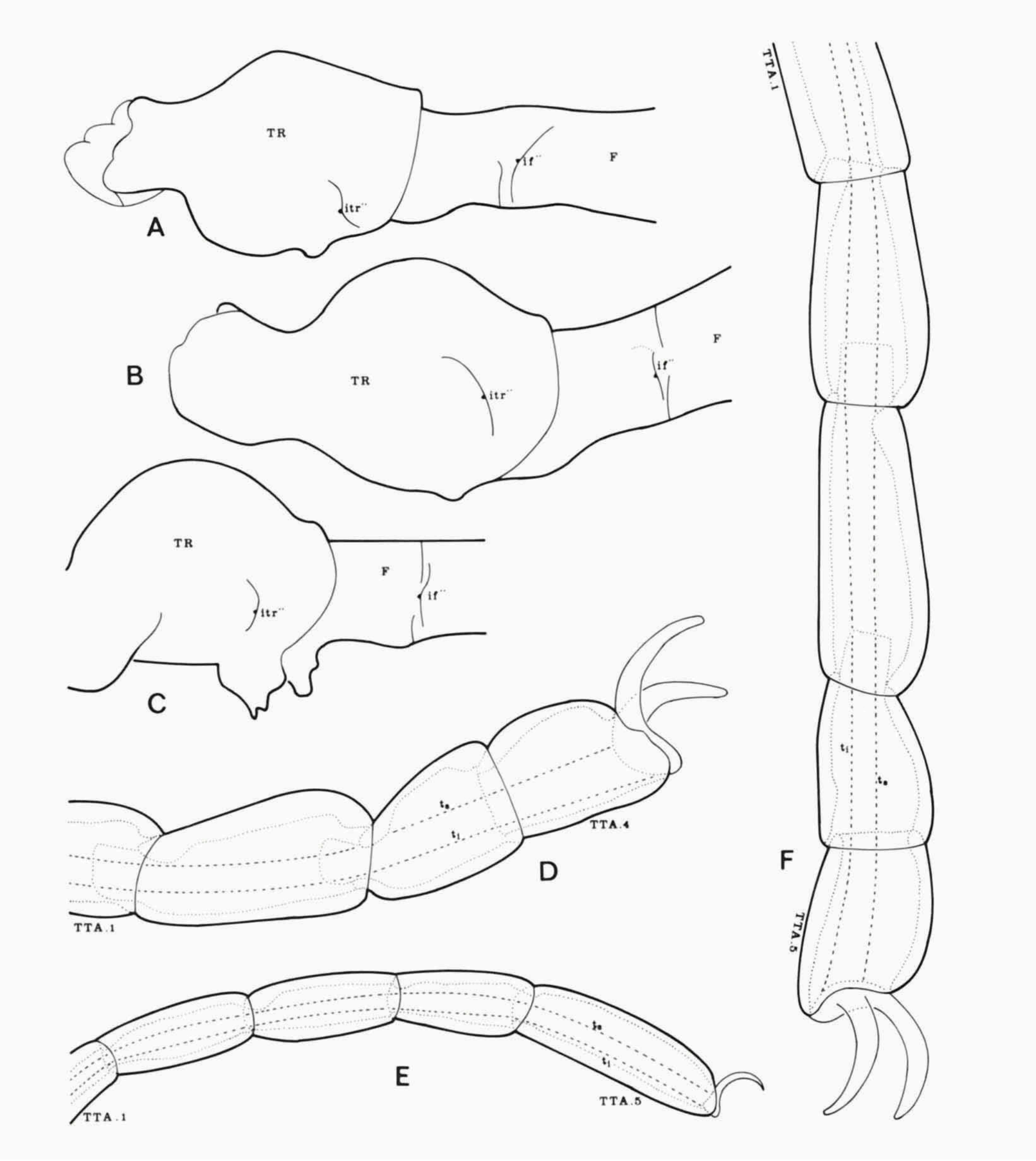

Fig. 31. *Scotolemon lespesi* Lucas, adult male; A, trochanter and proximal part of femur of right leg II, lateral (posterior) view; B, trochanter and proximal part of femur of right leg III, lateral (posterior) view; C, trochanter (basal part omitted) and proximal part of femur of right leg IV, lateral (posterior) view; D, terminal part of right leg III, lateral (posterior) view; E, terminal part of right leg II, lateral (posterior) view; F, terminal part of right leg IV, lateral (posterior) view; A, B, × 155; C, E, × 118; D, F, × 246.

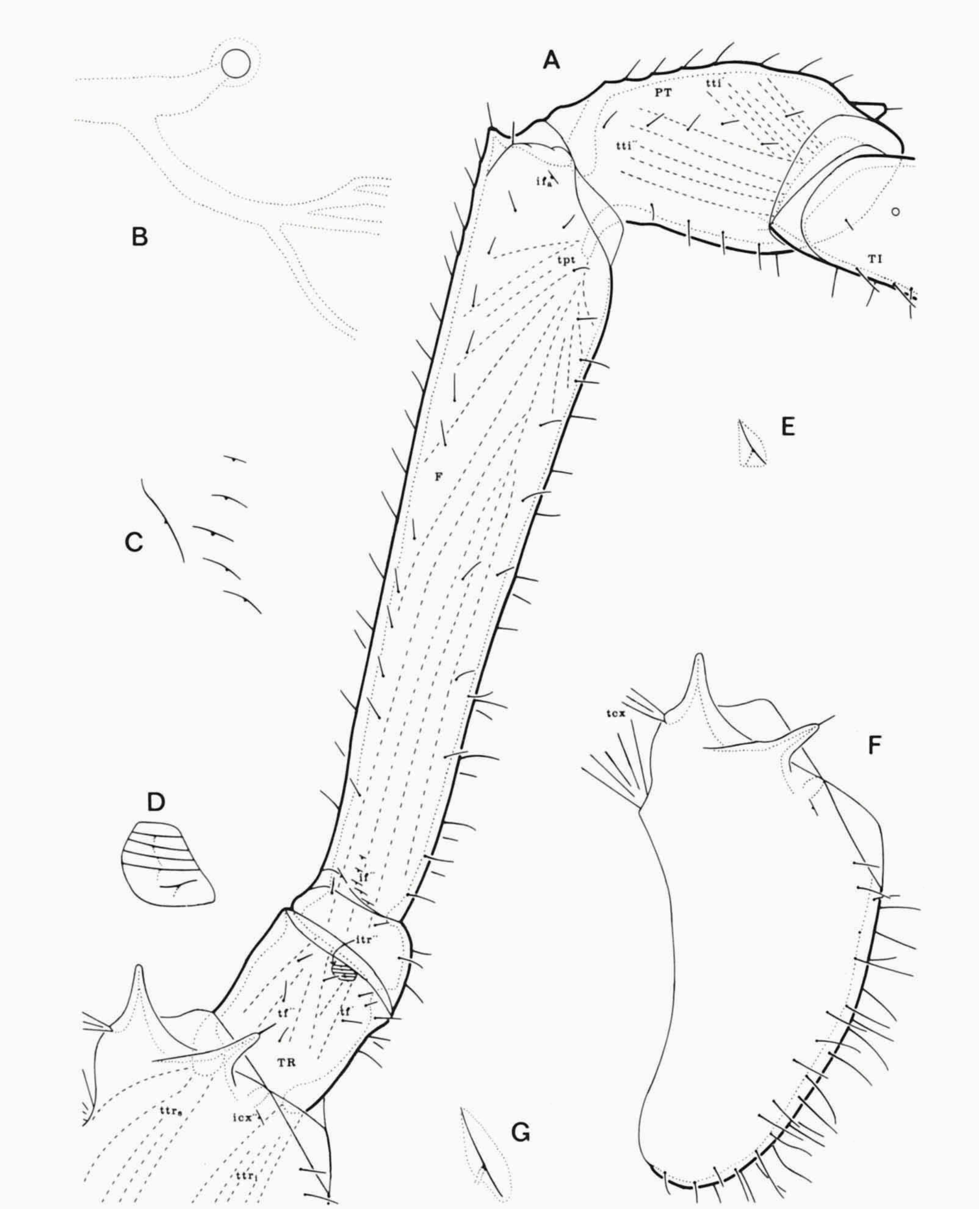

Fig. 32. *Paroligolophus agrestis* (Meade), proximal part of right leg I of adult male, lateral (posterior) view; A, distal part of coxa, trochanter, femur, patella and proximal part of tibia; B, tibial stigma and tracheae; C, posterolateral lyrifissures associated with basifemoral ring; D, posterolateral lyrifissures of trochanter; E, distal posterolateral lyrifissure of femur; F, coxa; G, posterolateral lyrifissure of coxa (B-G have the same orientation as A); A, F, × 73; B-E, G, × 246.

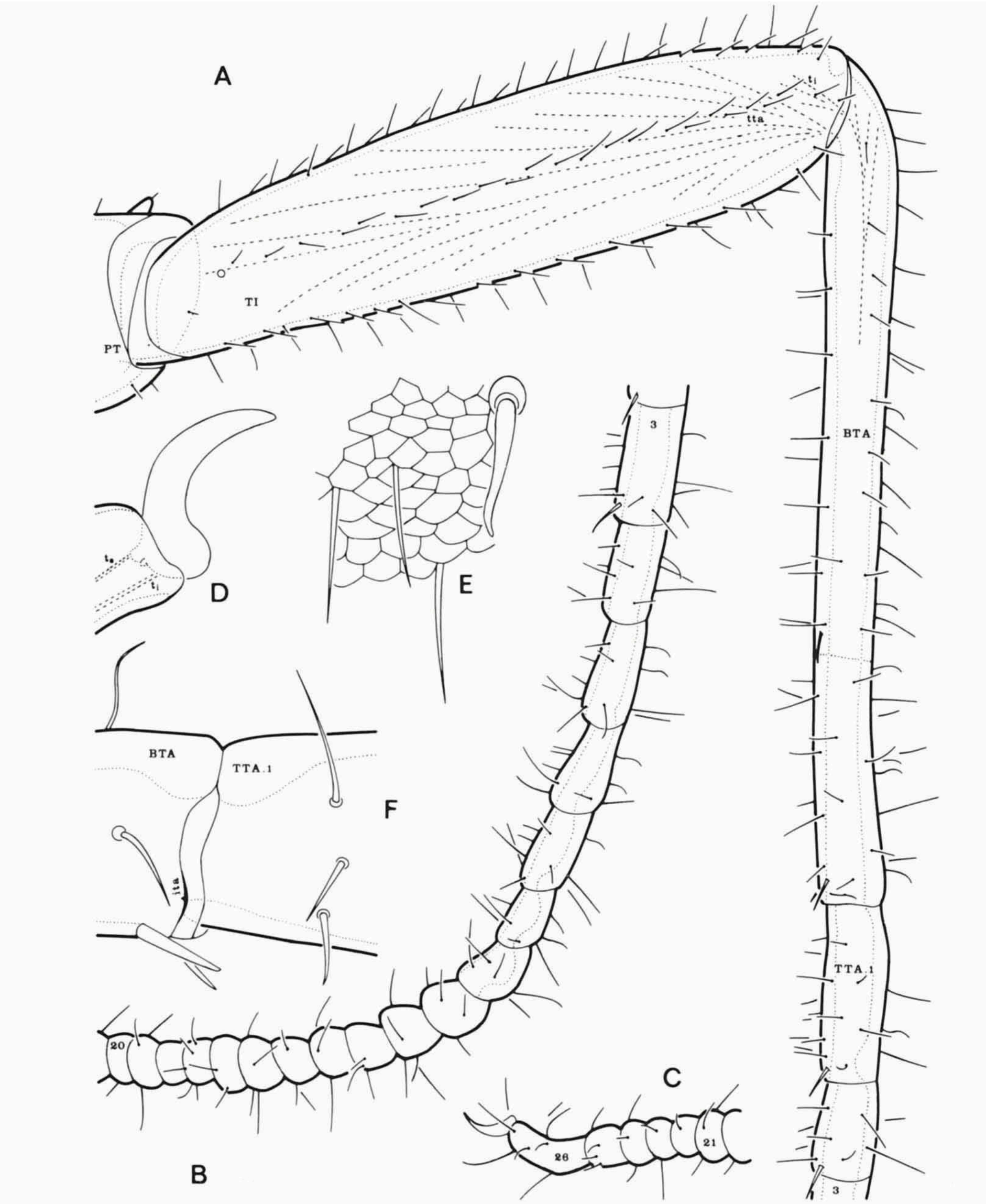

Fig. 33. *Paroligolophus agrestis* (Meade), distal part of right leg I of adult male, lateral (posterior) view; A, distal part of patella, tibia, basitarsus and telotarsi 1-3; B, telotarsi 2-21; C, telotarsi 20-26 and apotele; D, terminal part of telotarsus 26 and apotele; E, reticulate aciculate microsculpture and seta of proximal part of basitarsus; F, articulation between basitarsus and telotarsus 1 (in figs. A-C, the phanerotaxy is represented schematically; in figs. A-D, F, the aciculate microsculpture is omitted); A-C, × 43; D, F, × 246; E, × 458.

The opisthosomatic musculature includes dorsoventral and longitudinal muscles; the last-mentioned muscles can have disappeared in the case of fusion of sclerites.

Embryonic development. — The opilionid embryonic development was studied, among others, by Winkler (1957), Moritz (1957, 1959) and Juberthie (1964: 65-75, figs. 20-25). According to Weygoldt & Paulus (1979: 114), chelicerate embryology furnishes hardly any characters which can be used in the study of chelicerate phylogeny. According to Anderson (1973), the base of the pattern of embryonic development in Opilionida (and Mites, Araneida, Uropygi, Amblypygi, Solifugae and Pseudoscorpionida) could lie in that of the Xiphosura, but not in that of the Scorpionida; among these chelicerate groups, Opilionida (and Mites) present a more generalized pattern than Araneida, Uropygi, Amblypygi, Solifugae and Pseudoscorpionida (which present more modified patterns with forwardly flexed opisthosoma).

Postembryonic development. — The opilionid postembryonic development was studied, among others, by Pabst (1953), Immel (1954, 1955), Winkler (1957) and Juberthie (1964, 1965); a general study of the evolution of the chelicerate life-cycle was published by Van der Hammen (1978). There are three phases: a larval phase, a nymphal phase and an adult phase. The larval phase consists of one instar (a stase), viz., the larva, which is an elattostase (Cyphophthalmi) or a calyptostase (Laniatores, Palpatores). Consequently, the first level of postembryonic development has been subject to regression (as in other groups of Chelicerata; the evolutionary phenomenon is called protelattosis). The nymphal phase comprises a variable number of nymphs (4-6, mostly 5 or 6); the number of nymphs can even vary within one species, but a smaller number of moults is generally associated with adults of smaller size (these adults are probably neotenous). A number of four nymphs (rarely met with, but mentioned for *Anelasmocephalus cambridgei* (Westwood) and *Lophopilio palpinalis* (Herbst)) corresponds with a so-called protostasic life-cycle of six instars (larva, four nymphs and adult). A higher number of nymphs (mentioned for the majority of Opilionids of which the life-cycle was studied) could either refer to a secondary increase of the protostasic number of instars (neostasy; see Van der Hammen, 1980: 103), or to the more primitive condition, with variable number of instars, which is supposed to have preceded the protostasic life-cycle. Judging from the data from literature, the various nymphs are not the result of growing moults or repetition moults (they are different from neighbour instars by distinct discontinuous characters), and consequently do not represent isophena. At the supraspecific level, a higher number of opilionid instars is generally not correlated with larger size. As far as now known, the opilionid "nymphs" are, generally, not idionymous and, in many cases, cannot be homologized with corresponding instars in other species of the same group; in these cases, the nymphal instars could represent stasoids and should be called nymphoids. As far as known, the opilionid adults (which, in hypogeous species, can live for several years) do not undergo growing moults.

IV. THE EVOLUTION OF THE CHELICERATE APPENDAGES

Recently (Van der Hammen, in press), I have made some remarks on the first stages in the evolution of the chelicerate appendages. Because of the importance of these remarks for the comprehension of chelicerate evolution and chelicerate affinities, they are repeated in the present section.

Because the six pairs of chelicerate appendages (chelicera, palp and legs) are homonomous structures which have developed by parallel evolution from lobopodia, the ancestral number of the segments of the chelicerae (three) could be the prototypal number for all the appendages; these three segments are usually called trochanter, body of the chelicera, and apotele (or claw-segment). This number of segments could have occurred in short-legged species which stood up on their legs. Vachon (1945) demonstrated that, in chelicerate embryos, palp and legs first divide into four segments which he named protocoxa (prototrochanter is more appropriate), protofemur, prototibia and prototarsus. A leg with these four segments and an apotele (i.e. five segments) could represent the first stage in the evolution of a hanging stance. All types of chelicerate palps and legs can be derived from this primitive type. A coxa is supposed (see Van der Hammen, 1977a) to have originated from a projecting coxal region at the base of a leg. This is not an exceptional phenomenon, because lobopodia must also be regarded as projections of the body; all proximal segments of the appendages could, in fact, have developed, after the origination of the distal part, from projecting parts of the body. In my study of the evolution of the coxa (Van der Hammen, 1977a: 13-15, fig. 21; see also fig. 1E-G), I pointed to the presence in *Eukoenenia* (Palpigradi) of the supracoxal seta *e* above the base of the palp; a similar seta is, however, also present on the legs, viz., on the trochanter of leg I, on femur 2 of leg II, and on the genu of leg IV (I have made no notes on its occurrence in leg III, where it is certainly present); this evidently supports the above-mentioned hypothesis. Because trochanter 2, in Cryptognomae, disappears by suppression (see Van der Hammen, 1981: fig. 6), it must originally have evolved by repetition of information. Because femur 2, in Epimerata, disappears by fusion of femur 1 and femur 2 (see Van der Hammen, 1982: 38), it must originally have evolved by subdivision of the femur. Patella and tibia must originally have evolved by subdivsion of the prototibia; it is interesting that this subdivision has manifested itself in two different ways: the patella-tibia articulation is, ancestrally, either a hinge joint or a pivot joint. Other evolutionary changes in the ancestral leg type include the origination of rocking joints from pivot joints, the origination of extensor muscles in hinge joints, the flattening and broadening of hinge joints, and further changes in the number of segments by reduction (integration or suppression) and multiplication (subdivision, or repetition of information).

The special characters of the opilionid palp and legs are constituted by the presence of rocking joints between trochanter and femur (associated with promotor-remotor, not with levator-depressor movements!), and between patella and tibia. These particular characters are present in Cyphophthalmi, Laniatores and Palpatores, which demonstrates the fundamental unity of Opilionida.

V. DIAGNOSTIC CHARACTERS OF OPILIONIDA

The opilionid body consists of prosoma and opisthosoma, which are broadly united without conspicuous line of separation; the prosoma comprises the precheliceral metameres and the segments I-VI, the opisthosoma consists of the segments VII-XVI. Prosoma with one pair of eyes (sometimes absent), and one pair of odoriferous glands (with lateral orifice). The mouthparts include the coxapophyses of palp and anterior legs, and constitute a myliosoma associated with coxisternal feeding. The orifice of the coxal glands has a ventral position, paraxial to coxa III. The respiratory system consists of tracheae and one pair of stigmata with ventral position (in segment VIII, posterior to coxa IV). Genital opening with advanced position, between the coxae. The adult female is characterized by the presence of an ovipositor, the adult male by the presence of a penis or spermatopositor. Chelicerae three-segmented. Palp with free coxa. Coxae of the legs with ventral position (immovable in the posterior legs; movable, in connexion with ingestion, in the anterior legs). Palp and legs with rocking joints between trochanter and femur, and between patella and tibia.

These characters (by many of which the Opilionida are distinctly different from most other Chelicerata) are shared by Cyphophthalmi, Laniatores and Palpatores. The first-mentioned group was recently separated from the Opilionida by Savory (1977: 9, 195-197) on the ground of characters which are either primitive or of low hierarchical value. The shared characters, mentioned above, clearly demonstrate the close affinity of the three opilionid groups.

VI. OPILIONID RELATIONSHIPS

Coxisternal feeding is known from Opilionida, Xiphosura and Scorpionida, and from the fossil Eurypterida; it could also have been present in other fossil groups, such as Architarbi (hypothetically classified by Van der Hammen, 1977, with Cryptognomae, but now removed from this group). Orifices of coxal glands near coxae III are found in Opilionida, Pseudoscorpionida, Xiphosura, Scorpionida and some Amblypygi and Araneida; in the last-mentioned two groups and in the related Uropygi, two or three glands (those of legs I-III) are originally present, with orifices near coxae I and/or III (which condition presents some similarities with the development in Opilionida). The legs of Opilionida, Xiphosura, Scorpionida, Uropygi, Amblypygi and Araneida, can be derived from a single common type with coxa, trochanter, femur, patella, tibia, basi- and telotarsus, and apotele; and with pivot joints between body and coxa, coxa and trochanter, trochanter and femur, and possibly patella and tibia (although the last-mentioned articulation could, originally, also have been a hinge joint). External openings of the respiratory system in the sternal part of segment VIII are known from Opilionida, Uropygi, Amblypygi and Araneida.

Up to now, the closest affinities of Opilionida were supposed to be with Mites (particularly Anactinotrichida). These affinities are not confirmed by the present investigations. Because of coxisternal feeding, Opilionida are related to Xiphosura and Scorpionida. Because of the development of the coxal glands and their orifices in segments III and/or V, and because of the presence of openings of the respiratory system in the sternal part of segment VIII, Opilionida are also related to Uropygi, Amblypygi and Araneida. In anticipation of further studies of chelicerate relationships, Opilionida could hypothetically be classified between Xiphosura and Scorpionida, on the one hand, and Uropygi, Amblypygi and Araneida, on the other. The phylogenetic relationships of the three groups, which are not yet completely understood, are dealt with in the following section.

VII. THE RELATIONSHIPS OF OTHER GROUPS OF CHELICERATA

As a result of the present study, it has now become evident that the closest relationships of Opilionida are not with Mites (which was the current opinion) but with other groups of Chelicerata. This conclusion has simplified the pattern of supposed chelicerate affinities, by which it is possible to prepare a model of the phylogenetic relationships of Epimerata (Palpigradi and Actinotrichida) and Cryptognomae (Anactinotrichida and Ricinulei). These two groups are now united to constitute a superclass Acaromorpha, characterized by: the ancestral position of the orifice of the coxal gland (near coxa I; the gland belongs to segment III) and its association with the mouthparts; the absence of a palpal coxa (possibly associated with the origination of a gnathosoma); the ancestral condition of the articulation between genu and tibia (a simple hinge joint; the term genu, instead of patella, could be preserved for all groups of Acaromorpha); the presence of a hexapod larva (not known from Palpigradi and Holothyrida; and an ancestral life-cycle of six stases. The ancestral marine Acaromorpha are supposed to have occurred (possibly as local populations) in the Cambrian, and to have been characterized by cuticular respiration, rostral (not coxisternal) feeding, a variable number of body segments, and the condition of appendages 2-6 (consisting of trochanter, femur, genu, tibia, tarsus and apotele). It is interesting that in three of the four Acaromorph groups (Actinotrichida, Anactinotrichida and Ricinulei), a gnathosoma has developed by parallel evolution (it consists for the greater part of homologous elements, but the ancestral transport of coxal gland secretions to the mouthparts must have been different from the beginning of the evolution of a gnathosoma (i.e. dorsal in Actinotrichida, ventral in Cryptognomae). It will now be important to make a detailed comparative study of the gnathosoma of the Oribatid family Epilohmanniidae and the Palpigradid mouthparts, because in both groups the epimera of palp and leg I have fused.

In the course of the Cambrian, the ancestral Acaromorpha must have split into ancestral Epimerata and ancestral Cryptognomae. Between the Cambrian and the Silurian (the beginning of the terrestrial period), Epimerata developed a number of seventeen body segments, legs with two femora and a tridactyl claw, and (possibly) mouthparts associated with a podocephalic canal; the opisthosomatic appendages of the segments X-XII have, moreover, been suppressed in a special way (they reappear in the course of postembryonic development). Between the Cambrian and the beginning of the terrestrial period, Cryptognomae developed: a number of nineteen body segments; legs with a coxa, two trochanters (in the case of legs III and IV), basi- and telotarsus, and a bidactyl claw; and a gnathosoma with a subcapitular gutter associated with sternapophyses. In the same period, Cryptognomae must have lost all but one pair of opisthosomatic appendages. Ancestral Epi-

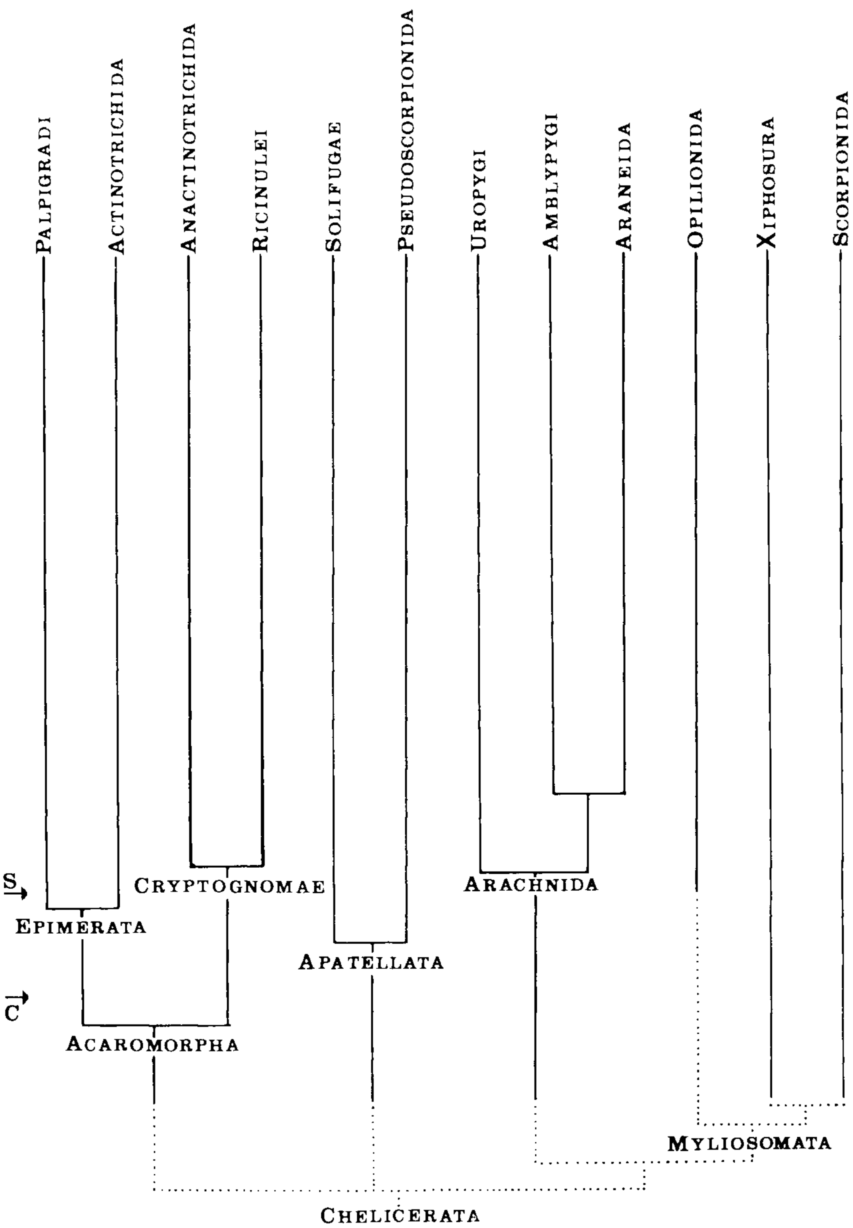

Fig. 34. Diagrammatic representation of the present (incomplete) view of chelicerate phylogenetic relationships. Dotted lines point to relationships which are not yet completely understood. *S* = lower border of Silurian; *C* = upper border of Cambrian.

merata could have split into Palpigradi and Actinotrichida just before the Silurian (see Van der Hammen, in press), whilst ancestral Cryptognomae could have split into Anactinotrichida and Ricinulei in the course of the Silurian. There are important differences in sperm morphology between the four acaromorph groups (see Alberti, 1979, 1980, 1980a, 1980b; Alberti & Palacios-Vargas, 1984). It may be remarked here that the Ricinuleid stigma is now supposed to be homologous with the stigma present in most Anactinotrichida.

Because changes in the ancestral segmentation of the legs, and the origination of various fixed numbers of body segments, in Acaromorpha, can now be attributed to a period extending from the Cambrian to the beginning of the Silurian, it is possible to extend the model of chelicerate phylogeny by applying these data to other groups of Chelicerata. The two groups of Apatellata (Solifugae and Pseudoscorpionida), in which the prototibia did not subdivide into a patella (or genu) and a tibia, present different numbers of body segments (seventeen, resp. eighteen), whilst Solifugae present moreover a second trochanter. For this reason, ancestral Apatellata must have split into Solifugae and Pseudoscorpionida at some moment in the period extending from Cambrian to Silurian. In the generally accepted model of the phylogenetic relationships of the subclass Arachnida s. str. (Uropygi, Amblypygi and Araneida), the first branching point is between Uropygi and the remaining Arachnida s. str. The subclass is homogeneous (same number of body segments, similar types of legs, etc.), and the separation of the three groups probably took place after the beginning of the Silurian. Opilionida, Xiphosura and Scorpionida, which are characterized by coxisternal feeding and the possession of a myliosoma, are now regarded as constituting a new superclass Myliosomata. Xiphosura (which are known since the lower Cambrian) and Scorpionida (known since the Silurian) constitute groups which must have been separated since the Cambrian; the separation of ancestral Opilionida from the other Myliosomata must have occurred still earlier. In fig. 34 an attempt is made to represent the present view of chelicerate phylogenetic relationships in a single diagram. It is still incomplete (see the dotted lines), because it is extremely difficult to reconstruct Precambrian branching points. It may be remarked, however, that the construction of hypothetical Cambrian ancestors could perhaps be helpful during the difficult last stage of the study of chelicerate phylogeny.

VIII. LIST OF NOTATIONS

acf, line of attachment of cheliceral frame to cheliceral trochanter.

am, arthrodial membrane.
AP, apotele.
ap.m, apodeme of myliosoma.
art, articulation point.
at, line of attachment of cheliceral frame to cervix.

b, mouth.
BF, basifemur.
BTA, basitarsus.

c, *c′ c″*, condyles.
CA.P, coxapophysis of palp.
CA.I, coxapophysis of leg I.
CA.II, coxapophysis of leg II.
CE, cervix.
CH, *CH′*, chelicera.
CX, coxa.
CX.P, coxa of palp.
CX.I, coxa of leg I.
CX.II, coxa of leg. II.
CX.III, coxa of leg III.
CX.IV, coxa of leg IV.

dgm, ducts of male postero-opisthosomatic glands.

F, femur.

gle′, *gle″*, glenoid cavities.
GEN, genital region.
gen, genital opening.

ibc, lyrifissure of body of chelicera.
ica.II, lyrifissures of coxapophyses of leg II.
icx, *icx″*, icx_1, icx_2, lyrifissures of coxa.
if′, *if″*, if_1, if_1'', if_2, if_2'', lyrifissures of femur.
if_a, distal lyrifissure of femur.
ita, lyrifissure of tarsus.
itr″, $itr_{1\text{-}3}'$, lyrifissures of trochanter.

LI, labium.

LS, labrum.

md, dorsal muscle of penis (spermatopositor).
ml, *ml′*, lateral muscles of penis (spermatopositor).
mv, ventral muscle of ovipositor.

OC, eye.
od, oviduct.
OE, oesophagus.
og, eugenital opening.
ogc, orifice of coxal gland.
oglo, orifice of odoriferous gland.
ogm, orifices of male postero-opisthosomatic glands.
op.an, anal cover (operculum anale).
opg, progenital opening.
op.ge, genital cover (operculum genitale).

PA, palp.
PH, pharynx.
PN, penis (spermatopositor).
PT, patella.

rs, receptaculum seminis.

SA.III, sternapophysis of the segment of leg III.
sc.d, dorsal sclerite of penis.
sc.l′, lateral sclerite of penis.
st, stigma.

t″, lateral tendon or muscle.
t_i, inferior tendon of apotele.
t_s, superior tendon of apotele.
TA, tarsus.
tap, lateral tendon of myliosomatic apodeme.
tcx, *tcx′*, *tcx″*, tendons of coxa.
tcx_i, inferior tendon of coxa.
tcx_r, retractor muscle of coxa.
tcx.P, tendon of palpal coxa.
tcx.I′, *tcx.I″*, tendon of coxa I.
tf′, *tf″*, lateral tendons of femur.

tf_i, tf_i', tf_i'', inferior tendons of body of chelicera.
tf_s, tf_s'', superior tendons of body of chelicera.
TI, tibia.
tm, median tendon of myliosomatic apodeme.
tpe, tendon of glans penis.
tpt, tendon of patella.
TR, trochanter.
tta, tendon of tarsus.
TTA, telotarsus.
TTA.1-5, telotarsus 1-5.
tti', *tti''*, lateral tendons of tibia.
ttr_i, ttr_i'', inferior tendon of trochanter.
ttr_s, ttr_s', superior tendon of trochanter.

x, base of median tendon of myliosomatic apodeme.

V-XVI, segments V-XVI.

3-26, telotarsus 3-26.

' (prime), anterior face of an appendage; the right one of two symmetrical structures.
'' (double prime), posterior face of an appendage.

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